DOCTORAL THESIS

Model-Based Reconstructions of Lake Environments in the Baltic States Using Subfossil Cladocera

Anna Lanka

TALLINNA TEHNIKAÜLIKOOL
TALLINN UNIVERSITY OF TECHNOLOGY
TALLINN 2025

TALLINN UNIVERSITY OF TECHNOLOGY
DOCTORAL THESIS
51/2025

Model-Based Reconstructions of Lake Environments in the Baltic States Using Subfossil Cladocera

ANNA LANKA

TALTECH PRESS

TALLINN UNIVERSITY OF TECHNOLOGY
School of Science
Department of Geology
This dissertation was accepted for the defence of the degree of Doctor of Philosophy in Earth Sciences on 30/06/2025

Supervisor: Prof. Siim Veski
School of Science
Tallinn University of Technology
Tallinn, Estonia

Co-supervisor: Dr. Inta Dimante-Deimantoviča
Latvian Institute of Aquatic Ecology
Riga, Latvia

Co-supervisor: Dr. Anneli Poska
School of Science
Tallinn University of Technology
Tallinn, Estonia

Opponents: Prof Thomas Alexander Davidson
Department of Ecoscience
Aarhus University
Aarhus, Denmark

Dr Helen Agasild
Institute of Agricultural and Environmental Sciences
Estonian University of Life Sciences
Tartu, Estonia

Defence of the thesis: 19/08/2025, Tallinn

Declaration:
Hereby I declare that this doctoral thesis, my original investigation and achievement, submitted for the doctoral degree at Tallinn University of Technology has not been submitted for doctoral or equivalent academic degree.

Anna Lanka

Signature

European Union
European Regional
Development Fund

Investing
in your future

ISSN 2585-6898 (publication)
ISBN 978-9916-80-335-6 (publication)
ISSN 2585-6901 (PDF)
ISBN 978-9916-80-336-3 (PDF)
DOI https://doi.org/10.23658/taltech.51/2025

Lanka, A. (2025). *Model-Based Reconstructions of Lake Environments in the Baltic States Using Subfossil Cladocera* [TalTech Press]. https://doi.org/10.23658/taltech.51/2025

TALLINNA TEHNIKAÜLIKOOL
DOKTORITÖÖ
51/2025

Subfossiilsete vesikirbuliste põhised järvekeskkonna mudelrekonstruktsioonid Läänemeremaades

ANNA LANKA

TALTECH
KIRJASTUS

Contents

List of publications

The list of the author’s publications, based on which the thesis has been prepared:

I **Lanka, A.,** Poska, A., Bakumenko, V., Dimante-Deimantovica, I., Liiv, M., Stivrins, N., Zagars, M. and Veski, S., (2024). Subfossil Cladocera as indicators of pH, trophic state and conductivity: Separate and combined effects in hemi boreal freshwater lakes. *Ecological Indicators*, *167*, p.112592. https://doi.org/10.1016/j.ecolind.2024.112592

II **Lanka, A.,** Dimante-Deimantovica, I., Saarni, S., Stivrins, N., Tylmann, W., Zawiska, I. and Veski, S., (2024). Urbanization-driven Cladocera community shifts in the lake-a case study from Baltic region, Europe. *Anthropocene*, p.100439. https://doi.org/10.1016/j.ancene.2024.100439

III Zawiska, I., Dimante-Deimantovica, I., Luoto, T.P., Rzodkiewicz, M., Saarni, S., Stivrins, N., Tylmann, W., **Lanka, A.**, Robeznieks, M. and Jilbert, T., (2020). Long-term consequences of water pumping on the ecosystem functioning of Lake Sekšu, Latvia. *Water*, *12*(5), p.1459. https://doi.org/10.3390/w12051459

Manuscripts:

I Bakumenko, V., **Lanka, A**., Belle, S., Poska, A., Vassiljev, J., Alliksaar, T., Heiri, O., Veski, S. A 14 500 - year multi-proxy reconstruction of climate and environment change in Eastern Baltics: case study from Southern Estonia.

Author’s Contribution to the Publications

Contribution to the papers in this thesis are:

I The author is the lead author of the publication and participated in sediment sample collection, water parameter measurements in the field, total phosphorus and chlorophyll-*a* analysis in the laboratory, loss on ignition, and subfossil Cladocera analysis. The author is also responsible for the statistical analysis, data visualization, and interpretation, and is the primary creator of the publication draft.

II The author is the lead author of the publication, participated in the sample collection, and is partially responsible for data analysis and visualization, the article’s conceptualization, and the draft's writing.

III The author participated in sediment collection and analysis, subfossil Cladocera analysis, and writing of the manuscript.

Manuscripts:

I The author was responsible for subfossil Cladocera analysis, participated in data analysis and visualization, preparation of the original draft, and editing.

Introduction

Humans have reshaped landscapes, habitats, and the climate for millennia, and this process has only accelerated since the Industrial Revolution (Ellis & Ramankutty, 2008; Ellis et al., 2013; Ruddiman et al., 2020; Steffen et al., 2015). The result is an ever-changing mosaic of agricultural, urban, forested, and aquatic environments, each exposed to varying intensities of anthropogenic pressure. Within this shifting planetary scene, lakes have been of notable importance for human societies throughout history. Early human settlements were closely connected to water bodies and were often established near the lake shores (Makohonienko et al., 2023; Meadows & Zunde, 2014; Tóth et al., 2019). In addition to the practical services lakes might have provided, they have also been influential as cultural and religious inspiration for pagan cultures in Europe (Hiiemäe, 2024; Mustonen & Huusari, 2020). Today, lakes continue to support human societies by supplying drinking water, food, and recreation opportunities (Reynaud & Lanzanova, 2017). At the same time, they remain indispensable ecological systems, providing habitat for diverse communities of fish, invertebrates, aquatic plants, and many other species groups (O'Sullivan & Reynolds, 2004). Despite the economic, ecological, and cultural importance of lake ecosystems, they are currently under threat from a multitude of stressors. These include eutrophication (Le Moal et al., 2019), salinization (Kaushal et al., 2021), acid deposition (Battarbee, 1990), and pollution with xenobiotics (such as heavy metals, microplastics, pesticides, etc.) (Amoatey & Baawain, 2019; Barone et al., 2024), as well as brownification (Williamson et al., 2016), climate warming (Woolway et al., 2020), and expansion of invasive species (Reynolds & Aldridge, 2021). Furthermore, many lakes are under several of these pressures, which can often interact with each other in complex ways (Moss et al., 2011**;** Radosavljevic et al., 2022; Smol, 2010).

Paleolimnology is a scientific discipline that utilizes physical, biological, and chemical information stored in the sediments of lakes, reservoirs, etc. to reconstruct past environmental conditions. Paleolimnological records provide valuable insights into past climatic conditions, landscape changes, and different types of stressors that have affected the lake ecosystems (Elias, 2025). This is information that most monitoring programs cannot provide due to their comparatively brief (a few decades maximum) observation time frames (Smol, 2019). The knowledge of past conditions is crucial for setting adequate lake restoration targets, evaluation of natural lake variability, as well as for predictions of the potential future development of lake ecosystems (Anderson et al., 2006; Bennion et al., 2011; Catalan et al., 2013). Furthermore, investigations of sedimentary records can enhance the understanding of contemporary species diversity within water bodies (Nevalainen, 2010; Tumurtogoo et al., 2022) and help to evaluate the success of restoration efforts and lake recovery (Smol et al., 1998).

Subfossil Cladocera, the chitinous remains left behind in the lake sediments by different Cladocerans, can be used as a proxy for assessing temperature, water level, trophic state, pH, electrical conductivity, as well as fish and macrophyte abundance of the past (Jeppesen et al., 2001; Rautio & Nevalainen, 2025). Furthermore, subfossil Cladocerans can be used to evaluate anthropogenic impacts and natural changes in the environment throughout the Holocene (Davidson et al., 2011a; Szeroczyńska, 2002). However, the methodology is not without its caveats, many of which overlap with other proxies used in paleolimnology. Environmental reconstructions using subfossil Cladocera could be classified as either descriptive (qualitative and semi-quantitative) or quantitative. For descriptive reconstructions, information on the ecology of each observed species is needed. This information is often obtained from literature focusing on contemporary Cladocera ecology (for example, such books as Flössner, 2000). However, not all Cladocera species have received equal attention in the research of limnology (Smirnov, 2017), and paleolimnological samples often contain higher diversity of littoral taxa than contemporary ones (Çakıroğlu et al., 2014; García-Girón et al., 2018; Nevalainen, 2010; Tumurtogoo et al., 2022). An alternative approach that solves this issue is the development of surface sediment training sets. Such training sets can be used to evaluate the correlations between Cladocera species and the environment, and to develop transfer functions for quantitative environmental reconstructions. In an ideal scenario, a surface sediment training set should encompass the regional variability of all the relevant environmental parameters. Furthermore, these parameters should be independent of each other (Birks et al., 2012; Juggins, 2013). This is rarely achieved, as researchers often maximize the training set's coverage on a single parameter of interest, which can lead to result misinterpretation (Davidson & Jeppesen, 2013; Velle et al., 2012), especially if the changes have occurred in multiple environmental parameters. The commonly used transfer function methods, such as Weighted Averaging Partial Least Squares (WA-PLS), have certain data distribution assumptions (Birks et al., 2012; Turner et al., 2021). Therefore, it might be a difficult task to build a training set with sufficiently covered and independent gradients across multiple parameters. This issue might be tackled by choosing more advanced machine learning methods such as random forest (RF) or Boosted Regression Trees (BRT), which do not have a priori assumptions of the data distribution or species response (Birks et al., 2012). However, these methods might not be suitable for small datasets (Elith et al., 2008). Independent of the preferred method, additional uncertainties can arise based on the chosen taxonomical resolution and measurement errors (Birks et al., 2012; Turner et al., 2021).

During this research, a subfossil Cladocera surface sediment training set was built for the Baltic states (Estonia, Latvia, Lithuania) across multiple environmental parameters, and the validity of different reconstruction methods for each of the studied environmental parameters was assessed. This is the first such training set of the region. The Baltic states are a region rich in natural lakes (Estonia 1,562, Latvia 2,256, Lithuania 6,714) (Apsīte et al., 2014; Taminskas et al., 2012; Terasmaa, 2018). The lakes of the Baltic states are mostly of glacial origin (Nikodemus et al., 2018; Teresmaa, 2018). However, some other types, such as bog and coastal lakes, are present (Nikodemus et al., 2018; Suursaar et al., 2024; Teresmaa, 2018), and at least one lake (Kaali) has formed due to a meteorite impact (Veski et al., 2004). Lakes in the Baltic states vary in their size (the largest Lake Peipsi 3,543 km^2), depth (deepest Lake Drīdzis 65.1 m) (Estonian Ministry of Climate, 2025; Latvijas Ezeri, 2010). Lakes in Baltic states also differ in catchment characteristics, such as bedrock (sand, silt, clay, limestone) and land cover (urban, agricultural, forested, or bog area) (Daubarien et al., 2011; Nikodemus et al., 2018; Teresmaa, 2018). As a result, lakes in this area vary in their trophic state, water hardness, pH, color, as well as in the organisms that inhabit them (Česonienė et al., 2020; Eņģele & Sniedze-Kretalova, 2013; LVĢMC, 2022; Teresmaa, 2018).

The **aim of this study** is to:

1. Identify the main abiotic drivers of subfossil Cladocera community species composition in lentic freshwater bodies of the Baltic states.
2. Find the optimal approach/model for reconstructing different environmental parameters based on subfossil Cladocera.
3. Apply the developed methods to reconstruct the environmental history of lakes in the Baltic States.

To achieve these goals, a list of **tasks** was executed:

1. Create a surface sediment training set that would include a variety of environmental conditions representative of lakes in the Baltic states. (2020–2021: Select lakes, collect sediment samples, find the available information from monitoring data, go to lakes for fieldwork to measure water parameters where data is not available, consult with recognized experts on subfossil Cladocera identification, analyze subfossil Cladocera, do preliminary data analysis, identify potential gaps in the training set. In 2022, do additional sampling to cover the gaps). (Article I)
2. Identify the major factors driving the subfossil Cladocera species composition in the surface sediment training set samples through correlation and ordination analysis. (Article I)
3. Analyze the relationship between subfossil Cladocera and main environmental parameters using the functional group approach.
4. Analyze the relationship between subfossil Cladocera and main driving environmental parameters using the indicator species approach (Article I).
5. Create a subfossil Cladocera training set based quantitative reconstruction models for the main environmental parameters using:
    1. WA-PLS
    2. BRT
6. Test how the model's performance changes with:
    1. The reduction of taxonomical resolution by merging *Bosmina (Eubosmina) coregoni* and *Bosmina (Eubosmina) longispina* into the *Eubosmina* spp. group.
    2. Targeted sampling site selection, by excluding the dystrophic lakes.
7. Analyze subfossil Cladocera species composition from sediment cores of 3 lakes with different time scales and levels of anthropogenic influence, two of which have available literature on the past conditions, for evaluation of various environmental reconstruction method performance (Article II, Article III, Manuscript I):
    1. With functional group approach
    2. With indicator species approach
    3. With quantitative reconstruction approach.
8. Compare the results between different subfossil Cladocera-based environmental reconstruction approaches and with the conclusions derived by other proxies (Article II, Article III, Manuscript I) and lake environmental observations recorded in literature sources.

While comparative evaluations between more traditional transfer function methods and machine learning algorithms such as BRT and RF, applied to pollen or diatom data, have recently been published (Wang et al., 2021; Sun et al., 2024), this study is the first to perform such an assessment for subfossil Cladocerans. Furthermore, this might be the first time the results of the quantitative reconstruction model outputs are compared to results obtained by indicator species, functional group approaches, environmental measurements from literature, and other proxies (such as Chironomidae, pollen, diatoms, sediment chemistry) in the same work.

This study has contributed to 3 research articles and one manuscript (see section "List of publications"), and results from work done as part of this PhD project have been presented:

1. International conference Lakes&Reservoirs, Hot Spots and Topics in Limnology, Mikorzyn, Poland. September 17-22, 2019. Dimante-Deimantoviča I., Lanka A. (poster), Zawiska I., Strivins N., Rzodkiewicz M., Luoto T., Tylmann W. "Prelimnary results of multi-proxy paleolimnological survey performed in anthropogenic impact limited lake, a case study from Latvia, Nort-Eastern Europe".
2. 12th Eastern European Young Water Professionals conference: Water research and innovations in a digital era – Virtual conference, September 31 – April 2, 2021. Lanka A. (oral presentation), Zawiska I., Stivrins N., Tylmann W., Dimante-Deimantovica I. "A Cladocera Based Paleolimnological Assessment of Recent Environmental Changes in Lake from Drinking Water Supply System in Riga Vicinity, Latvia".
3. Preliminary results of the subfossil Cladocera training set was presented in CenTrain 500 workshop in Budapest, Hungary (October 2021), EPD open science meeting in Prague, Czech Republic (June 2022), 11th international shallow lakes conference in Tartu, Estonia (June 2023) and XVII subfossil Cladocera workshop in High Tatra mountains, Slovakia (October 2023).

Abbreviations

BP	Before Present (0 years BP = 1950 CE)
BRT	Boosted Regression Tree
CE	Common Era
Chl-a	Chlorophyll-*a*
CV	Cross-validation
EC	Electrical Conductivity
LIA	Little Ice Age
MA	Modern Analogue
MAPE	Mean Absolute Percentage Error
ML	Maximum Likelihood
N	Nitrogen
P	Phosphorous
PCA	Principal Component Analysis
PLS	Partial Least Squares
Q	Quartile
RDA	Redundancy Analysis
RF	Random Forest
RMSEP	Root Mean Square Error of Prediction
SAL	Salinity
SD	Secchi Depth
T_{ann}	Mean Annual Air Temperature
TN	Total Nitrogen
TP	Total Phosphorous
TS	Trophic State
TSI	Trophic State Index
WA	Weighted Averaging
WA-PLS	Weighted Average Partial Least Squares

1 Background

1.1 Cladocera

Cladocera, also known as water fleas, are a diverse group of microscopic zooplanktonic crustaceans that belong to the class Branchiopoda (subphylum Crustacea) (Smirnov, 2017). A characteristic trait of all brachiopods and therefore Cladocera is leaf-like limbs with epipodites whose function can be compared to branchiae (Fryer, 1987). Cladocera bodies are segmented and are covered by a bivalved chitinous carapace that does not cover the head (Smirnov, 2017; Van Damme & Kotov, 2016). Cladocerans are also characterized by parthenogenetic reproduction, swimming antennae adapted for locomotion, and a large, immobile eye formed by the fusion of a pair of eyes and asymmetrical mandibles. However, each of these features can also be characteristic of other crustacean groups, or there are exceptions within the superorder Cladocera itself where some of these features are not present (Fryer 1987; Van Damme & Kotov, 2016).

Cladocera are an evolutionarily old group with the earliest possible cladocera-like fossils dating back to the Devonian and Carboniferous periods (Anderson et al., 2003; Womack et al., 2012). Although these fossils are attributed to Cladocerans, many diagnostic features that would truly classify them as Cladocera are missing (Van Damme & Kotov, 2016). The first fossils fully recognizable as Cladocera can be found around the Jurassic period (Kotov, 2007; Sun et al., 2016), and it is considered that most specimens of the modern species have diverged during the Pleistocene (Van Damme & Kotov, 2016). However, while the group itself might be ancient, some of the species have diverged very recently during the Holocene (Faustová et al., 2011). Cladocera can be found in all of the zoogeographical regions of the World, and there are approximately 700 known currently living Cladocera species (Forró et.al., 2008; Smirnov, 2017). However, it is estimated that the actual number of species should be twice as high, due to the existence of cryptic species and the fact that Cladocera diversity in some regions is insufficiently described (Adamowicz & Purvis, 2005).

1.1.1 Habitat preferences

Cladocerans are predominantly water-associated crustaceans that inhabit brackish and marine habitats, freshwater (lakes, bog pools, rivers, temporary ponds), some species can live as stygobionts (Brancelj & Dumont, 2007; Forró et.al., 2008; Stenert et al., 2017), and there are even reports of semi-terrestrial Cladocera inhabiting different types of wet mosses of tropical rainforests several meters above the ground (Glime, 2017). Nevertheless, it is considered that Cladocerans have primarily evolved in lentic freshwater habitats (Van Damme & Kotov, 2016).

Cladocera species found in lakes can be categorized by their habitat preference into pelagic species, which live in the open water column, and littoral species. While many Cladocera researchers tend to classify species as pelagic or littoral, this division is somewhat artificial, as the littoral species category often includes species that are non-pelagic, rather than strictly tied to the littoral zone (Nevalainen et al., 2011; Rautio & Nevalainen, 2025). Littoral zone by definition is the area in the lake where light reaches the bottom of the waterbody allowing for macrophyte and benthic algae growth (Rose, 2024), however, there are Cladocera species, that while sometimes referred to as littoral, actually inhabit rock, sand and mud substrates (Rautio & Nevalainen, 2025) and therefore have no direct connection to light and macrophytes associated to littoral zone. The pelagic/littoral species division is even more complicated by the fact that many pelagic species prefer to inhabit the water column among littoral vegetation (Kuczyńska-Kippen & Nagengast, 2006), existence of neustonic species (Rautio & Nevalainen, 2025), and littoral species such as *Chydorus sphaericus*, that can be found in pelagic zone due to their ability to attach themselves to floating filamentous algae (Fryer, 1968).

1.1.2 Cladocera in aquatic food webs

Cladocera have an essential role in aquatic food webs, as they feed on algae, bacteria, and detritus, linking primary producers to higher consumers that feed on Cladocerans. Cladocera are primarily filter feeders or scrapers, however there are also some predatory species (Smirnov, 2017). Pelagic Cladocera are primarily filter feeders, and their diet mainly consists of phytoplankton, and in some cases also bacterioplankton and fine detritus (Ebert, 2005). It is considered that, in general, small green algae, as well as diatoms, are a better-suited food source for Cladocera (Smirnov, 2017), however, there are some species that are well adapted for consuming blue-green algae and therefore have a competitive advantage under conditions with cyanobacteria blooms (Tõnno et al., 2016).

Littoral and bottom-dwelling Cladocerans are primarily scrapers or grazers and obtain food by scraping periphyton or by feeding on detritus from the substrate they inhabit (Smirnov, 2017). Sediment-associated species can feed on sediment-dwelling bacteria, protozoans, and algae or directly feed on detritus derived from various sources (Lemke et al., 2007; Smirnov, 2017). Detritus can come from both allochthonous (terrestrial) and autochthonous (in-lake) sources. It is known that the type of allochthonous matter present can significantly shape the zooplankton species composition (Yıldız et al., 2025). Allochthonous organic matter is considered a food source with low nutritional value, and with an increase in trophic state, the relative contribution of allochthonous matter to the zooplankton biomass decreases (Cole et al., 2006; Wilkinson et al., 2013), however, the optimal food sources for sediment-associated Cladocera are largely unknown (Smirnov, 2017). It is unclear whether autochthonous and allochthonous sources of detritus are equally suitable for the detritivorous Cladocera, or to what degree the diversity of detritus sources is connected to the diversity and abundance of substrate-dwelling and detritivorous Cladocera.

There are several carnivorous Cladocera species (such as *Pseudochydorus*, *Leptodora*, *Polyhemus*, *Bythotrephes*, and *Anchistropus* spp.), which prey primarily on other zooplankton organisms, such as ciliates, rotifers, hydras, and other Cladocerans (Packard, 2001; Smirnov, 2017; Young & Taylor, 1988). The mechanisms of prey detection differ, with some Cladocerans like *Polyphemus pediculus* being visual predators (Young & Taylor, 1988), while others, like *Leptodora kindtii*, are mainly tactile (Browman et al., 1989). The targets of prey can overlap between several predatory Cladocera species, nevertheless, several carnivorous species can coexist within the same lake due to different spatial niches, which reduces competition (Cavaletto et al., 2010).

Cladocera serves as a food source for other animals. One of the primary predators of Cladocera are planktivorous fish, which can significantly influence Cladocera communities and lake ecosystems by selectively feeding on larger Cladocerans (Jeppesen et al., 2001). Cladoceran communities can also be affected by invertebrate predation, however, invertebrates tend to affect small-sized species and individuals more severely (Gliwicz & Umana, 1994). Fish have been preying on Cladocerans for millions of years (Richter & Baszio, 2001). Cladocerans, in turn, have developed different anti-predation strategies. These strategies can be divided into behavioral and morphological adaptations.

Diel migrations are among the best-documented antipredator strategies in zooplankton. In the most common pattern of diel vertical migration, zooplankton sinks into deeper water levels during daytime and returns to upper water levels during nighttime. As fish are visual predators, Cladocerans are more vulnerable during the day, and diel vertical migration can be helpful to avoid predation due to worse light conditions in the deeper water layers (Dodson, 1990; Wojtal-Frankiewicz et al., 2010). It is also known that some Cladocera species are more hypoxia tolerant than fish, therefore temporary refuge in the anoxic water layer can provide additional protection from fish predation (Vanderploeg et al., 2009). However, many Cladocera species are hypoxia intolerant; therefore, in lakes with hypoxic hypolimnion, diel vertical migration might be disturbed and could potentially lead to higher planktivorous fish pressure (Doubek et al., 2018; Vanderploeg et al., 2009).

This diel migratory behavior of Cladocerans can switch its direction in some cases. For example, in shallow lakes, diel vertical migration can be replaced by diel horizontal migration, where some Cladocerans seek refuge in the macrophytes during the day, but return to the pelagic zone at night (Burks et al., 2002). If the primary predators of Cladocerans are nocturnal invertebrates, these migratory patterns can change to reverse diel vertical migration, where Cladocerans migrate to deeper water layers during night, but to upper water layers during daytime (Wojtal-Frankiewicz et al., 2010). Another behavioral pattern is swarming, which is exhibited by several Cladocera species in the presence of chemical cues released by fish, in this way reducing capturing risk, however this behavior is not universal even with the individuals of the same species (Pijanowska & Kowalczewski, 1997; Smirnov, 2017).

To avoid predation by fish and invertebrates, many Cladocera species have evolved to undergo rapid morphological changes triggered by the presence of predators. One of the best-known examples is the cyclomorphosis, or changes in morphology of the same species within a year. Changes can include elongation of carapace, tail spine, or growth of new appendages such as neck teeth (Johnsen & Raddun, 1987; Korosi et al., 2013; Pijanowska, 1990; Tollrian, 1995), and some Cladocerans can develop populations with less pigmented eyes or more transparent bodies in the presence of Fish (Tollrian & Heibl, 2004; Zaret, 1972). These adaptations, such as an increase in Cladoceran relative size due to the elongation of appendages, reduce the possibility of being ingested by predators (Kolar & Wahl, 1998) but come at a cost of energy expenditure (Black & Dodson, 1990). Therefore, in conditions with no predation pressure, the defensive morphological features of Cladocerans tend to disappear (Herzog et al., 2016).

Cladocerans can be hosts of different fungal, bacterial, single-celled parasites, as well as other invertebrate organisms (Decaestecker, 2005). The known effects on Cladocerans include decreased fecundity and a decrease in population (Decaestecker, 2005; Duffy et al., 2015). Nevertheless, the true diversity of parasites of Cladocera is most likely underdescribed (Goren & Ben-Ami, 2013), and its ecological impact on host communities is therefore incompletely described as well. Additional mortality of Cladocera can be a result of predation by *Utricularia* spp. (Kurbatova & Yersov, 2009), however thus far there are no reports of this macrophyte species having significant effect on overall Cladocera populations or species assemblages.

1.1.3 Reproduction

Cladocera reproduction is characterized by cyclical parthenogenesis, which means that Cladocerans are capable of reproducing both sexually and asexually. For most species, the parthenogenic and sexual reproduction is cyclical (one cycle includes parthenogenic and gametogenic reproduction). The cyclicity is species and environment specific, and different species under different conditions can undergo one or more cycles per year (Klemetsen et al., 2020; Smirnov, 2017).

In the parthenogenic (asexual) phase, females produce other genetically identical females from unfertilized eggs (Decaestecker et al., 2009). Under favorable conditions, such as optimal temperature and abundance of good quality food sources, Cladocerans can continue to reproduce parthenogenetically for several generations (Koch et al., 2009; Smirnov, 2017). This strategy allows Cladocerans to rapidly expand their populations and exploit resource-rich periods (Tessier, 1986).

Cladocerans tend to switch to gametogenic (sexual) reproduction mode in the presence of cues for unfavorable environmental conditions (Koch et al., 2009), as well as under changes in photoperiod (Kleiven et al., 1992). In the presence of unfavorable conditions, females can produce eggs that develop into males that can participate in sexual reproduction (Ebert, 2005; Smirnov, 2017). After sexual reproduction, resting eggs are formed. In some cases, resting eggs are encapsulated in thick-walled shell called ephippium. Resting eggs can be preserved within the water column, macrophytes, or lake sediments (Gyllström & Hansson, 2004). The resting eggs can survive in a variety of unfavorable conditions (such as cold temperatures and drought) (Smirnov, 2017) and can remain viable for hundreds of years (Burge et al., 2018). Ephippia can not only be useful for survival of the population under environmental stressors, but also for the dispersal into new water bodies (Pinel-Alloul et al., 2021; Reynolds & Cumming, 2015). When certain environmental cues that suggest improvement of the conditions are met, resting eggs hatch into new female Cladocerans (Gyllström & Hansson, 2004), and the cycle can be repeated.

1.1.4 Relation to abiotic factors

Cladocera communities are strongly influenced by abiotic factors such as pH, ionic content of the water body, xenobiotics, temperature, light, and water transparency, as well as water depth, phosphorus, nitrogen, and oxygen concentration. Many of these factors have indirect effects. For example, oxygen concentration and light conditions can impact the predatory pressure on Cladocerans (Vanderploeg et al., 2009; Zagars et al., 2025). Phosphorus and nitrogen concentrations can impact algae growth, and therefore food abundance and quality, as well as availability of macrophyte habitats (Naderian et al., 2025; Nürnberg & Shaw, 1998; Rattray et al., 1991). As these effects are discussed in the previous sections, the focus of this chapter will be the direct interactions between Cladocerans and abiotic factors.

Temperature can directly affect Cladocera either by controlling physiological processes or by changing different aspects of metabolism. Generally, rising temperatures are associated with increased activity (Smirnov, 2017). Most Cladocerans can't maintain sufficient activity in temperatures close to 0 °C and overwinter by producing resting eggs. However, there are some exceptions, for example, *Chydorus sphaericus* can maintain activity even under ice (Kalinowska & Karpowicz, 2020; Klemetsen et al., 2020; Smirnov, 2017). The optimal temperature for many temperate zone Cladocerans is somewhere between 10 °C and 20 °C, and becomes lethal around 30 °C (Smirnov, 2017). However, that is not the case for all Cladocerans, as researchers have found that some species can inhabit hot springs with temperatures close to 40 °C (Padhye & Kotov, 2010).

The pH tolerance between Cladocera species might differ, however, most Cladocerans prefer neutral pH (Bērziņš & Bertilsson, 1990; Smirnov, 2017). Few species can survive under conditions with a pH < 3 (Deneke, 2000). Acidic stress and ion uptake inhibition can be some of the reasons why many Cladocerans cannot tolerate low pH conditions (Gao et al., 2022; Smirnov, 2017). Ecotoxicology studies have also shown that metal toxicity for some Cladocerans increases at low pH (De Schamphelaere et al., 2025). However, this effect might be less pronounced in dystrophic than in acidic clearwater lakes (Korosi & Smol, 2012). Nevertheless, other properties of acidic water bodies might influence Cladoceran distribution. For example, softwater acidic lakes often have low calcium (Ca) concentrations (Murphy, 2002). Ca is necessary for different bodily functions of Cladocerans (Smirnov, 2017). Additionally, a lack of Ca can increase the toxicity of various substances, such as heavy metals and road salt (NaCl) in Cladocerans (Buren & Arnott, 2025; Smirnov, 2017). Ca demand is species-specific, and as some species have lower Ca demand than others, it is sometimes used as an argument for why some Cladocerans can thrive in acidic or softwater lakes, while others disappear (Hessen et al., 1995; Jeziorski et al., 2015; Shapiera et al., 2011). The opposite end of the lake condition spectrum could be considered alkaline, hardwater, or even saline water bodies. Most Cladocerans inhabit freshwaters, with few species living in saline waters (Boronat et al., 2001; Smirnov, 2017). It is considered that the species' ability or inability to occupy waters with certain salinity or hardness depends on its osmotic regulation mechanisms (Smirnov, 2017). Electrical conductivity is a commonly used parameter to describe the concentration of ions in the water (Jones & Smol, 2024). It is considered that for many Cladocerans the optimal electrical conductivity range is between 50 and 500 µS/cm (Boronat et al., 2001; Smirnov, 2017).

Many researchers have found that lake depth can significantly influence Cladocera assemblages. Some Cladocerans can live in water depths greater than 100 m (Smirnov, 2017), but as most lakes do not reach such depths, the effects of depth might rather be connected to other associated parameters. Lake depth can influence the distribution of macrophytes (Jones & Smol, 2024), which can be important for many Cladocerans, as well as provide refuge from fish through diel vertical migration (Dodson, 1990). Inhabiting deeper water layers can also protect Cladocerans from harmful ultraviolet (UV) radiation. In conditions when sufficient vertical migration is not possible or is costly, some Cladocerans develop melanized shells to minimize UV radiation's impact (Rhode et al., 2001). This adaptation is absent or reduced in waters with fish presence, as this makes Cladocerans more vulnerable to visual predation (Tollrian & Heibl, 2004). Light can also be an important cue to terminate the diapause of the resting eggs (Gyllström & Hansson, 2004); therefore, in cases where resting eggs have settled deep below the photic zone, their hatching might be limited (Rother et al., 2010).

1.1.5 Subfossil Cladoceran use in paleoenvironmental reconstructions

Cladoceran body is covered by chitinous exoskeleton and after the individuals death or molting different body parts are settled into the sediment layer. The preserved exoskeleton elements can be retrieved from the sediments, providing information on the Cladocerans and their related environments of the past (Korhola & Rautio, 2001). The first publications using Cladocera subfossils date back to the first half of the 20th century (Deevey, 1942).

Subfossil Cladocera species assemblages can be used to assess the changes in water depth, trophic state (TS), pH, electrical conductivity (EC), calcium concentrations, climate, macrophyte abundance, and planktivorous fish density in lake ecosystems (Jeppesen et al., 2001; Jeziorski & Smol, 2017; Rautio & Nevalainen, 2025). Other information, such as Cladocera community size structure, can be informative of changes in climate, as well as fish and invertebrate predation (Sysoev et al., 2025). Information on the melanin content and size of ephippia can be informative of the UV radiation in the past (Kultti et al., 2011; Nevalainen & Rautio, 2014), while isotopic composition can provide insights into trophic web structure (Rautio & Nevalainen, 2025). Reconstructions using subfossil Cladocera mainly focus on human impact in the Holocene time scale (Korhola et al., 2005; Jensen et al., 2020; Szeroczyńska, 2002), but they are sometimes used for earlier geological periods as well (Suchora et al., 2025).

When using subfossil Cladocera, the changes in lake environment are most often presented in a descriptive (qualitative or semiquantitative) manner, and quantitative models are rarely used. This does not mean there are no models for the environmental quantitative reconstructions using subfossil Cladocera. Early attempts at quantitative pH reconstruction involved a combination of indicator species and linear regression approaches (Krause-Dellin & Steinberg, 1986), while most researchers after that use such well-known palaeoecological statistical methods as Weighted Averaging (WA), Partial Least Squares (PLS), Weighted Averaging Partial Least Squares (WA-PLS), Modern Analogues (MA), Boosted Regression Trees (BRT), and Random Forest (RF) (Table 1).

Table 1. *Summary of published subfossil Cladocera based quantitative reconstruction models.*

Parameter	Method	Country	Training set size	Reference
Planktivorous fish	WA	Denmark	30	Jeppesen et al., 1996
Mean summer temperature	WA-PLS	Switzerland	68	Lotter et al., 1997
TP	WA-PLS	Switzerland	68	Lotter et al., 1998
TP	WA	Denmark	32	Brodersen et al., 1998
SAL, Depth	WA	Canada	33	Bos et al., 1999
Depth	WA-PLS, WA, PLS	Finland	53	Korhola et al., 2000
Planktivorous fish, SAL, TP	WA	Denmark	36	Amsinck et al., 2005
Lake surface water temperature	PLS	United Kingdom, Norway	68	Kattel et al., 2008
TP	WA-PLS, WA, PLS	Ireland	33	Chen et al., 2010
Macrophytes, Planktivorous fish	WA, ML	United Kingdom, Denmark	39	Davidson et al., 2010
Depth	WA	Greenland	53	Davidson et al., 2011b
Depth	MA, WA, WA-PLS, PLS, ML	Finland	55	Nevalainen et al. 2011
Maximum depth	PLS	Sri Lanka	51	Yatigammana et al., 2017
Macrophytes	BRT	China	64	Dong et al., 2020
Depth	WA, WA-PLS, MA, RF	China, Mongolia	136	Wang et al., 2024

2 Methods

The work of this thesis consists of four major blocks:

1. Training set development
2. Assessment of the relationship between environmental factors and subfossil Cladocera assemblages
3. Development of methods for subfossil Cladocera based environmental reconstructions
4. Analysis of subfossil Cladocera in sediment records and lake environmental reconstruction

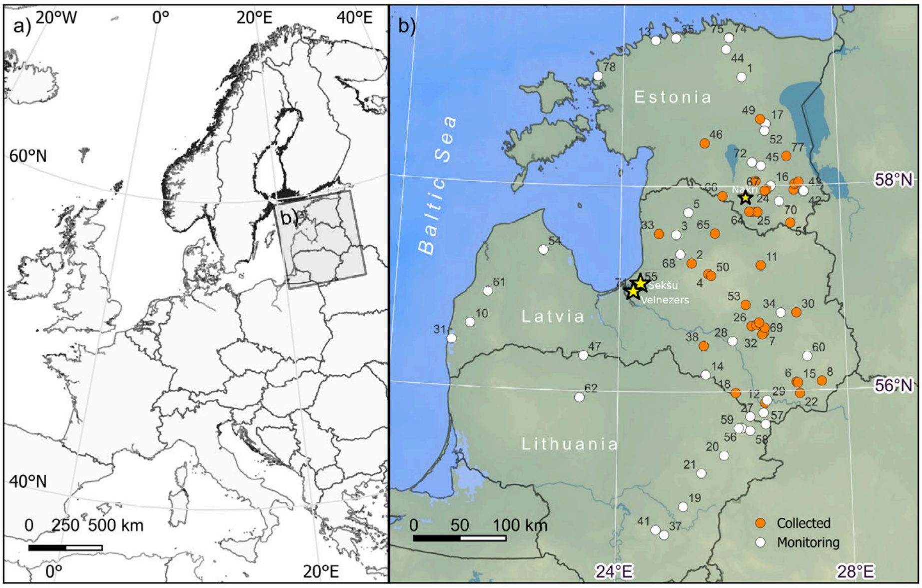


Figure 1 *Location of the sampling sites. a – location of the Baltic states in Europe. b – map of the lakes included in the surface sediment training set. White circles - sites for which environmental data was obtained from monitoring programs; Orange circles – environmental data collected by the author of the thesis or co-authors of Article I. Yellow stars – the sites for which sediment cores were investigated.*

2.1 Training set development

78 lakes, bog pools, and artificial water bodies across Estonia, Latvia, and Lithuania were selected to create a surface sediment training set with an aim to encompass the diversity of freshwater environmental conditions found throughout the Baltic states. In particular, sites that captured variations in pH, electrical conductivity (EC), trophic state (TS), lake maximum depth (Depth), and lake surface area (Area) were targeted. Furthermore, sites with different levels of anthropogenic disturbance were selected, ensuring that the resulting training set accurately represents the variety of conditions of the Baltic region. The artificial water bodies (3 sites) were included in the training set to improve the coverage of hypereutrophic lake conditions, as, after the preliminary data analysis, it was found that there was a shortage of such sites among natural water bodies. These artificial water bodies with considerable sediment layers are at least 100 years old. Therefore, their functioning should be comparable to that of natural lakes.

2.1.1 Sediment collection

Lake surface sediments were collected during the fieldwork campaigns of 2021 and 2022. Where possible, surface sediments were taken in the deepest part of the lake using a Willner-type gravity corer. The upper two cm of sediments were preserved for further analysis. This amount of sediments could accumulate in approximately 2–10 years of lake history (Heinsalu & Alliksaar, 2009; Liiv et al., 2018; Mikalauskienė et al., 2015; Punning et al., 2007; Stivrins et al., 2018; Stivrins, 2023; Veski et al., 2005). Therefore, it was assumed that the upper two cm of surface sediment should represent the modern situation (up to 10 years) while avoiding the one-year extreme event bias. However, the represented period might also be shorter for highly productive lake ecosystems (Article II).

2.1.2 Lake water descriptive parameters

The information on the lake water descriptive parameters was collected by the author of this thesis (28 sites), obtained from the monitoring data of Lithuania (11 sites) (Aplinkos Apsaugos Agentūra , 2024), Latvia (16 sites) (LVĢMC, shared upon request), and Estonia (15 sites) (Keskkonnaseire infosüsteem, 2024), from published literature (3 sites) (Zagars et al., 2025) or collected by other co-authors of Article I (5 sites). As many parameters were only measured by a few of the mentioned sources, this thesis will focus on the ones with no missing values that could be potentially used for subfossil Cladocera based environmental reconstructions. These parameters are surface water pH, EC, dissolved oxygen (DO), Secchi depth (SD), total phosphorus (TP), and Chlorophyll-*a* (Chl-a). Additional parameters analyzed include lake Depth, Area, and mean annual air temperature (T_{ann}).

The author collected water samples and measurements during the fieldwork campaigns of 2021 and 2022 to obtain data from smaller lakes outside the scope of the monitoring programs, which primarily focus on lakes with an Area of > 50 ha. Measurements were taken one to three times per vegetation season (April to October). The author measured pH, EC, and DO on site using a ProDSS probe and SD using a white Secchi disk. The author measured TP and Chl-a concentrations in laboratory conditions. More information on the methodology of these measurements can be found in Article I.

The monitoring program's information was extracted for up to five years before and one year after the sediment collection on lake water pH, EC, TP, total nitrogen (TN), DO, and SD. The five years were chosen as this period should approximately correspond to the period in which the collected surface sediments could have accumulated (see section 2.1.1). Only measurements from the growing season (April to October) were included in the data analysis, as this period is the most important for the development of Cladocera (Smirnov, 2017; Walther & Linderholm, 2006). There were differences in the number and frequency of measurements between data providers, such as measurements done every year vs. every few years, every month vs. one or few times per vegetation season, therefore the existing measurements of each parameter for each lake were combined as the average value of all the measurements of Table 2. While the relationship between TN and subfossil Cladocera was not analyzed directly, this information was included in the trophic state index (TSI) calculations where available (see section 2.4).

Auxiliary parameters such as Depth and Area were extracted from literature (Estonia: kalapeedia.ee; Latvia: ezeri.lv; Lithuania: zvejogidas.lt). Information on the T_{ann} for each lake was compiled from the ERA5 dataset (Copernicus Climate Data Store) (Hersbach, 2020).

Table 2. *Time of measurements for each lake. Lake names with a white background are missing total nitrogen measurements. Under each year, the months in which the data was collected are written. When a hyphen is used between numbers, it relates to time, which includes every month in the range. Months of data collection are color-coded according to the data provider: Estonian (EST), Latvian (LV), and Lithuanian (LT) monitoring programs, Anna Lanka (AL), Matīss Žagars (MZ), and Inta Dimante-Deimantoviča (IDD).*

Lake	2015	2016	2017	2018	2019	2020	2021	2022	Lake	2015	2016	2017	2018	2019	2020	2021	2022
1. Äntu sinijärv		5; 7-9			5; 7-9				40. Neitsi							5;8;9	
2. Āraiši							7;9		41. Nestrėvantys			5;7-9			5;7;8;10		
3. Augstroze					5;8		4-10	5-8	42. Nohipalo Mustjärv	5;7-9	5;7-9	5;7-9	5;7-9	5;7-9	5;7-9		
4. Bānūži							6;7;9		43. Nohipalo Valgõjärv	5;7-9	5;7-9	5;7-9	5;7-9	5;7-9			
5. Burtnieks		6;8	5;8	4-10	5;8	6;8			44. Ohepalu	5;7-9				6;8;10	5;7-9		
6. Čertoks							7;9		45. Pangodi						5;7-9		
7. Ciematnieku							5-8;10		46. Pärsti							5;8;9	
8. Dagdas							7;9		47. Petraičių tvenkinys			5;7-9			4;7-9		
9. Dervanišķu				5;8;10					48. Pikämäe								9
10. Durbes					5;8				49. Prossa							6;8;9	
11. Galgauskas							6;7;9		50. Rijas							6;7;9	
12. Gubišče							6;7;9		51. Ruusmäe							5;8;9	
13. Harku							4-6;8;9		52. Saad		5;7-9						
14. Ilze/Garais							4-10		53. Salas							6;7;9	
15. Jazinks							7;9		54. Sasmakas					5;8			
16. Jõksi		5;7-9							55. Sekšu					4;6;10			
17. Kaiavere		5;7-9							56. Šiurpys			5-10	4;6-10	4;6-10	4;6-10	4;6-10	
18. Kaminča							6;7;9		57. Skirna				5;8;10			4-10	
19. Karvys							4;7-9		58. Šventas			5-10	4;6-10	4;6-10	4;6-10	4;6-10	
20. Kemešys						5;7-9			59. Zalvas						5;7;8;10		
21. Kirneilis						5;7-9			60. Zosnas		4-10					5;8;10	
22. Kombuļu							6;7;9		61. Zvirgzdu			5;8;10					
23. Kuulma								9	62. Talkša			4;7-9			4;7-9		
24. Kooraste Linajärv							5;8;9		63. Tolkjāja							5-7;10	
25. Köstrijärv				5;7-9			5;8;9		64. Tollari							5;8;9	
26. Kurtava							5-8;10		65. Trikāta							6;7;9	
27. Laucesa			5;8;10			5;7;8;10	4-10		66. Udsu							5;8;9	
28. Laukezers		4-9				5;8;10			67. Uiakatsi							5;8;9	
29. Lielais Stropu ezers		8	8	8	5;7;10				68. Ungurs		4-10					5;8;10	
30. Lielais Svētiņu							6;7;9		69. Vaboles							5-8;10	
31. Liepājas							4-10		70. Vagula		5;7-9						
32. Liepsalas							5;6;8;10		71. Velnezers					4;6;10			
33. Limbažu dūņezers		6;10		4-10			5;7;8;9	5-8	72. Verevi			5;7-9					
34. Lubāns					5;8;10	4-10			73. Vērtezis							5;6;8;10	
35. Maardu	5;7-9						5;7-9		74. Viitna Linajärv							5;8;9	
36. Mikila							5;8;9		75. Viitna Pikkjärv	5;7-9	5;7-9	5;7-9	5;7-9	5;7-9		5;9	
37. Margis						5;7;8;10			76. Viroste								9
38. Mazsunākste							6;7;9		77. Võnnu							6;8;9	
39. Nakri							5;8;9		78. Vööla meri						5;7-9	5	

2.2 Study sites for analysis of sediment cores

We selected three lakes from Latvia and Estonia with different levels of human impact and temporal coverage for environmental reconstruction. All these lakes are small-sized (Velnezers 3.5 ha, Sekšu 7.9 ha, Nakri 0.9 ha) brown water lakes (Līcīte, 2017a, 2017b; authors' observations). Lake Sekšu and Velnezers nowadays do not have any inlet or outlet, while Lake Nakri receives water from a small spring. Currently, Lake Sekšu, Lake Velnezers, and Lake Nakri can be described as eutrophic lakes with neutral to alkaline pH (Article I).

2.2.1 Lake Velnezers

Lake Velnezers (56.97' °N, 24.24' °E) (average depth 3.5 m, maximum depth 6 m, elevation 4.6 m) is located within Riga, Latvia (Dručka, 2014). The catchment area of Lake Velnezers has undergone significant changes in the last 200 years, transitioning from a forested to an agricultural to an urban landscape. These changes have resulted in increased eutrophication as well as water pollution with heavy metals (Article II).

Samples for Lake Velnezers were collected in February 2019 using 8 cm diameter Kayak-type gravity corer. The sediment profile was 33 cm long and was sliced into 1 cm thick sub-samples in the field conditions. The core chronology was obtained using ^{210}Pb dating (Blaauw & Christen, 2011; Tylmann et al., 2016). In Article II, sediment chemistry was also analyzed to better evaluate changes in Lake Velnezers.

2.2.2 Lake Sekšu

Lake Sekšu (57°03'N, 24°35') is a shallow lake (average depth between 2.3 and 3.3 m, maximum depth 6 m, elevation 2.5 m a.s.l) located in the vicinity of Riga (Bauze-Krastiņš, 2009; Jansons, 1997; Latvijas Ezeri, 2010). Lake Sekšu has been part of the "Baltezers" water supply system for Riga since 1904. Currently, the lake is part of a restricted area, limiting more direct influences from pollution of agriculture and recreation (LVĢMC, 2015). The utilization of Lake Sekšu in the water supply system has led to considerable water level fluctuations (Bauze-Krastiņš, 2009; Jansons, 1997). Between 1953 and 1965, attempts were made to increase the water level in Lake Sekšu by pumping water from nearby Lake Baltezers via pipeline (Dziļuma, 2003). The influence of this pipeline led to increased erosion and eutrophication of Lake Sekšu (Article III).

Samples for Lake Sekšu were collected in February 2019 using 8 cm diameter Kayak-type gravity corer. The sediment profile was 46 cm long and was sliced into 1 cm thick sub-samples in the field. The core chronology was obtained using spheroidal carbonaceous particles, ^{137}Cs, and ^{210}Pb dating (Rose, 1990; Tylmann et al., 2016). In addition to subfossil Cladocera analysis, for this core, we also have information on pollen, non-pollen palynomorph, diatom, Chironomidae, and sediment chemical composition (Article III).

2.2.3 Lake Nakri

Lake Nakri (57°53' N, 26°16' E) (maximum depth 3 m, 48 m a.s.l.) is a small, shallow lake in Southern Estonia. The low swampy shores of Lake Nakri are characterized by a floating mat, with vegetation composed of *Phragmites australis* and different *Sphagnum* and *Carex* species. Macrophytes of Lake Nakri mainly consist of submerged species, with a few floating-leaved plants (authors' field observations). The catchment (0.25 km^2) (Amon et al., 2012) of Lake Nakri is dominated by coniferous and birch forests. Nowadays, some potential influences for Lake Nakri include drainage ditches from the nearby forest and a gravel road passing by the northern end of the lake (Keskkonnainvesteeringute keskus, 2024). However, this might not have always been the case as historical maps show that in the 19th and the beginning of the 20th century, some parts of the northern shore of Lake Nakri were covered by pasture instead of forest (Üheverstane kaart, 1911).

Several publications have used sediment archives from Lake Nakri to investigate the climatic and vegetation patterns of late glacial (14,700 to 11,700 years BP) and early Holocene (11,700 to 8,000 years BP) periods (Amon et al., 2012, 2014; Väliranta et al., 2015; Veski et al., 2015). The area of Lake Nakri deglaciated approximately 14,000 years ago. The pollen and macrofossil data show that during the late glacial period, the area underwent different stages of tundra vegetation, with a transition to forest vegetation at the beginning of the Holocene, approximately 11,650 years BP (Amon et al., 2012).

Sediment sampling of Lake Nakri was done on three separate occasions. In the year 2007 the glacial and early Holocene sediments were cored (sediment depths used in this thesis 10.5 to 7.4 m), in 2009 (sediment depth selected from these cores 7.3 to 6 m), and in 2018 (sediment depth 6 m to 0.25 m) using a Russian corer. In 2018 Willner corer was used for the surface sediments (sediment depth 0.25 to 0 m).

Sediments were sampled for Cladocera analysis (for more details on Cladocera analysis, see section 2.3) with an interval of every 10 cm for the upper 3 m to capture the potential anthropogenic influence on the lake ecosystem. In the rest of the sediment profile, the author sampled sediments with an interval of every 20 cm. There were some deviations in this sampling strategy in cases when some parts of the core were missing due to the material being used to analyze some other proxies, but also when transitioning to cores taken at different times (for example, switching from cores taken in 2018 to the ones taken in 2009). The author also sampled sediments with a smaller interval in the transition zone between late glacial and Holocene sediments. For more information on the selected samples and sediment dating, see Manuscript I.

2.3 Cladocera analysis

For subfossil Cladocera analysis, 1–2 cm^3 of sediment samples were taken and prepared according to the standard procedure described in Szeroczyńska & Sarmaja-Korjonen (2007). Sediment samples were placed in 100 ml of 10% KOH, then heated in an 85 °C water bath for 30 minutes. Afterward, samples were sieved (mesh size 40 µm). In this step, 10% HCl was applied if the sediments were carbonate-rich. After the treatment, sediment samples were diluted with water. The volume for the sample dilution was 10 ml for the samples of the surface sediment training set, Lake Sekšu, Lake Velnezers, and most of Lake Nakri. However, for some of the samples, it was visible already during the sample treatment process that the concentration of the remains was low, so the dilution volume was adjusted accordingly. The diluted sediments were stained with Safranine O. A few drops of ethanol were added to the diluted sample, and it was stored in a fridge until further investigation.

To prepare the microscopy slides, 100 µl of the homogenized subsample was taken with an automatic pipette. The prepared slides were investigated under a light microscope at 100x, 200x, and 400x magnification. All the recognizable remains (heads, shells, postabdomens, postabdominal claws, etc.) within each slide were counted. After counting each slide, the maximum number of individuals present for each species and how many individuals could be present in total were calculated, and this procedure was repeated until the number of individuals was at least 70. This number is considered to be sufficient to characterize the species assemblages (Kurek et al., 2010). After this, one additional slide was investigated, marking the presence of the species not previously found in the sample (Figure 2).

Species identification was primarily based on the identification key by Szeroczyńska and Sarmaja-Korjonen (2007). For the determination of rare species, or species and skeletal elements not described in this book, additional literature was used (Bjerring et al., 2008; Błędzki & Rybak, 2016; Sinev & Gavrilko, 2021; Van Damme & Nevalainen, 2019).

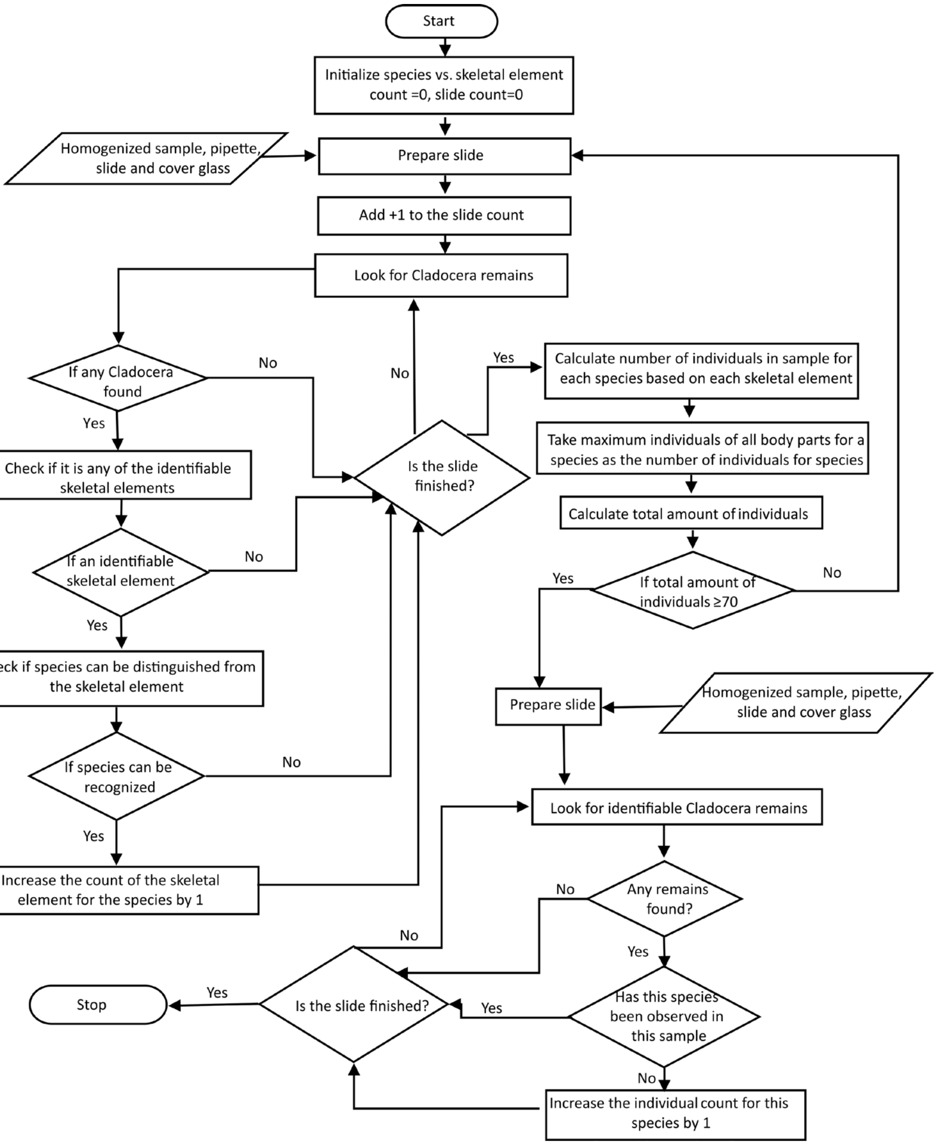


Figure 2 *Subfossil Cladocera microscopy analysis scheme.*

2.4 Data analysis

2.4.1 Dataset manipulations and data subset creation

To give a general description of Cladocera species assemblage samples of the surface sediment training set and the cores of Lake Velnezers, Lake Sekšu, and Lake Nakri, species counts were converted to relative abundances. All of the species were included in the functional group analysis and species diversity analysis (see section 2.4.3), but for ordination analysis (section 2.4.2), indicator species analysis (section 2.4.4), and model development (section 2.4.5) all the species that appeared in 5 samples or less were excluded from the dataset. Before it was done, it was graphically assessed whether the observations clustered around some areas of the tested environmental gradients (which they did not).

The pH, EC, Chl-a, TN, TP, and SD values for each lake were expressed as the average value of all the measurements for each parameter. This was done due to uneven data coverage among lakes (Table 2). Eutrophication and trophic state (TS) of lakes is one of the focus points in paleolimnological research (Davidson & Jeppesen, 2013). However, TS is a complex variable that can be assessed based on several parameters (such as TP, TN, SD, and Chl-a). To simplify the TS evaluation of the lakes, a combined parameter-trophic state index (TSI) (Brezonik, 1984; Carlson, 1977; Carlson, 2007) was calculated and added to the data analysis. First, TSI was calculated based on each of the measured TS-related parameters (SD, Chl-a, TP, and TN).

$$TSI(SD) = 60 - 14.41\ln(SD)$$
$$TSI(Chl-a) = 9.81\ln(Chl-a) + 30.6$$
$$TSI(TP) = 14.42\ln(TP) + 4.15$$
$$TSI(TN) = 54.45 + 14.43\ln(TN)$$

Then the average TSI index was calculated depending on the limiting nutrient, if information on TN was available. If TN data was missing and it was not possible to determine the limiting nutrient, an assumption of TP limitation was made. In dystrophic lakes, SD is water color limited due to the humic substances (Gray et al., 2022); therefore, in these lakes, SD was excluded from the TSI calculation, and the average value calculation was adjusted accordingly (division by two instead of three).

Nutrient balanced lakes (10≤TN/TP≥30)

$$TSI = \frac{TSI(Chl-a) + TSI(SD) + 0.5(TSI(TP) + TSI(TN))}{3}$$

P-limited lakes (TN/TP>30)

$$TSI = \frac{TSI(Chl-a) + TSI(SD) + TSI(TP)}{3}$$

N-limited lakes (TN/TP<10)

$$TSI = \frac{TSI(Chl-a) + TSI(SD) + TSI(TN)}{3}$$

The taxonomical level to which species are determined, and training set data coverage, can influence the model performance and statistical analysis results (Heiri & Lotter, 2010; Turner et al., 2021). Therefore, smaller data subsets were created and used in ordination analysis and model building. Subsets were created by excluding lakes from the training set with pH < 6. This lake group mainly consisted of dystrophic lakes and is mostly addressed separately from clear water lakes in limnological research. Another subset type was created by merging *Bosmina* (*Eubosmina*) *longispina* and *Bosmina* (*Eubosmina*) *coregoni* under the group *Eubosmina* spp. The taxonomy and determination of Eubosmina species is complicated due to its cyclomorphic forms and high morphological variability (Błędzki & Rybak, 2016; Johnsen & Raddum, 1987). However, while merging these two groups lessens the probability of subfossil remain misidentification, some information may be lost this way.

The resulting datasets are:

- "all" – dataset that includes all the species that have been observed in more than five sites and consists of all 78 sites of the training set;
- "Eubosmina"– dataset similar to "all", with the only difference of *B*. (*E*.) *longispina* and *B*. (*E*.) *coregoni* being merged into *Eubosmina* spp.;
- "pH > 6" – dataset with excluded lakes with average pH < 6;
- "Eubosmina (pH < 6)" – excluded lakes with average pH < 6 and *B*. (*E*.) *longispina* and *B*. (*E*.) *coregoni* being merged into *Eubosmina* spp.

2.4.2 Cladocera species relation to environmental parameters

Cladocera species relation to environmental parameters are primarily investigated in Article I. For data preparation in this step, subfossil Cladocera data were square root transformed, and species that had fewer than five observations were excluded from the analysis. Environmental data was natural logarithm transformed. The main environmental factors affecting subfossil Cladocera species composition were determined by redundancy analysis (RDA) (Birks et al., 2012) with a forward selection algorithm to reduce the number of explanatory variables. The analysis was performed for all of the created data subsets to determine whether the driving factors of the species composition differed. The analysis was done in R (v4.3.3, R core team 2024), using library "vegan" (Oksanen et al., 2022). Only parameters identified as significant in the RDA analysis were further investigated for environmental reconstructions.

2.4.3 Cladocera composition description

Cladocera species diversity was described in the samples based on Shannon's species diversity index, species evenness, and rarefied richness (Birks, 2012). Rarefied species richness was calculated in program R (v4.3.3, R core team 2024), using library "vegan" (Oksanen et al., 2022). Species diversity and evenness were calculated in program "Past 5.2.1" (Hammer et al., 2001).

Functional characteristics of a community can reveal aspects of ecosystem functioning that may be overlooked when focusing on individual species, mainly due to factors like competition for resources and functional redundancy (Laureto et al., 2015). Therefore, in addition to analyzing Cladocera community on a species level, the observed species were also divided into groups based on the average female size of the species (Small < 0.5 mm, Medium 0.5–1 mm, Large > 1 mm), habitat preference (Pelagic, Littoral unspecified (Littoral generalists), littoral Macrophyte-associated, littoral Sediment-associated). Species were divided into groups based on the species description in Błędzki & Rybak (2016). The relationship between the environmental parameters identified by RDA analysis and the functional groups of the training set samples was assessed via Pearson's correlation coefficient (Berman, 2016). Species composition was further evaluated by PCA analysis (Birks et al., 2012), which was carried out for each of the data subsets.

2.4.4 Indicator species analysis

Cladocera are commonly used in paleolimnology as indicators to assess the changes in lake environments (Chen et al., 2010; Davidson et al, 2010; Zawiska et al., 2025). To evaluate which species could be used as indicators for past environmental reconstructions, IndVal.g analysis was used (Cáceres & Legendre, 2009). This method evaluates species fidelity and observation frequency within the group (Dufrêne & Legendre, 1997). IndVal.g differs from IndVal by taking into account the number of samples within the analysed group (Cáceres & Legendre, 2009). The indicator species analysis was performed in program R, using "indicspecies" package (Cáceres et al., 2010). Within the analysis, it is possible to define whether each species can be indicative of only one group or several groups. Researchers more commonly use one species –one group indicator species approach, however, allowing a species to be indicative of several environmental groups can allow inclusion of species with wider environmental niches (Cáceres et al., 2010) and could be potentially more informative in cases when species environmental preference lays within a border of two environmental groups. Indicator species analysis was performed by applying both approaches. One species – one group approach is further referred to as "IndVal.g^1", and multiple group indicator species analysis is referred to as "IndVal.g^{all}".

Each of the important environmental variables identified by RDA analysis was analysed using the IndVal.g method. The environmental groups were pre-defined by the author of the thesis. Trophic state (TS) groups were defined based on the TSI values, as TS is a complex variable. The TS groups were oligotrophic, mesotrophic, eutrophic, hypereutrophic (Table 3), and dystrophic. Dystrophic lakes were identified based on the literature, as dystrophic lake definitions vary and are often based on catchment characteristics more than water chemistry (Eņģele & Sniedze-Kretalova, 2010; Gray et al, 2022; Ingmar Ott, personal communication).

Table 3. *TS descriptive water parameters and the threshold values between different trophic states according to Nürnberg (1996) and Carlson (2007).*

Trophic state	Trophic State Index	Secchi depth (m)	Total Phosphorus (µg/l)	Total Nitrogen (µg/l)	Chlorophyll-*a* (µg/l)
Oligotrophic	< 40	> 4	< 10	< 350	< 3.5
Mesotrophic	40–50	2–4	10–30	350–650	3.5–9
Eutrophic	50–70	1–2	30–100	650–1200	9–25
Hypereutrophic	> 70	< 1	> 100	> 1200	> 25

Lakes were grouped based on their average pH value into groups "< 6", "6–8", and "> 6". The selected electrical conductivity (EC) groups were "0–100", "100–200, "200–300", "300–400" and "> 400". The selected Depth groups were defined with a 5 m step ("< 5", "5–10", "10–15", "15–20", "> 20"). Lake Area (ha) groups were defined as "< 10", "10–25", "25–50", "50–100", "100–400", "> 400". The division of EC and Depth groups with a step was chosen due to a lack of clear definitions within limnological literature. Indicator species analysis and its pH, EC, and TS results are described in depth in Article I. The only new result of pH, EC, and TS indicator species was regarding *Eubosmina* spp., whose indicator species potential was not assessed in Article I.

2.4.5 Model development

This work aimed to find suitable models for reconstructing past environmental changes in the Baltic states. We developed and tested weighted averaging partial least squares (WA-PLS) and boosted regression tree (BRT) models for the reconstruction of pH, EC, Depth, and TS descriptive parameters (such as TSI, TP, Chl-a). WA-PLS is one of the most commonly used methods for constructing transfer functions in paleolimnology (Heiri et al., 2011; Turner et al., 2021). This method combines two commonly used methods – weighted averaging (WA) and partial least squares (PLS) – each with its own advantages and limitations. WA is a popular method for environmental reconstructions that captures unimodal species-environment relationships well. However, it is rather sensitive to uneven data distribution along the gradient and tends to overestimate the values at the lower end of the gradient and underestimate the higher values. On the other hand, PLS is a method that can effectively use several components for environmental predictions but has a tendency for model overfitting (Birks et al., 2012). It is considered that combining these two methods into WA-PLS results in improved model performance (Ter Braak & Juggins, 1993).

Even though WA-PLS has been shown to be an effective method for environmental reconstruction, it has some limitations, such as the model assumption of unimodal species response distributions (Ter Braak et al., 1993). Furthermore, uneven environmental gradient distribution can significantly impair the model's predictive power (Turner et al., 2021). As most of the data in the developed training set for Baltic States has uneven coverage along the environmental gradients (Appendix 5), machine learning methods that do not have fundamental assumptions might be more appropriate. Despite the rapid development of machine learning techniques, subfossil Cladocera research and the field of paleolimnology have shown relatively few attempts to integrate this knowledge into past environmental reconstructions (Dong et al., 2020; Salonen et al., 2014; Sun et al., 2024; Wang et al., 2021). Therefore, the author tested whether BRT could be a suitable method for reconstructing past lake conditions of the Baltic states.

The BRT approach combines regression tree and boosting algorithms. Regression trees are non-parametric models that subset the data with similar response values. They are capable of capturing complex, nonlinear relationships and interactions between species and environmental variables. Boosting, on the other hand, is an ensemble learning method that incrementally builds a strong predictive model by combining many weaker models, reducing bias and improving performance. While boosting enhances accuracy and robustness, it can be computationally intensive and prone to overfitting if not properly tuned (Elith et al., 2008). The integration of these two approaches in BRT allows to account for non-linear, non-monotonic relationships and interactions, which are common in species-environment datasets (Birks et al., 2012).

Data analysis was done using program R (v4.3.3, R core team 2024), the WA-PLS model was developed using package "rioja" (Juggins, 2022), while the BRT model was developed using package "gbm" (v 2.2.2, Ridgeway & Developers, 2024). To make the model results comparable for both models, k-fold (k = 10) cross-validation (López et al., 2022) with fixed folds predefined by the author (Appendix 6) was used. The WA-PLS model was tested for five components, and for the final model, the component with the lowest average RMSEP value was chosen.

The BRT workflow development was based on the article by Elith et al. (2008). The author did grided automated hyperparameter tuning to find the inner model parameters that would give the best results for the BRT model (López et al., 2022). The model performance was tested for distributions (“gaussian”, “laplace”, “tdist”), shrinkage (0.1, 0.05, and 0.01), bag fraction (0.6, 0.65, 0.7 and 0.75), interaction depth (1, 2 and 3), a minimum number of observations in the terminal nodes (2, 3, 5, 10) with a maximum number of 2000 trees. The best set of hyperparameters was chosen by selecting the hyperparameter combination that would give the smallest mean square error. The seed was set before the hyperparameter tuning, and a matching seed was used before the usage of the model to ensure the reproducibility of the model result. The best hyperparameters can be found in Appendix 7.

To make the data distribution more suitable for the WA-PLS model, Cladocera data was square root transformed, species present in less than five samples were excluded, and environmental data (except pH) was natural logarithm (ln) transformed. It was done as most of the parameters had a right-skewed distribution. However, pH has a slightly left-skewed distribution (Appendix 5). Therefore, natural logarithm transformation would not improve the distribution of the pH data (Birks et al., 2012).

Separate BRT and WA-PLS models were built using data subsets “all” and “Eubosmina” for pH, EC, TSI, TP, Chl-a, and Depth. Models based on datasets “pH > 6” and “Eubosmina (pH > 6)” were built for TSI, TP, Chl-a, and Depth.

The cross-validation (CV) results for all the developed reconstruction models for each parameter (pH, EC, TSI, TP, Chl-a, Depth) were compared by RMSEP, R2, and slope values for model CV results. Residuals vs. Predicted values were tested for heteroskedasticity using the Breusch-Pagan test in the package “lmtest” (Zeileis & Hothorn, 2002), and for the normality of distribution using the Shapiro-Wilk test (Shapiro & Wilk, 1965). Residuals vs. Observed values were analysed using Pearson's correlation coefficient (Berman, 2016) to identify if models are displaying any trends in their predictions in relation to the observed values.

2.4.6 Environmental reconstructions

The stratigraphic diagrams for Lake Velnezers, Sekšu, and Nakri were created in the program Tilia (Grimm, 2011). For sediment core investigations, to recognize the important shifts in the Cladocera species community, temporally constrained hierarchical clustering (CONISS) was employed (Grimm, 1987). The number of significant clusters was chosen using the broken stick method (Jackson, 1993).

The author tested the developed pH, EC, TSI, TP, Chl-a, and Depth models on the core of Lake Velnezers (Article II), Lake Sekšu (Article III), and Lake Nakri (Manuscript I). All of the developed models were applied to these sites and evaluated how well the model output aligns with the conclusions drawn in Article II, Article III, and Manuscript I, as well as with information from literature sources. Additionally, the author evaluates pH, EC, TS, and Depth based on the indicator species and functional group approach findings of this work. LOESS 10-point smoothing was applied to the graphical representations of all the reconstructed parameters for each lake. It was hypothesized that sediment core samples that have a similar species composition to the ones in the training set in reconstruction will provide more realistic results. The similarity between each sample in the core of Lake Sekšu, Lake Velnezers, and Lake Nakri was determined by first calculating the sample similarity as one minus Bray dissimilarity times 100 (Faith et al., 1987) between the sediment core sample and each of the training set samples. The 10 highest dissimilarity values were then selected to represent the dissimilarity results. This procedure was repeated for all four data subsets The past environment reconstructions, their representations as well as similarity calculations were done using program R (v4.3.3, R core team 2024) and libraries “rioja” (Juggins, 2022), “gbm” (v 2.2.2, Ridgeway & Developers, 2024) and “vegan” (Oksanen et al., 2022).

3 Results

3.1 Training set development

3.1.1 Cladocera relation to environmental parameters

RDA triplot shows that pH, TSI, and Depth are the main environmental parameters influencing subfossil Cladocera species communities (Figure 3). These parameters have a significant explanatory power independently of the tested dataset. Parameters, that were selected as significant by the forward selection criteria in some of the tested datasets, but not others are TP and Area (“all”, “Eubosmina”), Chl-a (“pH > 6”, “Eubosmina (pH > 6)”), EC (“All”, “pH > 6”, “Eubosmina (pH > 6)”). The explanatory power of the RDA1 and RDA2 axes is constant, regardless of whether *Bosmina* (*Eubosmina*) *longispina* and *B.* (*E.*) *coregoni* are left as separate groups (“All”) or merged into *Eubosmina spp.* (“Eubosmina”). However, it can be observed that changes in RDA1 and RDA2 axis explanatory power change from the dataset “pH > 6” to “Eubosmina (pH > 6)”, with increasing explanatory power for the RDA1 (from 20.65% to 23.97%) and a slight reduction of RDA2 explanatory power. The parameters excluded from further analysis as insignificant based on the RDA were DO, SD, and T_{ann}.

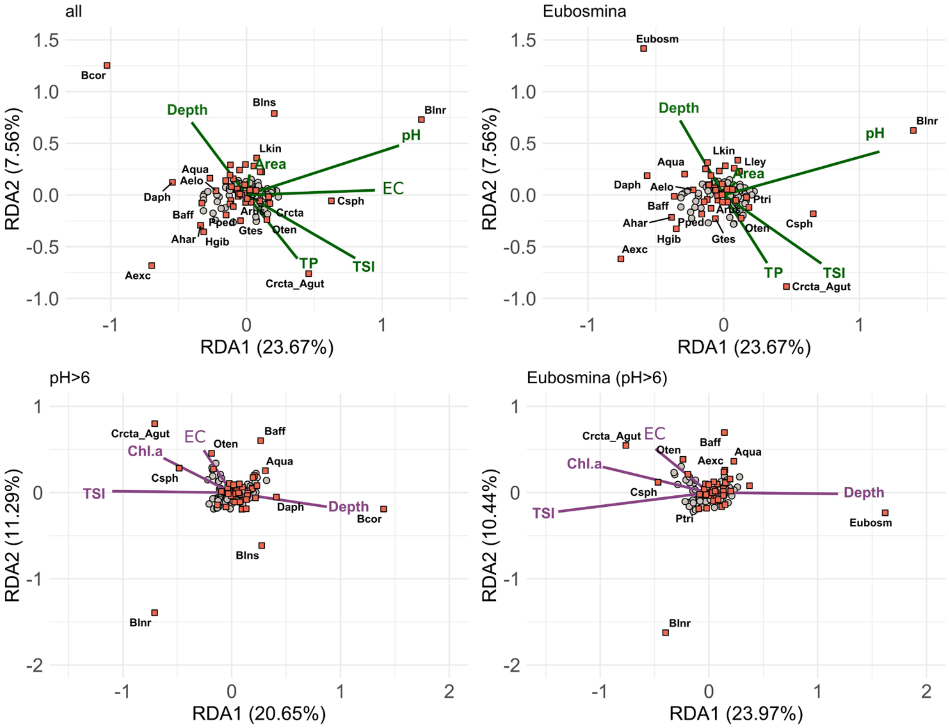


Figure 3 *Redundancy analysis (RDA) for each of the sub-datasets (“all”, “pH > 6”, “Eubosmina”, “Eubosmina (pH > 6)”).*

3.1.2 Environmental parameters

The median values of TSI and Depth do not noticeably differ between pH groups, however there is a difference in data range. The pH < 6 lakes do not exceed lake Depth of 10 m and have generally higher TSI values. While on average, pH < 6 lakes are smaller, the smallest and largest lakes belonged to pH groups 6–8 and > 8. (Figure 4). All of the pH < 6 lakes also belonged to the EC 0–100 group, but not all the lakes with EC 0–100 belonged to the pH < 6 group. There is no clear relationship between EC and TSI. There appears to be a relationship between lake Depth and lake TSI. Oligotrophic lakes were the deepest, and with increased TS the median lake Depth decreases, hypereutrophic lakes rarely exceeding 5 m. Shallow lakes (Depth < 10 m) tend to be smaller, but there seems to be generally little connection between lake Area and any other parameter.

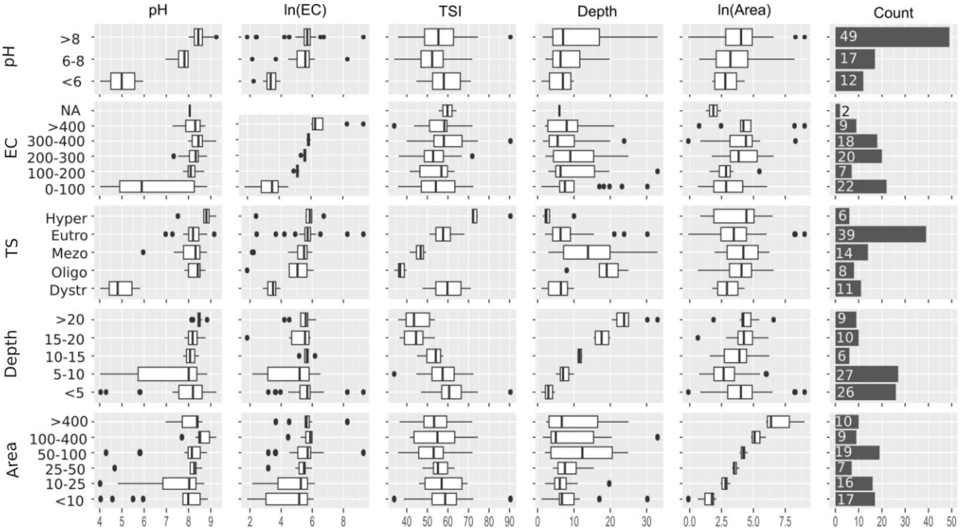


Figure 4 *Distribution of pH, EC (Electrical Conductivity, µS/cm), TS (Trophic State), Depth (maximum depth, m), Area (lake surface area, ha) groups across pH, EC, TSI (Trophic State Index), Depth, and Area values. In the column "count" a number of lakes in each group are represented by histograms.*

3.1.3 Cladocera relation to environmental parameters

Lakes with pH < 6 seem to have noticeably higher species evenness and slightly higher species richness and diversity (Figure 5). Species richness, evenness, and diversity tend to reduce with increasing TS. Data points are scattered in all of these cases, especially for eutrophic lakes. Therefore, results cannot be interpreted unequivocally. Species diversity and richness reduce with the increase of EC. On the other hand, evenness is higher in lakes with EC < 100 µS/cm, but does not differ much between lakes with EC > 100 µS/cm. Lake Area and Depth seem to have little connection to diversity descriptive parameters.

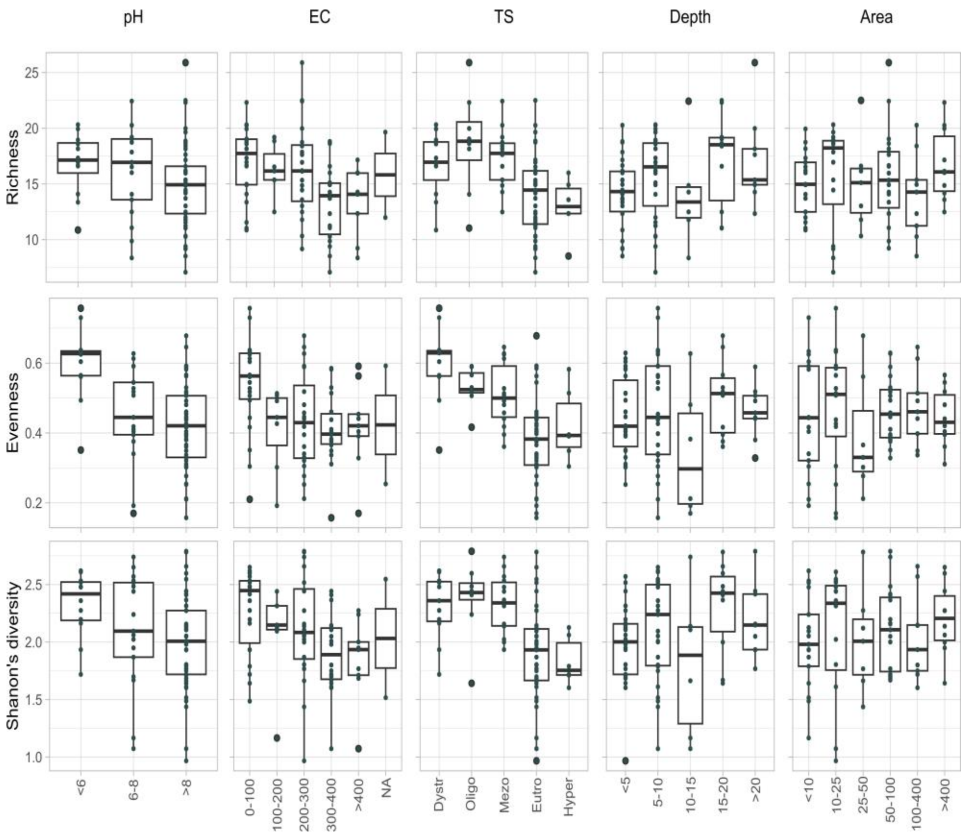


***Figure 5** Diversity descriptive parameters (Richness, Evenness, Shannon's diversity index) to pH, Electrical Conductivity (EC), Trophic state (TS), lake maximum depth (Depth, m), and surface area (Area, ha).*

Functional groups that most correspond to pH and EC are Large-sized Cladocera (r = –65 and r = –51) (Figure 6). Small and Medium Cladocera strongly correlate to TSI (r = 0.62 and r = –0.63). However, this group also has a noticeable correlation to Depth (r = –0.41 and r = 0.40). Small Cladocera also has a positive relation to pH (r = 0.41). In addition to Small and Medium-sized Cladocera, lake Depth correlates with relative abundance of Pelagic Cladocera (r = 0.45) and Macrophyte-associated Cladocera (r = –0.55). Littoral generalists (littoral unspecified) show no significant relation to any of the analyzed parameters. There was no functional group related to the lake area.

PCA analysis shows that subfossil Cladocera species compositions cluster according to trophic groups and pH (Figure 7). The Small Cladocera group coincides with the direction of eutrophic lake distribution, while the Medium-sized Cladocera vector points towards oligotrophic conditions. Large species seem to be characteristic of dystrophic lakes; however, for the datasets where acidic and dystrophic lakes were excluded, the vector points towards oligotrophic lakes. Macrophyte-associated species show a connection to both hypereutrophic and dystrophic lakes. Sediment-associated species seem to be connected to oligotrophic and mesotrophic lakes, but Littoral generalist species and pelagic species do not display a clear connection to any of the pH or trophic groups.

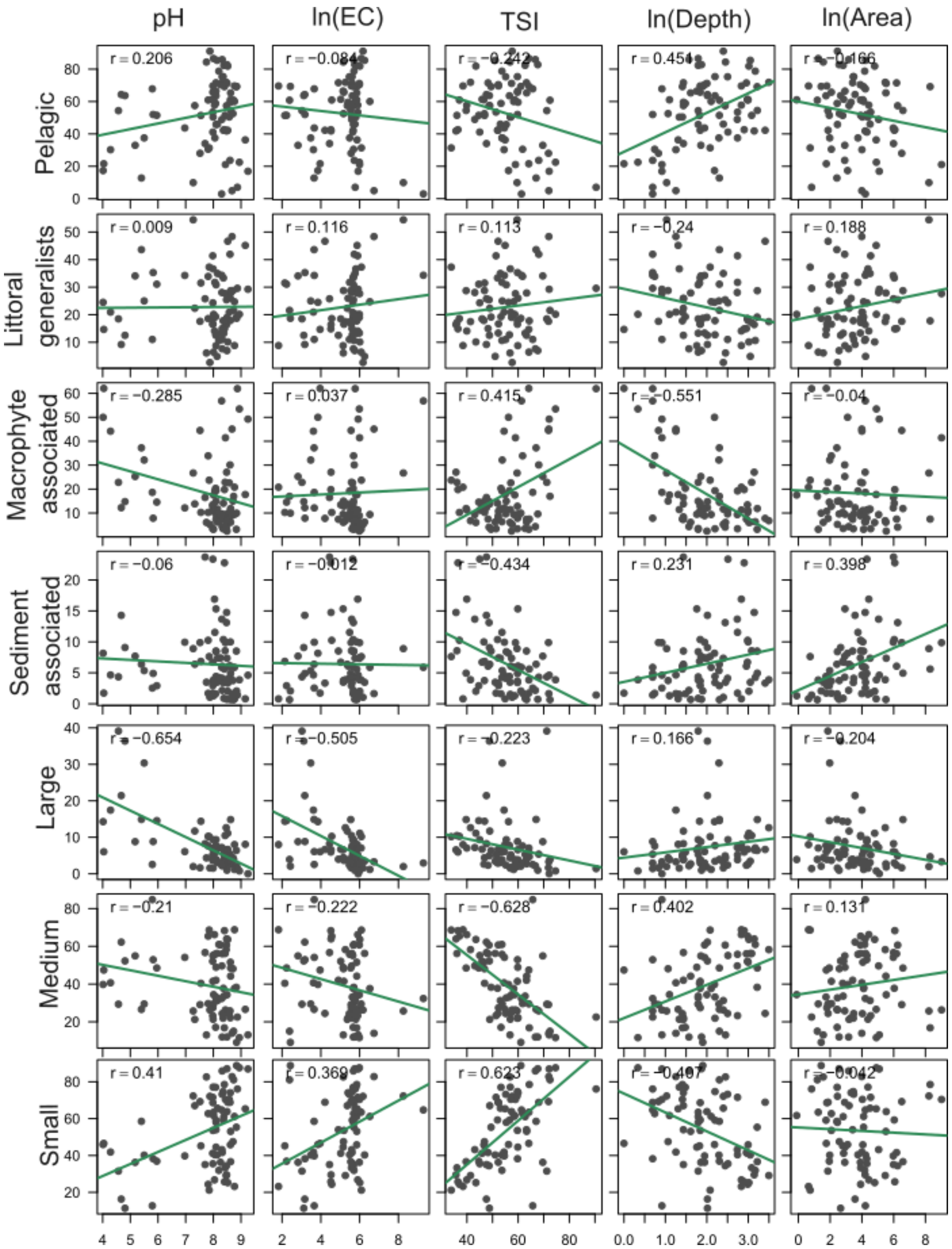


***Figure 6** Cladocera functional group relation to pH, Electrical Conductivity (EC), Trophic State Index (TSI), maximum depth (m; Depth), surface area (ha; Area). The top left corner of each plot Pearson's correlation coefficient (r) is displayed.*

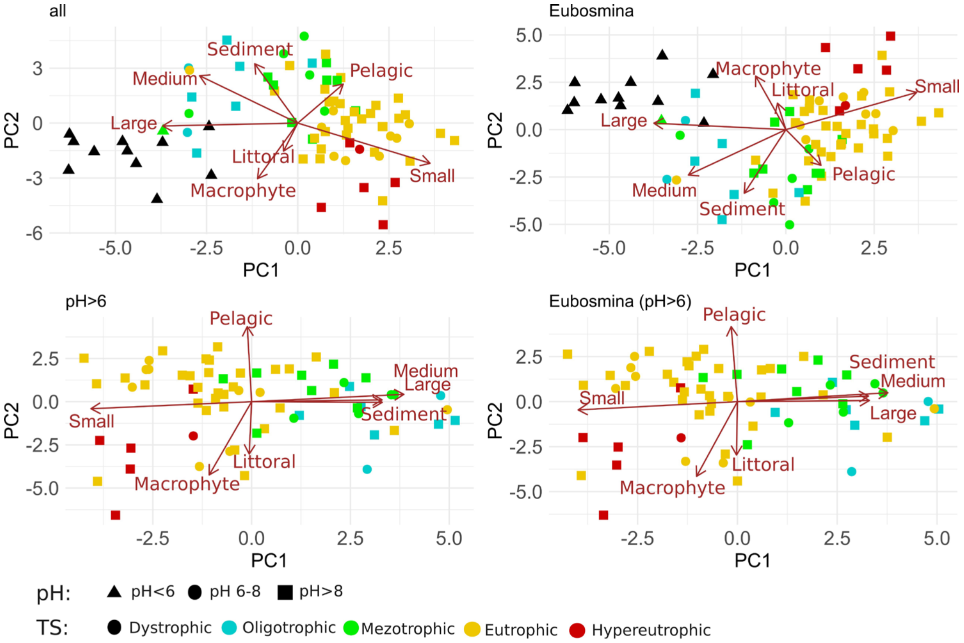


Figure 7 *Principal Component analysis (PCA) results for each of the data subsets ("all", "pH > 6", "Eubosmina", "Eubosmina (pH > 6)"). The relationship between lakes and functional groups is illustrated with arrows.*

3.1.4 Indicator species analysis

Cladocera indicator species in relation to lake pH, EC, and TS were examined in Article I. Initial indicator species analysis showed, that there are two distinct species communities for lakes with pH < 6 and with pH > 6, while for EC similar result was observed with the dividing value being 100 µS/cm, with an exception of *Alonopsis elongata* and *Polyphemus pediculus* which are indicative of EC < 200 µS/cm (Figure 8).

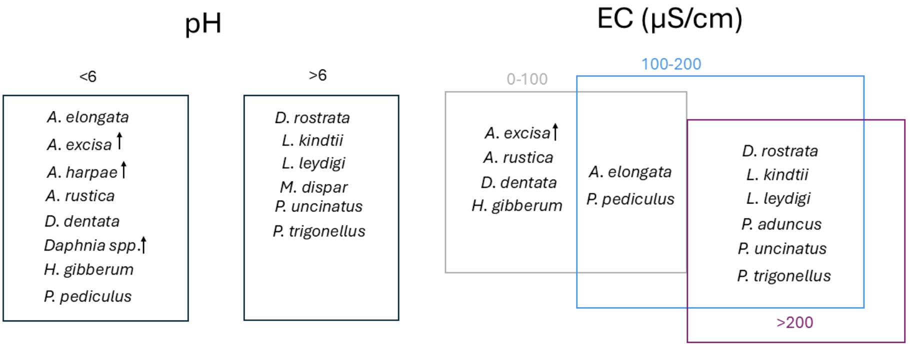


Figure 8 *Species identified as indicators of pH < 6, pH > 6, EC < 100 µS/cm, EC < 200 µS/cm, EC > 200 µS/cm in Article I. Upwards arrow indicates that species is an indicator based on increase in relative abundance, not presence-absence.*

The Cladocera identified as an indicator species by Article I displays a more complex pattern in relation to TS (Figure 9). Several species were found to be indicative of more than one trophic group. The presence of *A. elongata* can indicate dystrophic, oligotrophic, or mesotrophic conditions, while the presence of *Monospilus dispar* can indicate both oligotrophic and mesotrophic conditions. High relative abundances of *Daphnia spp*. can indicate dystrophic, oligotrophic, or mesotrophic conditions. Nevertheless, several species were found to be indicative of only one of the TS groups. Species whose presence indicates dystrophic conditions are *Alona rustica*, *Drepanothrix dentata*, *P. pediculus*, and *H. gibberum*. The presence of *Ophryoxus gracilis* and *Paralona pigra* can indicate oligotrophic conditions. The presence of *Oxyurella tenuicaudis* can indicate hypereutrophic conditions. An increase in relative abundance and dominance of *Alonella excisa* indicates dystrophic conditions, and an increase of *B. (E.) coregoni* suggests a reduction in the TS; the dominance of *B. (E.) longispina* is typical for mesotrophic conditions. The dominance of *B. longirostris* indicates eutrophic conditions, while the dominance of *Coronatella rectangula/ Alona guttata* and *Chydorus sphaericus* indicates hypereutrophic conditions.

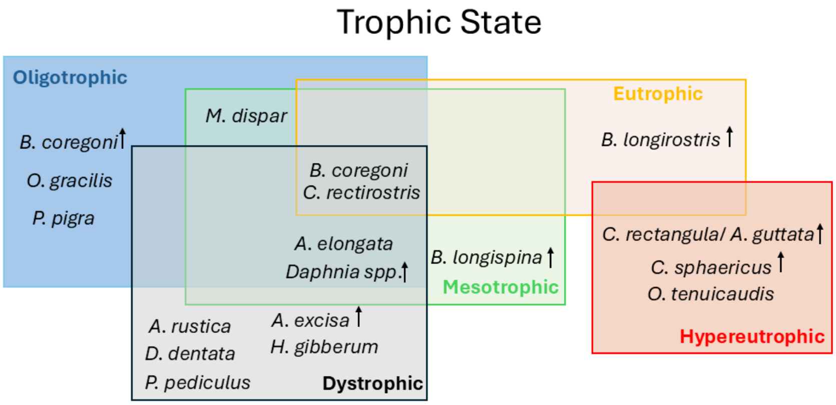


Figure 9 *Species identified as indicative of oligotrophic, mesotrophic, eutrophic, hypereutrophic, dystrophic conditions, or some combination of these groups. As identified in Article I. The upward arrow indicates that species is an indicator based on the increase in relative abundance.*

Indicator species analysis identified *Eubosmina* spp. as indicative of oligotrophic conditions. Testing the indicator species approach on lake Area resulted in four more potential indicator species (*Alonella exigua*, Area < 50 ha; *Alona quadrangularis*, Area > 400 ha; *Kurtzia latissima*, Area 10–50 ha; *Latona setifera*, Area 10–25 ha) (Figure 10). All of these results are statistically significant; however, they are of comparatively low significance ($0.05 < p > 0.01$). Results of Depth indicator species analysis classified as indicators species that were already mentioned as indicators of pH, EC, or TSI in Article I. *A. elongata* is a potential indicator of lakes with Depth of 5–10 and > 15 m. *B. longirostris* and *Leydigia leydigi* are potentially indicative of a lake Depth of 10–15 m. *P. pigra* might be indicative of lakes with a Depth of > 15 m.

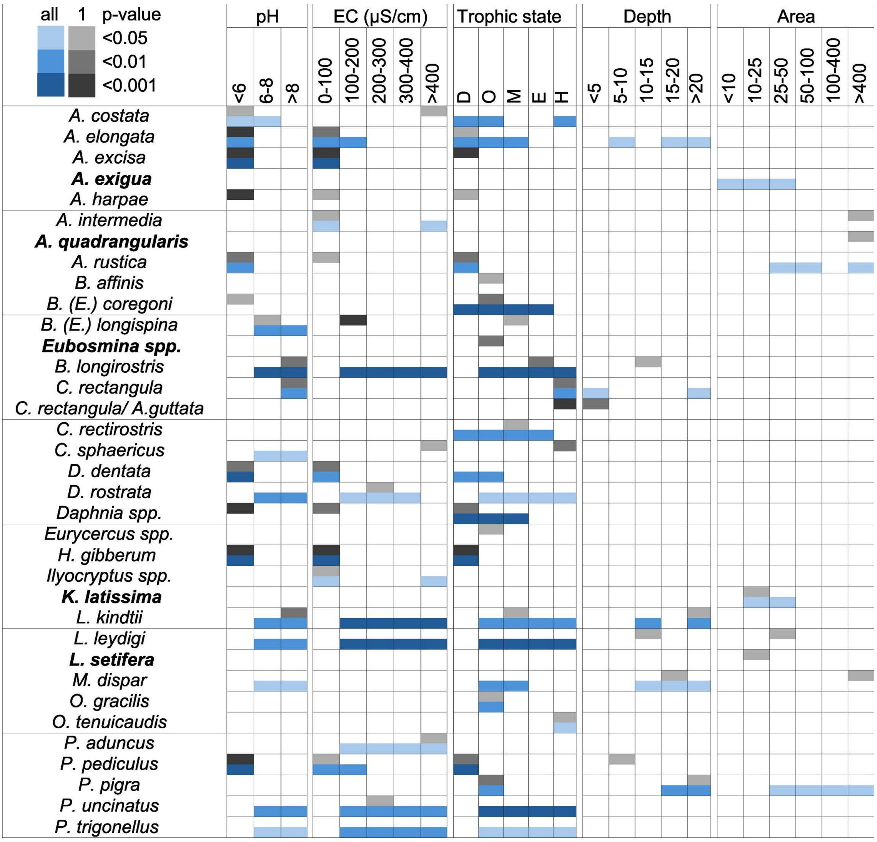


Figure 10 *Indicator species results based on 1 group limited and group combined IndVal.g analysis. Species that are shown to be indicators by IndVal.g analysis and were not part of the indicator species list in Article I are displayed in bold.*

Most of the species that were identified as new potential indicators can only be observed in small relative abundances (< 4%) (Figure 11). The exceptions are *A. quadrangularis* (maximum 15%), *C. rectangula/ A. guttata* (maximum > 40%), and *Eubosmina spp*. (maximum > 60%). *A. quadrangularis* has a larger relative abundance in lakes with a larger surface area (> 400 ha), but it can be found in lakes of all sizes. *Eubosmina spp*. relative abundance decreases with an increase in TSI and a decrease in Depth. However, this species was not identified as indicative of any particular Depths (Figure 10). *C. rectangula/ A. guttata* displays an opposite trend to *Eubosmina* spp. – it increases its relative abundance with an increase of TSI, and the highest relative abundance values for this species can be observed at lakes with Depth < 5m.

A. exigua can be observed in lakes of all sizes. However, this species is found in slightly higher relative abundances (> 2%) at lakes with Depths < 10 m. *K. latissima* observations are strictly limited to lakes with an Area < 50 ha. *L. setifera* was only observed in lakes with an Area between 10 and 400 ha. A similar result was found for *P. pediculus* (Figure 11), which was not identified as indicative of any particular Area size but instead is recognized as an indicator of depth between 5 and 10 m. In this Depth, *P. pediculus* reaches its highest relative abundance (3%). Results also show that *P. pediculus* was not found in any lakes that are deeper than 10 m.

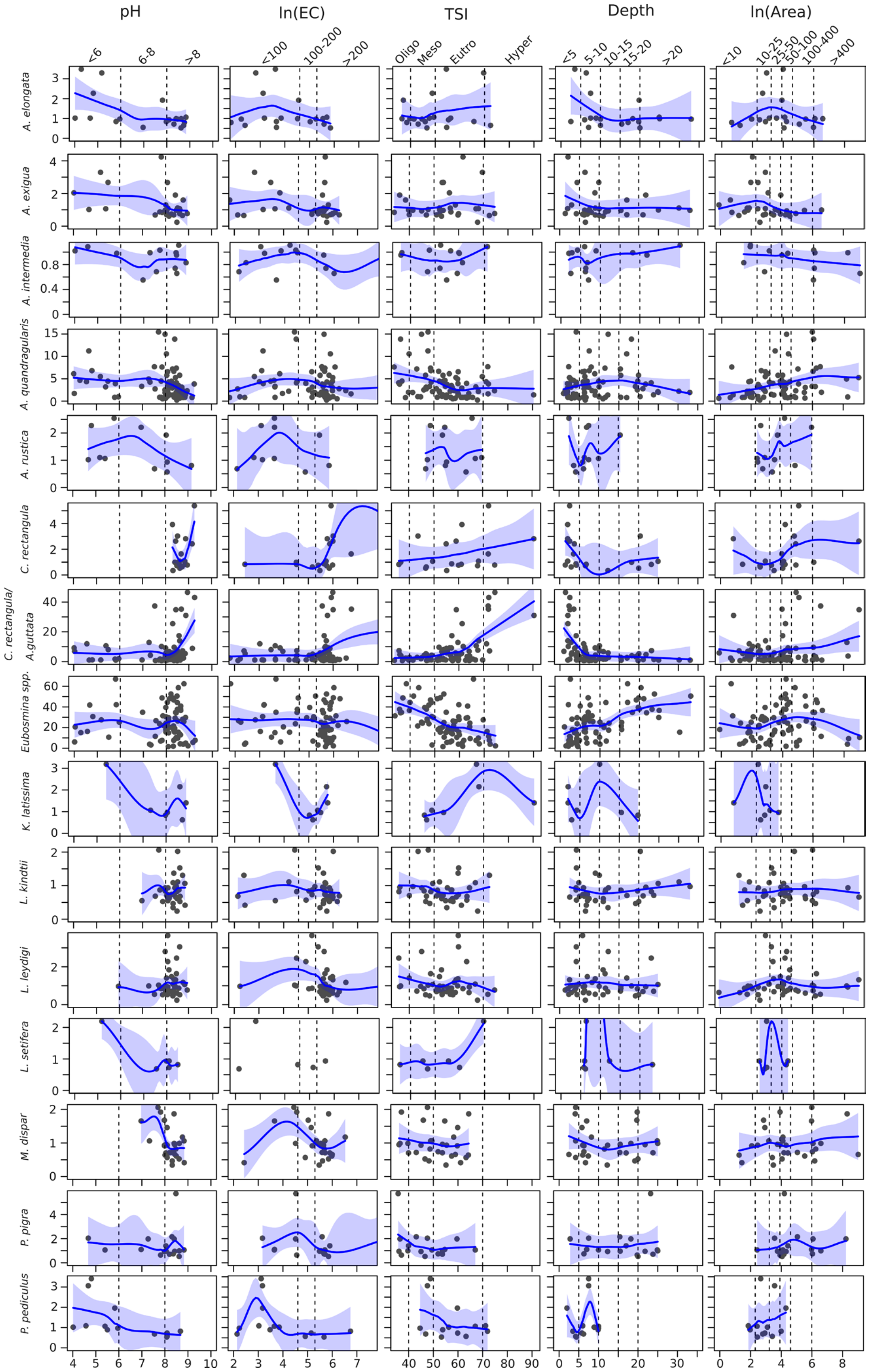


Figure 11 *Relative abundance of potential indicator species of Depth and Area in relation to pH, EC, TS, Depth, and Area. Additionally, Eubosmina spp. results are shown, as this species group was not analyzed before in Article I.*

3.2 Model development: WA-PLS and BRT cross-validation results

Model cross-validation (CV) results show that model performance descriptive parameters differ between the selected models (BRT vs. WA-PLS) and datasets (“all”, “Eubosmina”, “pH > 6”, “Eubosmina (pH > 6)”). Removing dystrophic lakes (datasets “pH > 6” and “Eubosmina (pH > 6)”) from the Depth, TSI, Chl-a, and TP models significantly improved the WA-PLS and BRT model performances (Figure 12). WA-PLS models’ performance results for datasets “all” and “Eubosmina” are, in general, more similar than the results for the same datasets using BRT models, and the same similarity can be noted between “pH > 6” and “Eubosmina (pH > 6)” results. When comparing the CV results for the same datasets between WA-PLS and BRT models, WA-PLS tends to have lower RMSEP values and higher R2 values. Exceptions to these results were found for the Depth model CV, where BRT had somewhat lower RMSEP values and higher R2 values, and for the TP model, where R2 values were similar between WA-PLS and BRT. Quartiles 1 and 4 tend to have higher RMSEP values than quartiles 2 and 3. No significant correlations were found between residuals vs. predicted values, and Breusch-Pagan did not indicate any anomalies within the distribution of the residuals.

Models with an R2 value below 0.5 will be excluded from further environmental reconstructions of Lake Velnezers, Lake Sekšu, and Lake Nakri. This criterion classifies only datasets “pH > 6” and “Eubosmina (pH > 6)” as suitable for reconstructions of Depth, TP, and Chl-a. While for EC, the BRT model based on the “Eubosmina” dataset does not fit into the R2 > 0.5 criteria. It can be seen that the excluded models also tend to have a higher correlation of residuals vs. observed values, despite the fact that none of these correlations were statistically significant (Figure 12).

WA-PLS overall showed lower RMSEP values for the pH model. The situation slightly changes when looking at the RMSEP values per quartiles, with WA-PLS performing better at quartiles 1 and 2, while BRT models performed better at quartiles 3 and 4. WA-PLS and BRT models based on datasets “pH > 6” and “Eubosmina (pH>6)” had little difference in RMSEP values between quartiles 1 and 2, had the smallest RMSEP values at quartile 3, and the highest RMSEP values in quartile 4.

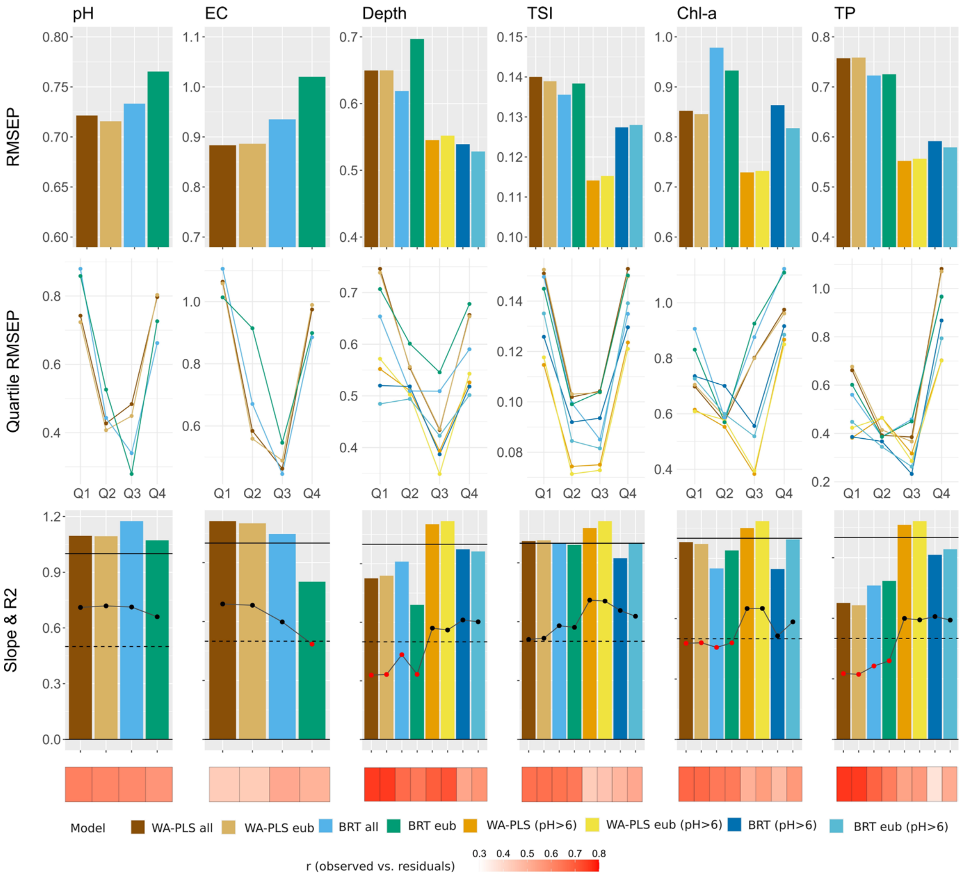


Figure 12 *Model cross-validation (CV) results. The performance of each metric of each model is portrayed in a unique color as per the color scheme. It must be noted that EC, TSI, Chl-a, and TP results were natural logarithm transformed before CV. Therefore, RMSEP values are also on a logarithmic scale. RMSEP (root mean square error of prediction) is portrayed first, and smaller RMSEP values are considered as desirable. However, they are dependent on the value range of the measured parameter, therefore, they can be compared between different models for the same parameter, but not between different parameters. In Slope & R2 plots, a horizontal line at 1 is drawn, as 1 is the ideal value for the slope. R2 values above 0.5 are portrayed with black dots, and the red dots represent R2 values below 0.5. Theoretical R2 values can range between 0 and 1, and the higher the R2 value, the higher the model's predictive power. Pearson's correlation of residuals vs. observed values is portrayed in the red color gradient under the Slope & R2 plots. A high correlation might indicate prediction bias at the ends of the environmental gradient.*

3.3 Environmental reconstructions

3.3.1 Lake Velnezers

Clustering results identified two major clusters for Lake Velnezers, with the lower part of the core being significantly different from the rest of it (Figure 13).

The first cluster spans 33 to 27 cm sediment depth (date unknown to the year 1920) (**Zone 1**). Other zones were selected based on historical environments and correspond to the same zoning used in Article II.

Zone 2 (sediment depth 27 to 20 cm, year 1920 to 1970). The period before the apartment complex construction around Lake Velnezers.

Zone 3 (sediment depth 20 to 14 cm, 1970 to 1990). The urbanized stage during the Soviet Union.

Zone 4 (sediment depth 14 to 0 cm, 1990 to 2018). Urbanized stage after the collapse of the Soviet Union. The selected borders of Zones 2–4 approximately correspond to clusters of lower significance.

The dominant species in Zone 1 are such lower TS indicators as *B.* (*E.*) *coregoni* and *B.* (*E.*) *longispina*, and an indicator of both low TS and low pH, *Daphnia* spp.. This is the only zone where the acidity indicator species *H. gibberum* is present. In Zones 2, 3, and 4, the eutrophy indicator *B. longirostris* becomes the dominant species. At the beginning of Zone 2, almost simultaneously appear such EC > 100 µS/cm indicative species as *Leptodora kindtii*, *Pleuroxus trigonellus*, *Disparalona rostrata, M. dispar*, and *L. leydigi*.

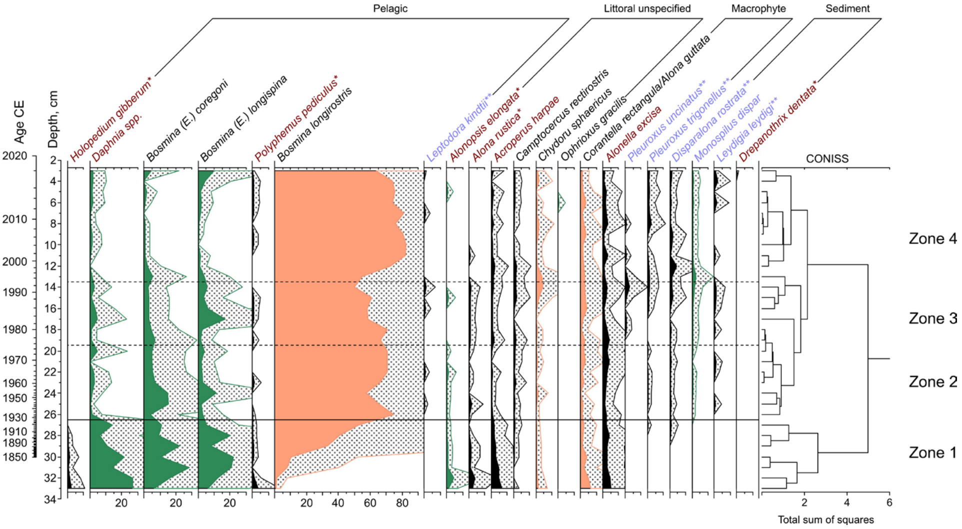


Figure 13 *Lake Velnezers stratigraphic diagram. Species are displayed based on their relative abundances. Only species identified as indicators in Article I (Figures 8, 9) are included. The names of species indicative of pH < 6 are colored brown, and the names of species indicative of EC > 100 µS/cm are colored purple. The relative abundance curves of species indicative of low TS (oligotrophic, mesotrophic) are displayed in green, while species curves or species indicative of higher TS (eutrophic, hypereutrophic) are shown in orange. Names of species not indicative of pH or EC are displayed in black, and curves of species not indicative of oligotrophic/mesotrophic/eutrophic/hypereutrophic conditions are also shown in black. The only exception is C. rectirostris, which is indicative of non-hypereutrophic conditions. Species are grouped according to their habitat preference.*

Functional groups and species diversity have similar patterns across the defined Zones. Zone 1 is characterized by a decrease in Littoral species, Large-sized and Medium-sized species proportion, and a small decrease in all species diversity descriptive parameters (richness, evenness, and Shannon's diversity index) (Figure 14). Zone 2 is relatively stable across all functional groups and species diversity descriptive parameters. In Zone 3, the proportion of Pelagic and Small-sized species gradually decreases in the sample, and an increase in all diversity descriptive parameters was observed. Zone 4 starts with a steep increase in Small-sized Cladocera and a sudden decrease in species richness, evenness, and diversity.

The dissimilarity analysis between Velnezers' samples and training set samples shows similar results across all of the tested datasets. The smallest dissimilarities were observed for the 4 topmost sediment layers, as the topmost sample was part of the surface sediment training set. Otherwise, the dissimilarity value between the closest training set sample and the sample of Lake Velnezers fluctuates between 0.2 and 0.3. In Zones 1 and 2, the lowest dissimilarity values are slightly lower between datasets "all" and "pH > 6" than those of datasets "Eubosmina" and "Eubosmina (pH > 6)" (Figure 14).

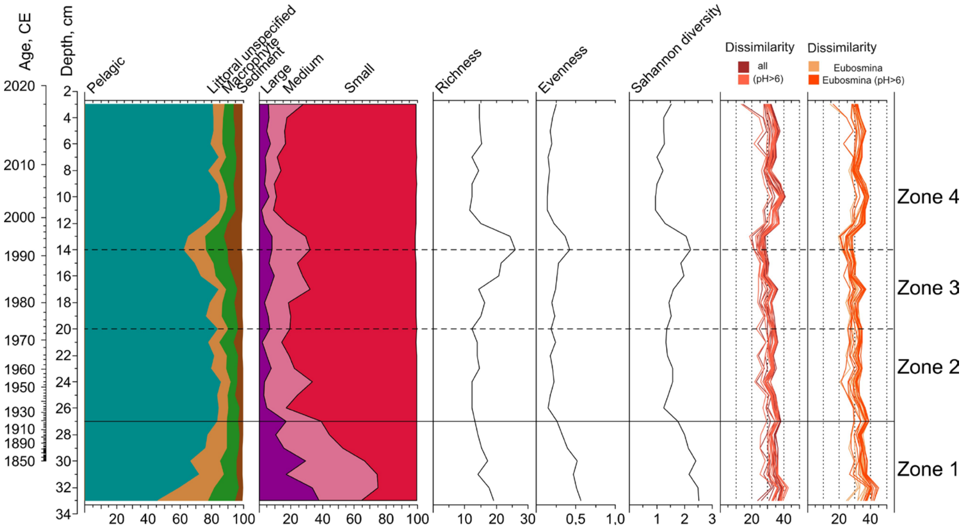


Figure 14 *Diagram of functional group relative abundances, diversity descriptive parameters, and 10 lowest Bray dissimilarity values between each sample of Lake Velnezers and datasets "all," "pH > 6", "Eubosmina", "Eubosmina (pH > 6)".*

All of the pH models agree that there has been an increase in the pH from pH < 6 to approximately pH = 8, but the rate of change differs between the models. BRT models predict a faster increase in pH, while WA-PLS models predict a gradual increase (Figure 15). In Zones 2–4, all of the models predict pH values in the range between 7 and 8.5. However, the predictions of BRT models seem to be closer to the Velnezers' pH values known from the literature. WA-PLS predicts EC from the bottom of the core to the top of the core, increasing from close to 0 µS/cm to 100 µS/cm, while BRT predicts similar values at the bottom of the core, and values as high as 200 µS/cm at the topmost samples. All of these EC model predictions are lower than values known from the literature. All of the developed models predict the lake Depth of Lake Velnezers to be higher than the present values during Zone 1. WA-PLS results show a gradual decrease from 13 to 7 m in Zones 2–4, with an increase of lake Depth to > 10 m from 2010 to 2018. The LOESS smoothing curve shows more stable results for lake Depth in Zones 2–4, which is also closely aligned with the known lake Depth values from the literature. However, when observing the individual points of BRT, it can be seen that they are dispersed more widely around the smoothing line than those of the WA-PLS models. Model reconstructions evaluate the TS of Lake Velnezers between mesotrophic and hypereutrophic (Figure 15). Almost all of the models identify a peak of TSI, Chl-a, and TP in Zone 4. The only models that do not register any significant changes in TSI are WA-PLS models based on “all” and “Eubosmina” datasets. WA-PLS consistently evaluates all of the TS-related parameters as lower than those evaluated by BRT models. BRT model values are closer to the values reported in the literature.

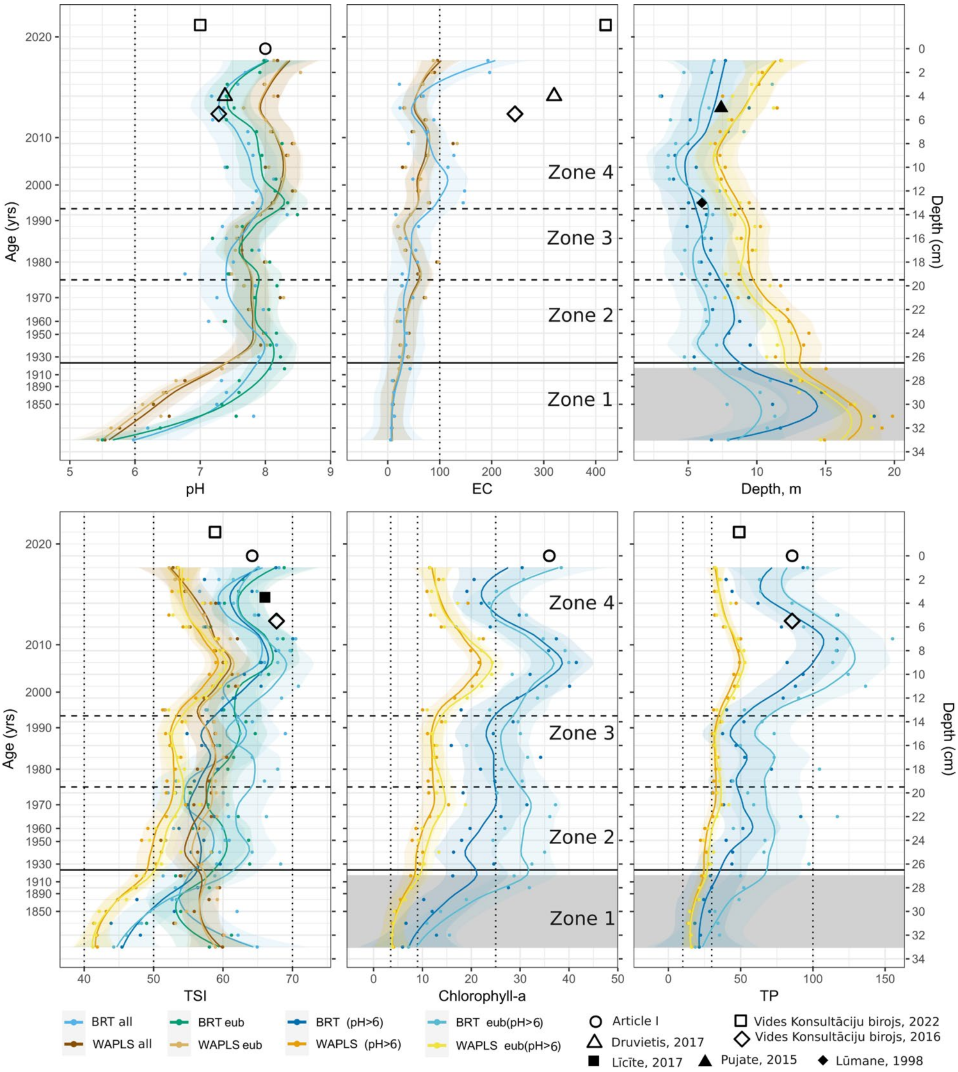


***Figure 15** Lake Velnezers pH, Electrical conductivity (EC), Depth, and trophic state descriptive parameters (Trophic State Index (TSI), Chlorophyll-a, Total Phosphorus (TP)) reconstructions. If parameter is reconstructions are only made with “pH > 6” and “Eubosmina(pH > 6)” datasets, then the Zone 1 area, which is suspected to have a pH < 6, is colored gray. Known values from literature are marked by differently shaped figures.*

3.3.2 Lake Sekšu

The results of the broken stick model based on subfossil Cladocera do not separate any of the clusters as significantly different from the others. For the purpose of result description, the zoning from Article III will be used, where different zones were distinguished based on Loss on Ignition (LOI) results.

Zone 1 describes the lower part of the core at the sediment depth 46 to 41 cm (year 1935–1947 CE).

In **Zone 2,** results from sediment depth 41 to 0 cm (year 1947–2018 CE) are described.

The most abundant species throughout the core are *B.* (*E.*) *coregoni*, *B.* (*E.*) *longispina*, *B. longirostris,* and *C. sphaericus* (Figure 16). There is a decrease in *B.* (*E.*) *coregoni* from the beginning of Zone 1 towards the end of Zone 2. Throughout the core *B.* (*E.*) *coregoni* varies between 6% and 22% relative abundance. The relative abundance of *C. sphaericus* varies between 6% and 26%. In Zone 1, *C. sphaericus* relative abundance values are consistently lower than in Zone 2 (Zone 1 max = 11.8%, min = 5.8%, median = 8.9%; Zone 2 max = 25.9%, min = 9.0%, median = 16.1%).

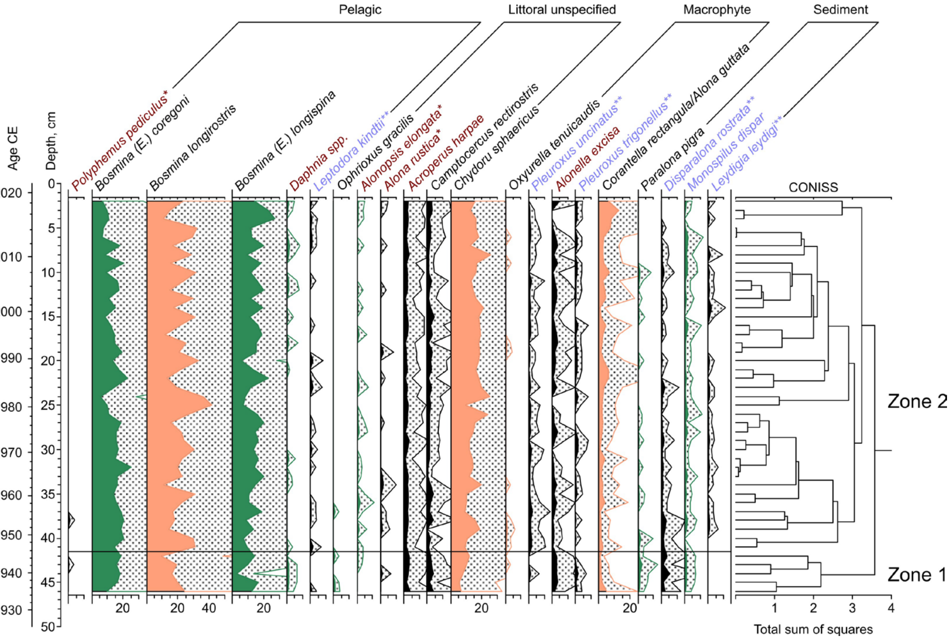


Figure 16 *Lake Sekšu stratigraphic diagram. Species are displayed based on their relative abundances. Only species identified as indicators in Article I (Figures 8, 9) are included. The names of species indicative of pH < 6 are colored brown, and the names of species indicative of EC > 100 µS/cm are colored purple. The relative abundance curves of species indicative of low TS (oligotrophic, mesotrophic) are displayed in green, while species curves or species indicative of higher TS (eutrophic, hypereutrophic) are shown in orange. Names of species not indicative of pH or EC are displayed in black, and curves of species not indicative of oligotrophic/mesotrophic/eutrophic/hypereutrophic conditions are also shown in black. The only exception is C. rectirostris, which is indicative of non-hypereutrophic conditions. Species are grouped according to their habitat preference.*

The species functional group composition for Lake Sekšu could be described as relatively stable. Sediment-associated species relative abundance is slightly higher in Zone 1 (Zone 1 max = 19.2%, median = 12.8%, Zone 2 max = 12.0%, median = 8.1%) (Figure 17). Small-sized species average relative abundance increases in the second half of Zone 2 (from 26th cm to 0 cm, year 1978–2018 CE), and can also be described as oscillating (before 26th cm max = 53.8%, min = 36.9%, median = 46.9%; after 26th cm max = 70.2%, min = 43%, median = 53%).

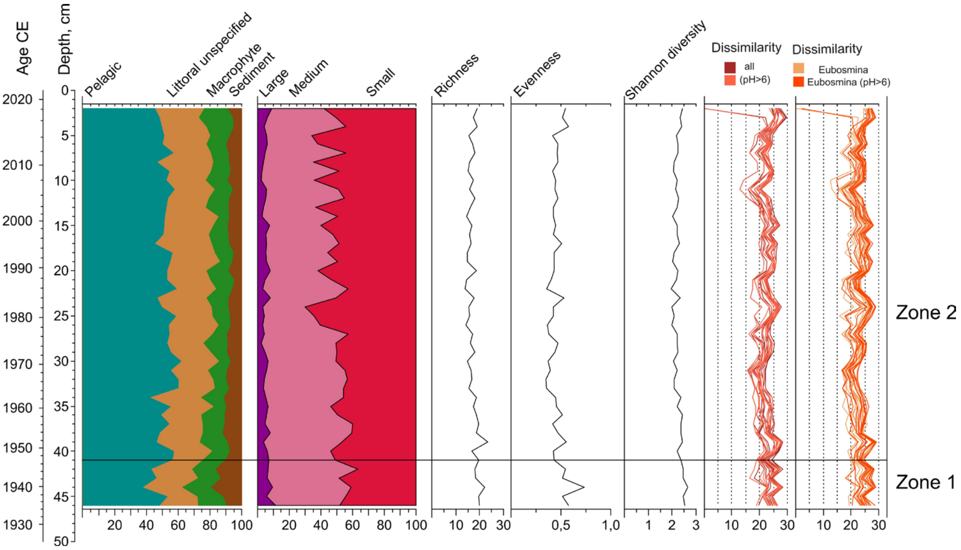


Figure 17 *Diagram of functional group relative abundances, diversity descriptive parameters, and 10 lowest Bray dissimilarity values between each sample of Lake Sekšu and datasets "all," "pH > 6", "Eubosmina", "Eubosmina (pH > 6)".*

All of the Lake Sekšu pH reconstructions evaluate the lake as neutral to slightly alkaline. WA-PLS models gave almost identical reconstruction results for models built based on datasets "all" and "Eubosmina" (Figure 18). WA-PLS evaluated the pH values to be slightly lower than those predicted by BRT. The closest pH values to those of the known literature are for the "Eubosmina" dataset based BRT model. Based on the model reconstruction, EC for Lake Sekšu varies between 25 and 350 µS/cm. WA-PLS again predicts almost identically based on both datasets, and its predictions are closer to the known EC value from the year 2013. The BRT model displays a large variation in the reconstructed values.

Lakes Sekšu Depth is evaluated to be between 2.5 and 24 m. All of the models show higher values in Zone 1. On average, BRT models produce lower values, which are closer to the Depth 7 m, as is known from the literature. However, the dispersal of the reconstructed values is also high. TS model reconstruction of Zone 1 returned values, which would classify Lake Sekšu as oligotrophic to eutrophic based on TSI, and as mesotrophic to eutrophic based on Chl-a and TP. The average values for all of the models in Zone 2 vary little.

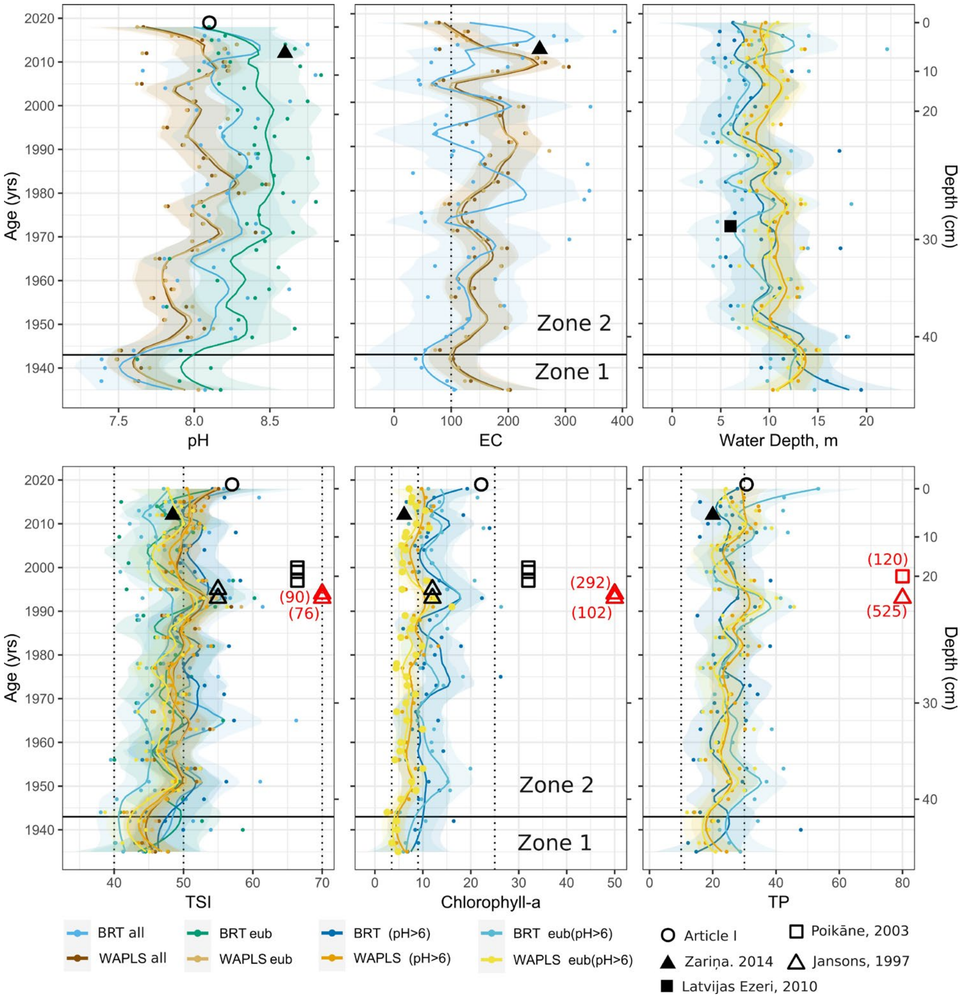


Figure 18 *Lake Sekšu pH, Electrical conductivity (EC), Depth, and trophic state descriptive parameters (Trophic State Index (TSI), Chlorophyll-a, Total Phosphorus (TP)) reconstructions. Known values from literature are marked by differently shaped figures. Outliers that fall beyond the displayed x-axis limits are shown in red, with their exact values given in brackets beside them.*

3.3.3 Lake Nakri

Four zones can be distinguished in the Lake Nakri sediment core, based on Subfossil Cladocera composition:

Zone 1 (sediment depth 1028–940 cm, calibrated year from 12,100 to 11,100 BP).

Zone 2 (940–620 cm, 11,100–7900 cal. years BP).

Zone 3 (620–349 cm, 7900–5330 cal. years BP).

Zone 4 (349–0 cm, from 5330 to –68 cal. years BP) (Figure 19).

For Lake Nakri, "BP" instead of the "BCE/CE" age scale is used. The record covers the whole Holocene and geological time periods, such as late glacial, Early Holocene, Middle Holocene, and Late Holocene, are usually described in BP time scale, thus simplifying the comparison with the literature.

The main dominant species throughout the core is *B.* (*E.) longispina.* In Zones 1 and 2, *B. longirostris* can be observed in relative abundances up to 20%, but becomes the dominant species in Zone 3 and onwards. In the period where Zone 1 transitions to Zone 2, *Daphnia* spp. and *B.* (*E.*) *coregoni* peaks occur. A similar peak of *Daphnia* spp. can be observed in the transition between Zones 3 and 4. Indicator species that appear in Zone 2 for the first time are *L. kindtii*, *O. gracilis*, *O. tenuicaudis*, *A. excisa*, *Pleuroxus uncinatus*, *P. aduncus*, *P. trigonellus,* and *P. pigra*. The appearance of *P. pigra* after the first observation could be described as sporadic. There were no indicator species that would be descriptive of Zones 1 and 2, but could not be found in Zones 3 and 4. On the other hand, such species as *D. rostrata* and *P. pediculus* are only found in Zones 3 and 4. Species that appear rarely in Zones 1 and 2, but appear regularly in Zones 3 and 4, are *L. kindtii*, *A. rustica*, *P. uncinatus*, *M. dispar*, and *P. aduncus*. *B.* (*E.*) *coregoni* and *L. leydigi* can be primarily found in Zones 1 and 4, while missing in the middle part. *A. elongata* is a species that can be observed in almost every sample during Zone 1, but afterwards appears rarely.

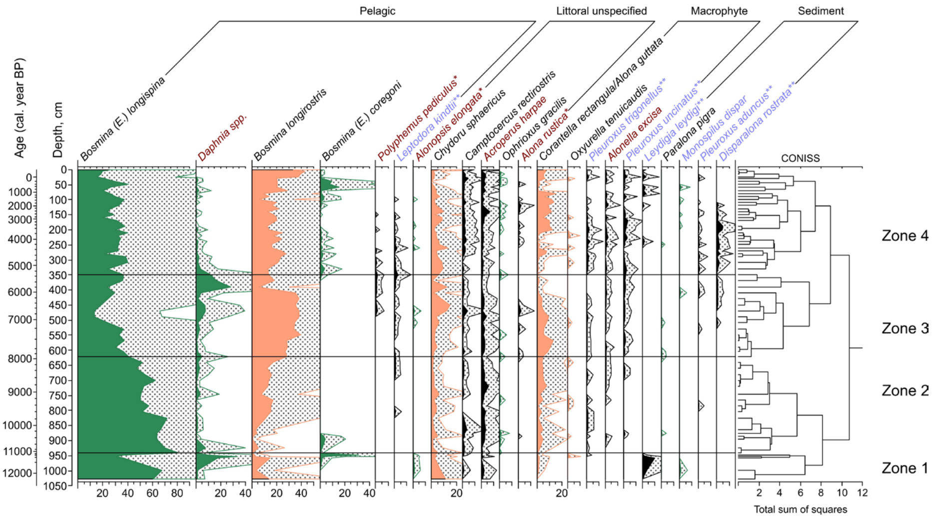


Figure 19 *Lake Nakri stratigraphic diagram. Species are displayed based on their relative abundances. Only species identified as indicators in Article I (Figures 8, 9) are included. The names of species indicative of pH < 6 are colored brown, and the names of species indicative of EC > 100 µS/cm are colored purple. The relative abundance curves of species indicative of low TS (oligotrophic, mesotrophic) are displayed in green, while species curves or species indicative of higher TS (eutrophic, hypereutrophic) are shown in orange. Names of species not indicative of pH or EC are displayed in black, and curves of species not indicative of oligotrophic/mesotrophic/eutrophic/ hypereutrophic conditions are also shown in black. The only exception is C. rectirostris, which is indicative of non-hypereutrophic conditions. Species are grouped according to their habitat preference.*

Pelagic species proportion reduces gradually throughout the sediment record of Lake Nakri (Figure 20), while species diversity increases. In Zone 1, there are almost no macrophyte-associated species, and the species richness is low. Macrophyte-associated species relative abundance remains rather constant throughout Zones 2 and 3 and increases in Zone 4. Sediment-associated species relative abundance is low in Zones 2 and 3. Samples' dissimilarity values reduce from the beginning of Zone 1 towards the end of Zone 2. In Zones 3 and 4, dissimilarity values are rather constant.

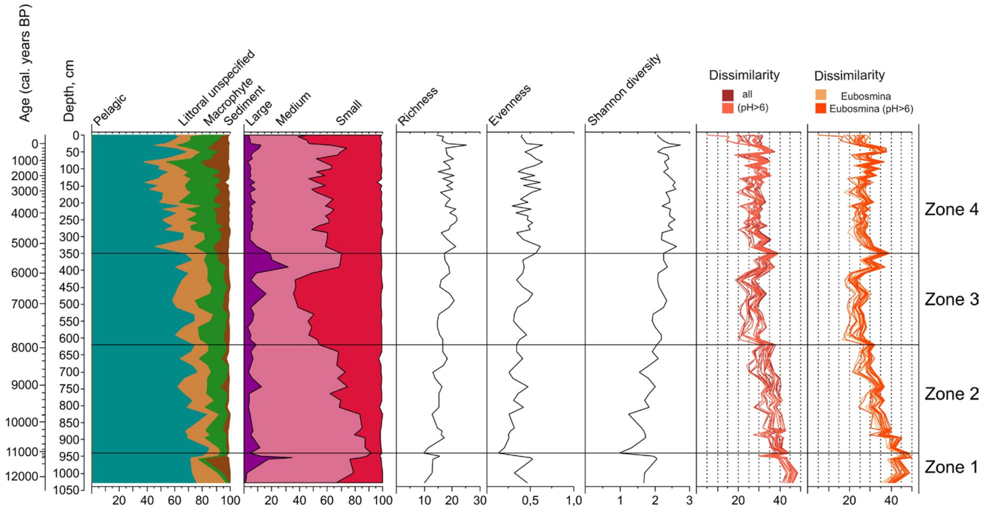


Figure 20 *Diagram of Functional group relative abundances, diversity descriptive parameters, and 10 lowest Bray dissimilarity values between each sample of Lake Nakri and datasets "all," "pH > 6", "Eubosmina", "Eubosmina (pH > 6)".*

Lake Nakri pH is predicted to be between 7 and 9 pH units (Figure 21). WA-PLS models on average predict that pH has not changed much throughout the Holocene. In comparison, BRT models evaluate that there has been a decrease in pH values by approximately 1 point between the beginning of Zone 1 and the beginning of Zone 2. During Zone 2, BRT predicted pH values stabilize between 8 and 8.5 units. Predicted pH values at the topmost sediment sample are close to the measured pH value for all tested models. On average, both WA-PLS and BRT models evaluated EC values between 100 and 400 µS/cm, occasionally decreasing below the 100 µS/cm threshold. BRT model predictions for the topmost sediment sample are the closest to the measured EC value. However, the BRT model also displays a considerable variation in the EC values, sometimes predicting Lake Nakri EC as high as 1200 µS/cm.

Lake Depth reconstructions predict values between 2.5 and 20 m. WA-PLS models evaluated Lake Depth as more or less constant in Zones 2–4. Based on the BRT model reconstructions, there was a noticeable increase in water Depth during the transition between Zones 3 and 4, with an average lake depth of 13 m. Nowadays, the approximate lake Depth is three meters. BRT model estimates are slightly closer to this value; however, on average, all the models seem to overestimate the water depth. The estimated values of TSI, Chl-a, and TP would correspond to those of a mesotrophic to hypereutrophic lake (Figure 21). In Zone 1, WA-PLS models evaluated TSI, Chl-a, and TP values as lower than those of the present day, while BRT model predictions would estimate these values to be higher than the contemporary ones. BRT "pH > 6" model consistently presents higher Chl-a values in comparison to other models.

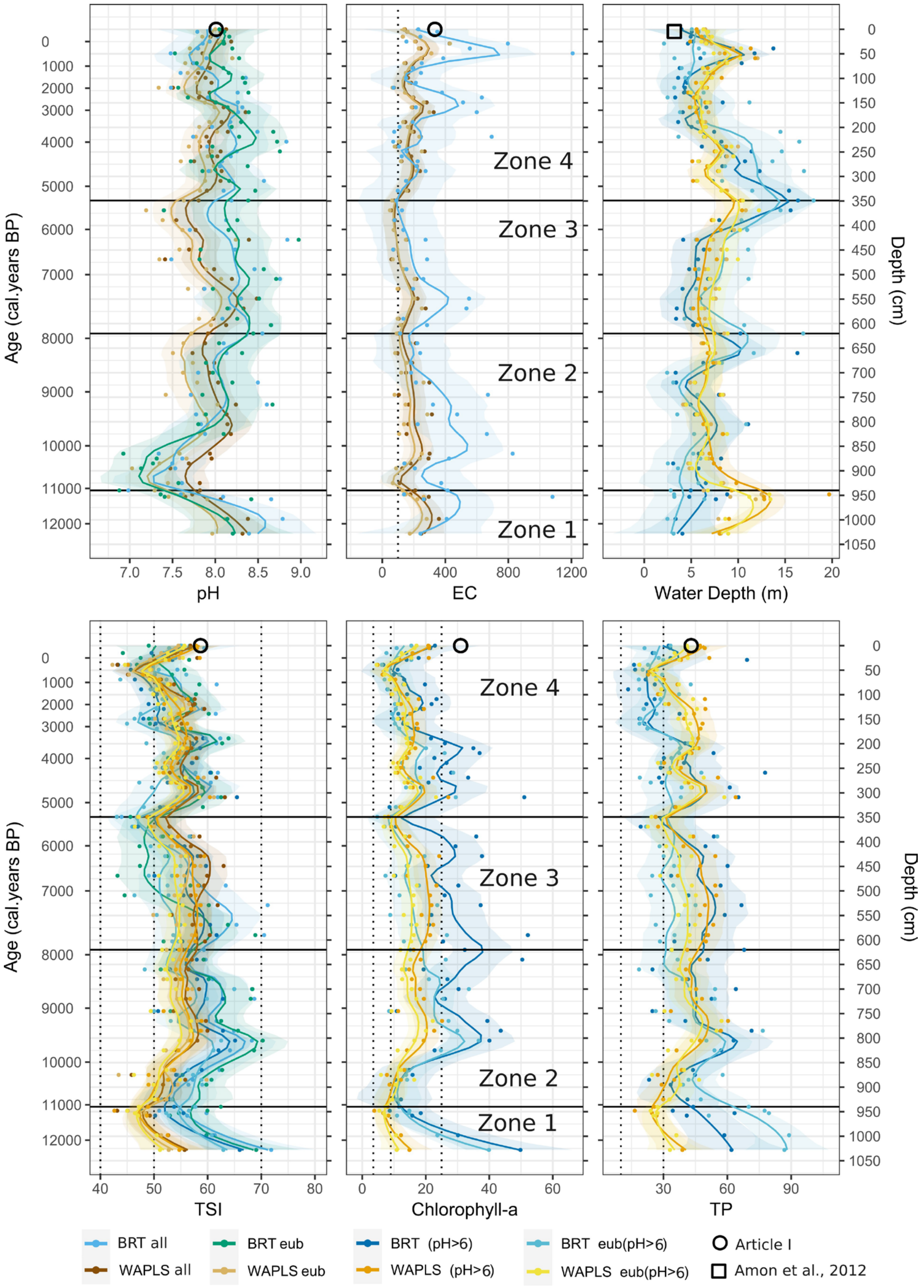


Figure 21 *Lake Nakri pH, Electrical conductivity (EC), Depth, and trophic state descriptive parameters (Trophic State Index (TSI), Chlorophyll-a, Total Phosphorus (TP)) reconstructions. Known values from literature are marked by differently shaped figures.*

4 Discussion

This study aimed to identify the main drivers of subfossil Cladocera species assemblages in lakes of the Baltic States, develop and apply various methods for reconstructing past lake environments, and assess each method's suitability for environmental reconstruction of each studied parameter. Based on the developed training set, several abiotic factors influence subfossil Cladocera assemblages, such as water pH, electrical conductivity (EC), trophic state (TS), maximum lake depth (Depth), and lake surface area (Area). However, it must be noted that other factors might have influenced cladocerans but were either not analysed due to incomplete observations and insufficient gradient (Article I), or were not assessed at all. Among such unexplored factors are some that have been reported to have a significant influence on subfossil Cladocera assemblages, such as planktivorous fish and macrophyte abundance (Davidson et al., 2010; Jeppesen et al., 2001). Assessing such parameters would have required labor-intensive extensive fieldwork and expertise beyond the scope and capacity of this thesis, as existing observations on fish and macrophytes for most of the studied lakes were not available.

The surface sediment training set methodology involves collecting surface sediment samples (typically the uppermost 1–2 cm), obtaining relevant environmental measurements, and analyzing the species assemblages preserved in the sediments. It is generally assumed that surface sediment samples represent environmental conditions over the past 1 to 20 years (Birks et al., 2012). In this study, the decision was made to collect the top 2 cm of sediments, as this amount should be representative of the current day situation (Article III; Heinsalu & Alliksaar, 2009; Liiv et al., 2018; Mikalauskienė et al., 2015; Punning et al., 2007; Stivrins et al., 2018; Stivrins, 2023; Veski et al., 2005). The choice to sample 2 cm, rather than just 1 cm, was intended to reduce the influence of seasonal variability and single-year extreme events, which might not have been fully captured by the environmental parameter measurements (Köster & Pienitz, 2006; Table 2). Environmental measurements used in the training set were selected from a time frame of up to five years before sediment sampling, assuming that these conditions reflect the period during which the Cladocera assemblages were deposited and preserved. Nonetheless, since the surface sediments in this study were not dated, it is possible that in lakes with higher or lower sedimentation rates than anticipated, the sedimentary Cladocera assemblages may not correspond well with the time period of the available environmental data, potentially creating a temporal mismatch between the environmental and subfossil Cladocera data.

Additional uncertainties regarding the alignment between environmental parameters and subfossil Cladocera assemblages in surface sediments arise due to variations in the sampling intensity of the environmental data. Some lakes in the dataset had up to 30 environmental measurements within the selected five-year period, while others were represented by only a single measurement (Table 2). Although it is not uncommon in surface sediment training sets to rely on a single environmental observation (Amsinck et al., 2005; Stivrins et al., 2022), such variability in sampling effort introduces the potential for mismatches between the recorded environmental conditions and the biological assemblages preserved in sediments.

4.1 Environmental factors and their interactions

Researchers have repeatedly reported a relation between subfossil Cladocera assemblages and pH, EC, Depth, TS, temperature, as well as fish and macrophyte abundance (Amsinck et al., 2005; Bjerring et al., 2009; Dong et al., 2020; Krause-Dellin & Steinberg, 1986; Lotter et al., 1997; Nevalainen et al., 2011). Our results align well with several of these findings, as it was found that pH, EC, TS descriptive parameters (TSI, Chl-a, TP), lake Depth, and Area had the highest explanatory power on subfossil Cladocera species assemblages. (Figure 3). Lake Area is not usually reconstructed using subfossil Cladocera; however, some researchers have found that this variable has some explanatory power (Pawlikiewicz & Jurasz, 2017). Although it is known that macrophyte and fish abundance can have significant explanatory power on zooplankton communities (Davidson et al., 2010), it was not studied within the scope of this work due to a lack of available data. This could contribute to the unexplained variability of lakes in this dataset and should be addressed in further research. We did not find a significant relationship between subfossil Cladocera and climate (regarding T_{ann}). This result is likely caused by the insufficient climatic gradient, as the T_{ann} difference between the warmest and coldest site was only 2.5 °C. Therefore, an extension of the gradient would be necessary to properly evaluate the influence of temperature on subfossil Cladocera.

Most authors who have attempted to reconstruct TS through transfer function have focused on TP as the main parameter (Amsinick et al., 2005; Brodersen et al., 1998; Chen et al., 2010). It is considered that more successful environmental reconstructions can be accomplished if the studied parameter is directly ecologically limiting to the study organism (Juggins, 2013). Because Cladocera are zooplankton that do not utilize phosphorus as a direct food source, there is no physiological basis for them to respond directly to TP. Nevertheless the TP can have a strong indirect effect on the Cladocerans, as TP concentrations influence algal and macrophyte growth and composition (Naderian et al., 2025; Nürnberg & Shaw, 1998; Rattray et al., 1991) and many Cladocera species feed on algae or prefer macrophyte habitats (Błędzki & Rybak, 2016; Smirnov, 2017) However, above mentioned lake's primary producers can be influenced by other factors as well, such as alkalintiy and ion content (Lewis et al., 2025; Šolcová et al., 2024), N concentration (Naderian et al., 2025), light limitation and temperature (Jeppesen et al., 2010; Rose, 2024). Our results showed that TSI had higher explanatory power than TP. As TSI includes several parameters (Carlson, 2007), it may be better at capturing the complex lake TS-related conditions necessary for Cladocera than TP.

Secondary gradients can affect the reliability of environmental reconstructions, and in an ideal scenario, all environmental variables should be independent from one another (Juggins, 2013). Data analysis revealed a strong relation between TS and Depth (Figure 4). Such a result has been reported by other authors as well (Zhou et al., 2022). While it has been argued that this effect is due to the geographical distribution of deep and shallow lakes, with deep oligotrophic lakes mostly being located in mountains, and shallow eutrophic lakes in lowlands (Zhou et al., 2022), this is not necessarily the case for the relatively flat Baltic states. It could be argued that many of the deeper oligotrophic lakes are located in forested areas and therefore have a lower human impact, but this argument would require a more thorough landscape analysis. Holocene sediment cores from some Baltic lakes can be up to 20 m thick (Rõuk, 1992). Accumulating that much sediment would lower the water column by about 20 m, turning a once-deep lake into a shallow one. Therefore, the inverse argument can also be made – some shallow lakes may be shallow due to human-induced eutrophication, which accelerates sediment accumulation and reduces water depth (Kornijów, 2023; Tammeorg et al., 2018).

Lake Depth is not only correlated with TS, but can also directly shape nutrient cycling processes and nutrient limitation regimes, thus playing a role in determining lake productivity. Nutrient limitation dynamics – specifically the relative availability of N and P – can influence both lake productivity and the ecological response of organisms such as Cladocera. Studies have shown that shallow, hypereutrophic lakes tend to be N-limited, eutrophic lakes are often co-limited, and deep oligotrophic systems remain primarily P-limited (Naderian et al., 2025). These dynamics may influence not only productivity metrics like the TSI but also the C:N:P stoichiometry of phytoplankton, which affects Cladocera food quality and growth rates (Sterner et al., 1992).

In both shallow and deep lakes, anoxia can alter nutrient availability through internal P loading from sediments and denitrification. Under anoxic conditions, P becomes more bioavailable, while denitrification converts nitrate and nitrite into nitrogen gases, effectively removing biologically available N from the system (Hakanson & Jansson, 1983; Qin et al., 2020). In deep lakes, stratification often restricts P availability to surface waters except during seasonal mixing events. In contrast, shallow lakes, which mix more frequently, may have continuous access to sediment-released P, leading to higher productivity. As a result, P availability is less likely to be a limiting factor in shallow lakes, and primary production can continue to increase until N, driven by a combination of denitrification and nutrient uptake by primary producers, becomes the limiting nutrient (Kornijów, 2023; Qin et al., 2020). The relationship between TS and Depth weakens in lakes deeper than ~15 m, because wind-driven mixing rarely extends deeper than this in most lakes (Qin et al., 2020). Similar results can be found in this work, as lakes in groups Depth 15–20 m and > 20 m did not differ in their TSI values (Figure 4). These considerations highlight the complexity of interpreting TS and Depth reconstructions, particularly since N data in this study are lacking (Table 2). Regardless of whether the relationship between TS and Depth is correlative or causal, the reconstructions of these parameters are likely to be influenced by one another.

Some relationship was found between pH and EC, as all of the acidic lakes (pH < 6) had EC < 100 µS/cm. This finding arises from the natural variability of acidic lakes in the Baltic States, as highly conductive acidic lakes do not occur in this region. A more thorough discussion on the relationships between pH, EC, and TSI can be found in Article I. Lake Area distribution seems to be independent of other parameters when looking at the group distribution along the environmental gradients (Figure 4). However, lake Area was not recognised as statistically significant for datasets “pH > 6” and “Eubosmina (pH > 6)”. Acidic lakes were on average smaller than lakes with pH > 6, which might have influenced this result.

4.2 Patterns of subfossil Cladocera assemblages

4.2.1 Relationship between environment and Cladocera species diversity

Species diversity is a community descriptive parameter that has interested ecologists for more than a hundred years (Gleason, 1922). It is suggested that information on species diversity can provide insights into ecosystem complexity and stability (Loreau & De Mazancourt, 2013; St. Pierre & Kovalenko, 2014). In this work, species diversity was assessed using Shannon’s diversity index. This index is one of the most commonly used and contains information on two key diversity components – species evenness (the distribution of individuals among the species) and species richness (Birks et al., 2012). Shannon's index and its two components were evaluated in relation to pH, EC, TSI, Depth, and Area.

One of the most commonly reported results is a decrease in species diversity with the increase of TS (Jeppesen et al., 2000; Whiteside & Hamsworth, 1967). This effect is attributed to (1) a decrease in species richness due to reduction of available niches, and (2) a decline in evenness caused by fewer species being able to use the abundant food resources effectively, and adverse effects of such stressors as oxygen depletion (Alexander et al., 2017; Barnett & Beisner, 2007). The decrease of species richness, evenness, and diversity with an increase of TSI was also found in this study (Figure 5). It must be noted that some authors have reported an increase in diversity and species richness with an increase in TS (Hessen et al., 2006). This difference is most likely caused by differences in regionally available environmental gradients. In this work, oligotrophic lakes exhibited higher species richness compared to all other lake types. However, the lowest TSI value of this training set was 34, whereas the minimum possible TSI value for oligotrophic lakes is one (Carlson, 2007), meaning that this study covered only a fraction of all the globally possible conditions for oligotrophic lakes.

In contemporary limnology, it is sometimes suggested that dystrophic lakes have lower species diversity and richness due to lower lake productivity, Ca deficiency, and acidity stress (Karpowicz & Ejsmont-Karabin, 2021; Smirnov, 2017). However, the results of this and other paleolimnological studies of dystrophic lakes (Zawisza et al., 2016) somewhat contradict these findings, as on average, the species diversity was higher in acidic (pH < 6) sites (Figure 5). The species richness in acidic (pH < 6) lakes was similar to that of non-acidic (pH > 6) lakes, and evenness was generally higher than that of non-acidic lakes. Contemporary zooplankton research tends to be biased towards pelagic species, and sweep net samples typically report lower species richness estimates when compared to surface sediment samples (Çakıroğlu et al, 2014; García-Gíron et al., 2018; Nevalainen, 2010). On the other hand, the dominant pelagic species in acidic/dystrophic lakes were *Daphnia* spp., *Holopedium gibberum*, and *Bosmina (Eubosmina) coregoni* (Article I). As *Daphnia* spp. and *H. gibberum* remains tend to preserve poorly (Szeroczyńska & Sarmaja-Korjonen, 2007), it is also possible that this has led to higher evenness estimates in this work due to pelagic dominant species comprising a smaller portion in the surface sediment samples than in the actual species community.

4.2.2 Relationship between environment and subfossil Cladocera functional groups

Sometimes, environmental studies prefer to analyse ecosystem changes in terms of functional groups/traits instead of species assemblages. Functional traits can be defined as morphological, biochemical, structural, behavioral, etc., characteristics of organisms that influence their fitness and performance in certain conditions (Nock et al., 2016). The functional traits approach makes datasets easier to compare and analyse due to the reduction of functional redundancies, and it is thought to provide a better insight into the mechanisms of ecosystem functioning (Laureto et al., 2015). This work tested the relationship between species-specific size and habitat preference against pH, EC, TSI, Depth, and Area. These functional traits (size and habitat preference) have relatively good literature coverage and are commonly used by other authors (Branco et al., 2023; Gomes et al., 2019). However, some uncertainties regarding the functional group approach of this work must be noted. Large-sized cladocera proportion might be overestimated, as *Daphnia* spp. in this work is in fact a combination of two groups – *Ceriodaphnia* spp. and *Daphnia* spp. While *Daphnia* spp. are usually large-sized, *Ceriodaphnia* spp. vary in their average size group from species to species (Błędzki & Rybak, 2016). Regarding the habitat preference, literature sources sometimes contradict each other (Błędzki & Rybak, 2016; Flössner, 2000). Depending on the tolerance, species can be driven into suboptimal niches (McGill et al., 2006). Therefore, given the differences in knowledge regarding optimal, realised, and fundamental niches of various species, it is likely that some of the species are misclassified.

Size is one of the most commonly used functional traits in zooplankton research, which is linked to such functions as growth, reproduction, survival, and feeding (Gomes et al., 2019; Nock et al., 2016; Sysoev et al., 2025). There are different proposed mechanisms for the change of the community size structure, such as the shift of species hypothesis, the population body size shift hypothesis, the population age-structure shift hypothesis, etc. (Daufresne et al., 2009). In contemporary zooplankton research, individual size can be measured with relative ease (Gomes et al., 2019), enabling the testing of various theories about the drivers behind changes in community size structure. However, this is not always the case for subfossil Cladocera. As full individuals are rarely found, some researchers have used the species-specific size from literature (Nevalainen & Luoto, 2017), while others have been measuring the remaining sizes of the dominant species (Korosi et al., 2013; Korponai et al., 2020). The direct measuring approach gives more precise information on the selected species than the size grouping based on the literature. However, there are several issues in the application of these results. The statistical analysis requires a certain amount of measured remains, and the decision to measure or not measure a remain could depend on taxonomical determination (Korponai et al., 2020). This means that a species would only be measured if the conditions are suitable enough to establish a sufficiently large population. The survival and reproduction of individuals belonging to particular species and their physical development can be influenced by unfavourable conditions (Gomes et al., 2019). However, if the number of remains is below the required minimum, the species' response to unfavourable conditions would not be recorded. In paleolimnological research, this could have the highest influence in core segments where species composition changes occur. A possible solution would be to measure all the remains of the sample. However, taking into consideration the issues with remains preservation and the differences in which skeletal elements are preserved for each species (Szeroczyńska & Sarmaja-Korjonen, 2007), this might be a very labor-intensive process that may still fail to provide the desired information about the actual community size structure. Therefore, for paleolimnological research, using literature-based information on the average size of a taxon might be considered an appropriate approach, despite the preference for direct size measurements in contemporary ecology literature (Brown et al., 2023). Nevertheless, it must be noted that this approach only accounts for the shift-of-species hypothesis and will not capture the whole complexity of the possible changes in Cladocera community size structure.

Subfossil Cladocera size groups had the strongest correlation to TSI (Medium $r = -0.63$, Small $r = 0.62$), with the exception of large-sized Cladocera, which had the strongest correlation to pH ($r = -0.65$) (Figure 6). Other researchers have found similar results regarding Cladocera size structure and lake TS (Beaver et al., 2020; Nevalainen & Luoto, 2017). Size limitation in nutrient-enriched (eutrophic and hypereutrophic) conditions can be influenced by multiple factors, such as oxygen and food availability, or fish predation pressure. Oxygen stress impacts negatively large-bodied zooplankton species due to their higher oxygen demand and reduced feeding efficiency under hypoxic conditions (Karpowicz et al., 2020; Sysoev et al., 2025). In contrast, small-sized Cladocerans have a competitive advantage under low oxygen conditions due to higher oxygen uptake efficiency (Seidl et al., 2005). In highly eutrophic and hypereutrophic conditions, an increase in bacteria and cyanobacteria biomass can be observed, which may benefit small-bodied Cladocerans that can utilize these particles as a food source (Geller & Müller, 1981; Gliwicz, 1990; Krztoń & Kosiba, 2020; Tõnno et al., 2016).

Fish predation pressure and warming can also result in changes of cladocera community size structure (Agasild et al., 2025; Albini et al., 2025; Beaver et al., 2020; Jeppesen et al., 1998). Due to a lack of data and an insufficient T_{ann} gradient, the effects of fish predation and temperature are not addressed in this study. However, they could potentially influence the results as confounding variables. The diminished fish pressure could explain the increase of large-sized species in dystrophic lakes (Figure 6). Fish in bog pools have been shown to feed primarily on benthic animals instead of zooplankton (Zagars et al., 2025), and large-sized Cladocera are usually impacted by predation more severely (Jeppesen et al., 2001). Even so, this increase in the large-sized cladocera in dystrophic lakes is not universal, as some other authors have observed a rise of small-sized Cladocera species in dystrophic conditions instead (Karpowicz et al., 2023; Locke & Sprules, 2000).

The functional groupings using habitat preferences are often used to assess changes in different environmental parameters. The Pelagic to littoral (Macrophyte-associated, Sediment-associated, and Littoral generalist species) ratio is commonly used to evaluate changes in water level (Nevalainen et al., 2011; Sarmaja-Korjonen, 2001). This work also shows that water Depth has the strongest correlation with Macrophyte-associated species ($r = -0.55$) and Pelagic species ($r = 0.45$) groups (Figure 6). However, no relationship was found between water Depth and Sediment-associated species or Littoral generalists. The main reasoning behind the Pelagic/Littoral species relation theory is the reduction of macrophyte-covered area due to light limitation with an increase in water depth (Hofmann, 1998). Therefore, the observed relationship between the Pelagic, Macrophyte-associated species and Depth aligns with the theory, even if the available data does not allow for further testing of the causes of this relation.

The Macrophyte-associated species were also correlated to TSI ($r = 0.41$), again highlighting the possible interaction between TS and Depth in lake ecosystems. The PCA analysis related the increase of Macrophyte-associated species to hypereutrophic and dystrophic lakes (Figure 7). While these two lake types are considered to be rather different, there are some similarities they share. Both of these lake types were relatively shallow (Figure 4). Other known similarities include light-limited conditions caused by brown-coloured humic substances in dystrophic lakes and light limitation due to algal blooms in hypereutrophic lakes (Nürnberg, 1996; Nürnberg & Shaw, 1999). Furthermore, bacteria tend to have a more significant influence on the food webs of dystrophic and hypereutrophic lakes (Jones, 1992; Karpowicz et al., 2023; Xu et al., 2015), and neither are considered to be macrophyte-rich (Gray et al., 2022; Szpakowska et al., 2021). Considering this, the connection between dystrophic and hypereutrophic lakes and Macrophyte-associated species seems counterintuitive. For the hypereutrophic lakes, the explanation might lie in the specific species composition. Macrophyte-associated *Coronatella rectangula*/ *Alona guttata* was identified as one of the dominant species in hypereutrophic lakes (Figure 11). However, it is more likely that these particular taxa are indicative of hypereutrophic conditions, not the macrophyte abundance. Even though dystrophic lakes are not considered rich in submerged macrophytes (Gray et al., 2022), the sphagnum mosses present in this habitat might be a sufficient replacement for some of the Macrophyte-associated species (Henrikson, 1993; Kuczyńska-Kippen, 2008). Another possible explanation could be the physical barrier that large-sized macrophytes create, hindering the in-lake transportation of subfossil cladocera remains. For other paleolimnological proxies, such as pollen, the assumption is that during the bi-annual water mixing event of stratified hemiboreal lakes, material that is in the water column will be sedimented in the deepest part of the lake (Elias, 2025). This might be true for the pelagic Cladocera, but research has shown that the distance of the sampling site to the macrophyte zone might bias the results of some littoral Cladocera (Nevalainen, 2011). In dystrophic lakes, large submerged macrophytes are typically underdeveloped, potentially reducing their physical barrier effect (Gray et al., 2022; Różańska-Boczula & Sender, 2025). The observed increase in Macrophyte-associated species may instead reflect two factors: (1) the presence of smaller suitable vegetation (e.g., sphagnum mosses), and (2) improved conditions for remnant transportation. However, validating this hypothesis requires macrophyte survey data.

The relative abundance of the Littoral generalist species group seems indifferent to any of the studied environmental parameters. On the other hand, the Sediment-associated species have a strong relationship to TSI (r = –0.43). The larger proportion of sediment-associated species in nutrient-poor (oligotrophic-mesotrophic) lakes could be due to several reasons, such as oxygen levels, food sources, and suitable habitat availability. The oligotrophic lakes are characterised by better hypolimnion oxygen conditions (Nürnberg, 1996). While it has been found that some sediment-associated species can survive under hypoxic and anoxic conditions, other individuals' fitness-related parameters, such as breeding and growth rates, might still be affected. However, the research on this topic is limited (Smirnov, 2017). Furthermore, some sediment-associated species prefer sand and rock substrate (Błędzki & Rybak, 2016), which might not be available in highly eutrophic lakes with high organic matter sedimentation rates. Consequently, with an increase in TS, the conditions necessary for Sediment-associated species might become unfavourable, as the diverse niches they inhabit disappear. The highest relative abundance of the Sediment-associated species functional group does not exceed 25% (Figure 6); therefore, it is unlikely that any individual species of this group significantly contributes to the zooplankton biomass. This could explain the gaps in the literature on the biology of the Sediment-associated species. Even though in hypereutrophic lakes most energy is accumulated in pelagial, these lakes are capable of sustaining complex benthic communities (Wang et al., 2020). Therefore, one possible explanation for a negative correlation between Sediment-associated species and TS involves the data presentation methodology: since species data is presented in relative abundances, the taxon's relative share could decrease solely due to an increase in pelagic species abundance under hypereutrophic conditions, while the actual abundance of Sediment-associated species might remains unchanged.

4.3 Indicator species analysis

An effective indicator species should be easy to find and identify, and its response to environmental parameters should be adequately predictable (Butler et al., 2012; Dufrêne & Legendre, 1997). As discussed in Article I and summarised in Figures 8 and 9, several Cladocera species fit this criterion when analysing species response to pH, EC, and TS.

In the text below, the indicator species analysis results not presented in Article I are discussed, such as indicator species for lakes of different Depth, Area and *Eubosmina* spp. as an indicator.

Eubosmina spp. group was created by merging *B.* (*E.*) *coregoni* and *B.* (*E.*) *longispina*. Both species were identified as indicators of nutrient-poor conditions, with *B.* (*E.*) *coregoni* being an indicator of oligotrophic conditions, and *B. (E.) longispina* – mesotrophic conditions (Article I). These results aligned with findings of some other paleolimnological investigations (Chen et al., 2010; Gąsiorowski & Hercman, 2005). However, in some sources, *B.* (*E.*) *coregoni* is mentioned as typical for nutrient-enriched lakes (Kamenik et al., 2007). When evaluating *Eubosmina* spp. indicator species potential, it was identified as an indicator species of oligotrophic conditions by IndVal.g[1] analysis (Figure 10), with no relation to any of the other parameters. This result is reasonable, as there seems to be a direct linear relationship between *Eubosmina* spp. relative abundance and TSI. As the results show, combining *B. (E.) coregoni* and *B. (E.) longispina* into a single *Eubosmina* spp. group still provides ecologically meaningful interpretations in relation to TS. Therefore, combining Eubosmina species appears to be justified in paleolimnological contexts, where taxonomic uncertainty and morphological fragmentation often limit species-level resolution.

Area and Depth are parameters that were tested by IndVal.g analysis but were not discussed in Article I. Lake Area has been proven to be an important explanatory variable in several other subfossil Cladocera community studies (Pawlikiewicz & Jurasz, 2017; Yatigammana & Cumming, 2017). But is the influence of lake size connected to an actual species response, or is it just connected to the distance the remains need to be transported for the deposition in the deepest part of the lake, could be debated (Nevalainen, 2011). Of the established indicator species, *Paralona pigra* was found to be an indicator of Area > 25 ha (Figure 10), and no individuals of *P. pigra* were found in lakes with Area < 10 ha (Figure 11). However, this result has less statistical significance than its relation to oligotrophic conditions. Most *P. pigra* observations were found in lakes with an Area between 50 and 100 ha. *Latona setifera* was found only in lakes with an Area < 50 ha, and IndVal.g analysis has identified it as an indicator of lakes with an Area of 10–50 ha, due to its seeming specialization. However, there were 16 lakes in this group, and in only 4 of them *L. setifera* was observed. In general literature, this species is described as a benthic species preferring deep, oligotrophic lobelia lakes with a wide range of pH (Bledzki & Rybak, 2016). The results show that *L. setifera* was found in various pH, EC, and TSI conditions (Figure 11). Therefore, it is most likely that this species is not specialized for lake size but was found randomly.

Some species emerged as potential Depth indicators with statistically significant associations, including *Leptodora kindtii* (10–15 m and > 20 m), *P. pigra* (> 15 m), and *C. rectangula*/ *A. guttata* (<5 m) (Figure 10). However, closer examination of these results leaves doubts on whether these species could truly be used for past water Depth reconstructions. For instance, *P. pigra* was identified as an indicator of both deeper lakes and oligotrophic conditions (Figure 10). Therefore, this may simply reflect the trend that deeper lakes in the dataset are generally more nutrient-poor (Figure 4). Similarly, other oligotrophy indicators like *Alonopsis elongata* and *Monospilus dispar*, associated with deeper lakes, had a stronger relationship with TS than Depth (Figure 10). These examples further illustrate the challenge of separating the effects of lake Depth and TS in sediment records.

Suppose we assume that lake Depth truly is the main driving factor for some of the species. In that case, there does not seem to be a reasonable explanation of why some species, as an example of *L. kindtii,* might prefer lakes with Depth 10–15 m and > 20 m, but avoid the lakes with Depth 15–20 m. Therefore, it is unlikely that species that have a gap in the Depth value groups for IndVal.g^{all} analysis are sensitive to the lake Depth. Such results were found for *L. kindtii* (10–15 m and > 20 m), *A. elongata* (5–10 m and > 15m) and *C. rectangula* (< 5 m and > 20 m). While there is a well-reported connection between lake depth and pelagic and littoral species relative abundances, there are few to no reports of specialised Cladocera species only living in lakes with specific depths (Hofmann, 1998; Nevalainen et al., 2011; Sarmaja-Korjonen, 2001). And for good reason. From the Cladocera viewpoint lake depth is a complex parameter, which includes the hypolimnion oxygen concentration, water mixing, temperature conditions, light penetration in water column and macrophytes associated to it, as well as possibilities to escape predation (Rose, 2024; Sysoev et al., 2025; Vogt et al., 2013). The problem with depth evaluation is also the fact that it is not actually just one number, as in this analysis – every lake with a Depth of > 20 m also has zones with depths of < 5 m, 5–10 m, 10–15 m and 15–20 m. Therefore, it can be concluded that the indicator species approach is not a valid method that could be used for lake Depth reconstructions, and more insights could be gained from other approaches, such as the functional group perspective.

4.4 WA-PLS and BRT model results

In this work, Weighted Averaging Partial Least Squares (WA-PLS) model results were compared to Boosted Regression Tree (BRT) results. In the cross-validation (CV) results, WA-PLS almost always outperformed BRT models (Figure 12). Some authors have noted, that WA-PLS tend to produce more robust estimations compared to some of the more complex machine learning algorithms (Sun et al., 2024), while others have found that BRT outperforms WA and WA-PLS in paleolimnological reconstructions (Salonen et al., 2014; Wang et al., 2021). When looking at the separate data points of BRT model predictions on the studied lacustrine sediment-core records, the data points seem somewhat scattered compared to WA-PLS (Figures 15, 18, 21). Such noisiness of the BRT model predictions has been reported by other authors as well (Elith et al., 2008). However, when looking at Predicted vs. Observed slope values, BRT often has a score closer to 1 than WA-PLS (Figure 12). The slope value of 1 means that with an increase of 1 unit in the observations, the predicted values also increase by 1 unit. The combination of higher Root Mean Square Error of Prediction (RMSEP) values, slightly lower R2 and Pearsons correlation of residuals vs. observed values together with the slope value of BRT being close to 1 could mean, that BRT captures the general data pattern rather well, but its sensitivity to noise results in higher scatter of the predicted values from the 1:1 line.

The RDA analysis recognised pH as one of the most important factors influencing subfossil Cladocera species assemblages (Figure 3). Therefore, it is no surprise that pH showed good CV results across models, with maximum bias no more than 1.7 pH units. According to the RMSEP value, WA-PLS based on the dataset “Eubosmina” might be the best model for the pH prediction. However, when comparing the reconstructed values with the literature data on Lake Sekšu and Lake Velnezers pH, the BRT “Eubosmina” model seems more precise (Figures 15 and 18), despite its slightly lower CV performance (Figure 12). One of the possible explanations for why BRT models perform well in the lake environment reconstructions, despite the lower CV performance, could be related to the CV process. In this work, k-folds (k = 10) CV was used, meaning that the dataset was divided into 10 approximately equal parts, then, on 9/10 parts, the model was built and the remaining 1/10 part was used for testing the model's predictive performance. The procedure was repeated until all of the 10 parts had been used as a test set. After the CV process, the final model was built using all samples in the dataset. This means the final model is built on more samples than the test models for CV. Several authors have successfully built reconstruction models using WA-PLS on smaller training sets than the one used in this work (Chen et al., 2010; Enache & Prairie, 2002). Meanwhile, the BRT method is more suitable for larger datasets (Elith et al., 2008; Wisz et al., 2008). Since the BRT method is more sensitive to the dataset size, it is possible that with the increased number of samples in the final model, its performance improved as well. Another possible explanation for the success of the BRT "Eubosmina" model can be found when looking at the quartile (Q) RMSEP data (Figure 12); it is notable that the BRT "Eubosmina" model has especially low values at the Q3. The values from literature that could be compared to the reconstructed values of sediment cores were between 7 and 8.5, which would place them in the data range best covered by the training set (Appendix 5). When looking at the Q RMSEP, it can be seen that in Q1, WA-PLS outperformed BRT (Figure 12). This could be due to the left-skewed data distribution of pH values in the training set. Only 12 out of 78 samples had pH < 6, and although BRT might be preferable in cases of non-Gaussian data distribution, this method is also somewhat sensitive to the number of samples (Elith et al., 2018; Birks et al., 2012), which could have led to WA-PLS outperforming BRT at the lower end of the pH gradient. However, when looking at the reconstructed pH values for Lake Velnezers and Lake Sekšu, the patterns of different models within each lake are similar, and the reconstructed values mostly don't differ by more than 1 pH unit (Figures 15 and 18). A water pH change of 1 unit or more is common within the same lake over a year, as well as in different microhabitats and lake depths (Erlandsson et al., 2008; Maberly, 1996; Martinsen et al., 2022). Therefore, the results of all the models could be considered as rather similar and suitable for past pH reconstructions.

EC was found to have a significant explanatory power of subfossil Cladocera species assemblages by the RDA analysis. However, the effect seems to have some collinearity with the pH (Figure 3). EC showed reasonable results during the model CV. EC WA-PLS models had little trend in the Residuals vs. Observed, and R2 values were comparable to pH WA-PLS models (Figure 12). However, all the models failed to reconstruct reasonable EC values for Lake Velnezers, and all the reconstructed values showed serious underestimation compared to the literature observations (Figure 15). EC and pH were correlated environmental parameters (Figures 3 and 4), and it is most likely due to the pH influence that subfossil Cladocera do not respond to the EC gradient in a way that could be captured by any of the models. Therefore, using any of the models developed in this work for lake EC reconstructions is not recommended.

The secondary environmental gradients most likely strongly influenced the Depth, TSI, Chl-a and TP models. This can be seen when comparing the "all" and "Eubosmina" dataset based models to "pH > 6" and "Eubosmina (pH > 6)" based models. TSI, TP, Chl-a and Depth models performed better if dystrophic lakes were excluded, and for these parameters, "pH > 6" and "Eubosmina (pH > 6)" based models showed considerably better CV results (Figure 12). WA-PLS models outperformed BRT models in CV for TS-related parameters; however, when comparing the WA-PLS and BRT model performances on the lacustrine sediment core samples, BRT models seem to generally reconstruct values closer to the values reported in literature than WA-PLS (Figures 15 and 18). It is especially pronounced in the reconstruction results of Lake Velnezers (Figure 15), where WA-PLS forms a smooth line of constant underpredictions of such parameters as TSI, Chl-a and TP. On the other hand, while BRT values are more scattered, their LOESS-smoothed curve values were closer to the observations from the literature. Some possible explanations exist for why WA-PLS models show good CV results but perform comparatively poorly when applied to the lake sediment records (core samples). One of the potential explanations could be related to the CV process and the increase in the number of samples for the final BRT model, as described above. Another possible explanation is connected to the data distribution of the training set. Both BRT and WA-PLS tend to perform poorly at the end of the environmental gradients (Salonen et al., 2014; Ter Braak et al., 1993; Wang et al., 2021), but it is possible that in some cases BRT might perform better at the gradient ends, as in case of Lake Velnezers TSI, Chl-a and TP predictions (Figure 15). The known historical values of Lake Velnezers' TS descriptive parameters result in the lake being classified as highly eutrophic to hypereutrophic, which would be closer to the 4th quartile values of the training set (Article I). In Velnezers Zone 3 and 4, the difference between WA-PLS and BRT TS descriptive parameter predictions is largest. However, the differences are smaller in Zones 1 and 2, where lower TS could be expected (Article II). If the failure of the WA-PLS model is indeed due to its low performance at high TS, then WA-PLS models based on the presented training set should not be used for lakes with high anthropogenic disturbance.

CV results showed that Depth reconstruction models were more successful if acidic lakes ($pH < 6$) were excluded from the training set. The most successful CV results for Depth models were for BRT "$pH > 6$" and BRT "Eubosmina ($pH > 6$)", as BRT models outperformed WA-PLS in R2, slope, RMSEP values, as well as for the residual distribution (Figure 12). BRT "$pH > 6$" models also predicted Depth values closer to the values from literature for Lake Sekšu and Lake Velnezers (Figures 15 and 18). However, in almost all cases, the model predicted a higher value for lake Depth than was reported in the literature. This could be due to the considerable variation in other environmental parameters and uncertainties connected to the acquisition of lake Depth data. Information on lake Depths was acquired using different literature sources (Estonia: kalapeedia.ee; Latvia: ezeri.lv; Lithuania: zvejogidas.lt), for which the year or method of the measurement was almost never mentioned. Therefore, it is unknown if the Depth value indeed corresponds to the period covered by the surface sediments. Lake Depth can also vary seasonally and annually (Evtimova & Donohue, 2016; Wrzesiński & Ptak, 2016; Zohary & Ostrovsky, 2011), which only adds to the validation uncertainty of the model reconstruction results. When other authors have attempted to reconstruct lake Depth using subfossil Cladocera, the training sets were often characterised by little variability in other parameters such as TS and pH (Davidson et al, 2011a; Nevalainen et al., 2011). Altogether, while the CV showed somewhat promising results for lake Depth modelling using subfossil Cladocera, the models were tested only on sediment records from relatively shallow lakes. For these lakes, a slight change in water depth might appear ecologically more significant than for deeper lakes (Zohary & Ostrovsky, 2011). Furthermore, the uncertainties connected to the training set data and relatively few observations reported in the literature must be considered. Therefore, to truly evaluate the Depth model performance, it would be necessary to test it on sediment records from lakes with better-monitored changes in Depth values and deeper lakes. As the Depth gradients correlate with the TS gradient, additional data collection and dataset filtering might be necessary to create a fully functional Depth reconstruction model.

4.5 Lake environmental reconstructions

4.5.1 Lake Velnezers

Lake Velnezers is a small lake located within the city of Riga. The landscape surrounding Lake Velnezers has undergone rapid changes within a relatively short time span.

The area changed from forested (19th century) to agricultural (beginning of 20th century) to urban area (1950 onward). The sediment record of Lake Velnezers can be divided into 4 zones based on clustering results and historical events. Zone 1 corresponds to the landscape of Lake Velnezers transitioning from forested to agricultural land (before 1920). Zone 2 is descriptive of the transition between the agricultural and urbanised stage of Lake Velnezers (year 1920 to 1970). Zone 3 is descriptive of the urbanised stage during the Soviet Union (1970 to 1990), and Zone 4 is representative of the urbanised stage after the collapse of the Soviet Union (1990 to 2018). These landscape changes have resulted in eutrophication, changes in pH, and heavy metal pollution of Lake Velnezers. More information on the lake can be found in Article II.

Based on subfossil Cladocera composition, the most significant changes in Lake Velnezers occurred during Zone 1 (before the year 1920) (Figure 13). While in Article II, it was recognised that during Zone 1, lake pH might have been lower than present day, indicator species analysis and model estimations (Figure 15) reveal that the change might have been more rapid and pronounced than previously anticipated. All of the models estimated pH < 6 at the beginning of Zone 1 and an increase to pH 7.5–8.5 by the beginning of Zone 2. The composition of the subfossil Cladocera indicator species supports these results, as the acidic softwater indicator *H. gibberum* (Article I) is only present in Zone 1. Other species indicative of acidic conditions, such as *A. elongata*, *A. rustica*, and *P. pediculus* (Article I), are present in every sample of Zone 1. Species that can be considered indicators of pH < 6 with increased relative abundance, such as *Daphnia* spp. and *Acroperus harpae*, were also observed in larger proportions during Zone 1 (Figure 13). Shift to pH > 6 at the beginning of Zone 2 (1920–1970) is supported by the simultaneous appearance of species with pH > 6 and EC > 100 µS/cm preference, such as *L. kindtii*, *P. trigonellus*, *D. rostrata*, *M. dispar*, and *L. leydigi* (Figures 10 and 13). However, during Zone 2, pH < 6, EC < 200 µS/cm and oligotrophy-mesotrophy indicator *A. elongata*, pH < 6 indicators *P. pediculus* and *A. rustica* remain present, but their appearance is less continuous. Therefore, the author's estimations of pH would better align with the BRT "all" estimates (Figure 15), which predict the pH values in Zone 2 to be between 6.5 and 8, allowing coexisting species with acidic and alkaline pH preferences. Based on similar reasoning, EC of Lake Velnezers should be < 100 µS/cm in Zone 1, and between 100 and 250 µS/cm in Zone 2. In the first half of the 20th century (end of Zone 1, beginning of Zone 2), Lake Velnezers was surrounded by agricultural lands (Military topographic map, 1908; NARA, 1940), which might have contributed to soil erosion. The cause of acidic conditions in the lakes of the Baltic States is most often the influx of humic substances from surrounding areas, and the most common source of humic substances is the peat bogs (Eņģele & Sniedze-Kretalova, 2013). Human-driven changes in the landscape could have reduced the influx of acids into Lake Velnezers due to the transition from forested/bog to agricultural land. This might have been one of the main driving factors of the pH increase during Zone 1. At the same time, erosion, nutrient and fertiliser input could have contributed to eutrophication and an increase in EC. As pH was identified to be the main driving factor influencing subfossil Cladocera species composition (Figure 3), it is difficult to estimate how other conditions, such as Depth or

TS, changed during Zone 1. However, the large relative abundance of *B. longirostris* confirms that at the beginning of Zone 2, Lake Velnezers was a eutrophic lake. Most of the models evaluate Lake Velnezers to be an eutrophic lake during Zone 2, except for Chl-a and TP BRT "Eubosmina (pH > 6)" models, which predict the values reaching hypereutrophic conditions.

In Article II, chemical analysis of sediments revealed lake condition deterioration at the end of Zone 3 (1970–1990) and the beginning of Zone 4 (1990–2018). During this time, heavy metal contamination and anoxic conditions in the lake were estimated. Subfossil Cladocera composition analysis somewhat supported this claim, as there was a reduction of species diversity (Figure 14), and *B. longirostris* relative abundance increased even more (Figure 13). However, subjectively, the changes in species composition do not seem as distinct as the ones described by sediment chemistry analysis. Despite this, the model predictions across all the TS descriptive parameters reconstructed the increase in trophic degree at the beginning of Zone 4 (Figure 15) with a very similarly shaped curve to that of sediment analysis (Article II). As BRT model evaluations are considerably closer to the TSI, Chl-a and TP values obtained from literature, the estimates from these models are more likely to be true for Zone 4. Both BRT "pH > 6" and BRT "Eubosmina (pH > 6)" have predicted that at the beginning of Zone 4, Lake Velnezers reached hypereutrophic conditions, with a later return to eutrophic conditions.

4.5.2 Lake Sekšu

Article III examines environmental changes in Lake Sekšu – a small eutrophic lake that has been part of Riga's drinking water supply system since the early 20th century (Dziluma, 2003) – using sediment chemistry, chironomid, diatom, pollen, non-pollen palynomorphs, and subfossil Cladocera data. To reiterate: nowadays this lake is part of a restricted zone, but during the Soviet Union period, an attempt was made to increase the groundwater levels of the area by pumping water from the nearby lake Mazais Baltezers into Lake Sekšu. The water pumping system for Lake Sekšu was active from 1953 to 1965 (Krutofala & Levins, 2006). In Article III, the beginning of this period was marked as the end of Zone 1 (1935–1947). Zone 1 in comparison to Zone 2 (1947–2018) had noticeably higher sediment organic matter content, C/N ratio, abundance of diatom species with oligotrophic – eutrophic environmental preference as well as larger proportion of *Isoetes lacustris*, which is widely considered as species typical for oligotrophic softwater lakes (Azzella et al., 2024).

Additionally, to increased erosion and nutrient input, it is also argued in Article III that the pipeline caused considerable water level fluctuations. However, that does not mean that the lake was pristine and undisturbed in the period before the construction of the pipeline. The core of Lake Sekšu only extends back to the sediments from the year 1935 and does not cover the period before it was part of the drinking water supply system "Baltezers". A literature source from before the period covered by the sediment record reported that the lake had a transparency of 5.6 m, and the presence of an indicator species of acidic conditions and EC < 100 µS/cm, *H. gibberum* (Kuptsch, 1927). The remains of this species cannot be found anywhere in the analysed sediment record, which would mean that the environmental shift had started before the studied period.

The pH reconstructions from the sediment core portray the pH conditions in Lake Sekšu as relatively constant, varying between 7.25 and 8.75, with slightly lower values in Zone 1 (1935–1947) (Figure 18). This result aligns with the findings based on indicator species approach, as the whole length of the core species indicative of pH > 6 and

EC > 100 µS/cm (such as *L. kindtii*, *P. uncinatus*, *D. rostrata*, *M. dispar)* are present (Figure 8). However, some evidence from the current study and literature suggests that during Zone 1, and possibly earlier, the lake's pH and EC may have been lower than present-day values. For instance, the already mentioned occurrence of *H. gibberum* (Kuptsch, 1927) is characteristic of acidic, softwater lakes (Article I; Błędzki & Rybak, 2016). Similarly, the macrophyte *Isoetes lacustris*, noted for its preference for softwater conditions (Azzella et al., 2024), shows higher relative abundance in the lower layers of the sediment core (Article III). Furthermore, Lake Sekšu is situated in a region with sandy soils (Nikodemus et al., 2018), and softwater lakes in such conditions are a common phenomenon (Murphy, 2002). These findings suggest that Lake Sekšu may have had lower EC and pH values earlier in the first half of the 20th century, as reported by the model and indicator species results.

In Zone 2 (1947–2018), *P. pediculus*, which is an indicator of pH < 6 and EC < 200 µS/cm, disappears, and another species (*L. leydigi*), which is indicative of pH > 6 and EC > 100 µS/cm, appears (Figure 16). The increase in pH and EC could be one of the possible explanations for these results. The initial causes for such a change are unclear, but a further rise in EC after the pipeline construction is possible. The lake from which water was pumped into Lake Sekšu – Mazais Baltezers is indirectly connected to the Baltic Sea, and it has been reported that sometimes seawater penetrates it (LVĢMC, 2015). Based on all of the information given above and the fact that such indicator species as *A. rustica* (pH < 6, EC < 100 µS/cm) and *A. elongata* (pH < 6, EC < 200 µS/cm) remain throughout the core, the author estimates that the EC of Lake Sekšu should be a little above 100 µS/cm in Zone 1, and somewhat close to 200 µS/cm in Zone 2.

The indicator species analysis and clustering results of Lake Sekšu subfossil Cladocera composition would point to relatively unchanging environmental conditions throughout the core (Figure 16). In the transition between Zones 1 and 2, the oligotrophic indicator species *O. gracilis* disappears (Figures 9 and 16). Still, other species indicative of oligotrophic to mesotrophic conditions, such as *A. elongata* and species indicative of hypereutrophic conditions, such as *O. tenuicaudis*, appear. While in Article III, the noticeable increase of *C. sphaericus* is mentioned as one of the arguments that proves the eutrophication of Lake Sekšu, the relative abundance values rarely exceed 20%. The threshold of 20% for *C. sphaericus* relative abundance was suggested in Article I, as in the training set and other studies this species could be commonly found in proportion between < 1% and 20 % in all lake types (de Eyto, 2001), but above 20% only in eutrophic and hypereutrophic lakes. However, this does not mean that Lake Sekšu did not experience eutrophication. Other evidence, such as the increase of relative abundance of small-sized Cladocera species (Figure 17), and results drawn from other proxies (Article III) still support this claim. It just might be that the extent of the effect was less pronounced.

The results of TS descriptive parameter reconstructions show, on average, slightly lower TSI, Chl-a and TP values in Zone 1 (Figure 18). Generally, all of the models evaluate the TS of Lake Sekšu to be on the border between mesotrophic and eutrophic conditions, with a few points predicted with values that would classify Lake Sekšu as highly eutrophic or hypereutrophic. These results might seem somewhat chaotic, or it could be argued that it is proof of poor model performance. However, the literature source Jansons (1997) has reported high Chl-a value fluctuations (Figure 18). It is mentioned that, on average, the Chl-a value is 12 µg/l (Jansons, 1997), which would classify Lake Sekšu as lightly eutrophic and later literature records would also classify Lake Sekšu as mesotrophic to eutrophic (Article I; Zariņa, 2014). At the same time, there are several reported events when Chl-a values exceed 100 µg/l, which would classify Lake Sekšu as highly hypereutrophic (Figure 18) (Jansons, 1997; Pujate, 2003). It can be seen that some of the higher prediction points coincide with the extreme values described in the literature (Figure 18). As fluctuations in the small-sized species proportion are observed (Figure 17), and every core sample contains approximately a 1–3 year period, model predictions may be "picking up" on these episodes.

On the other hand, the average predictions of TSI, Chl-a and TP are relatively stable, which would be more in accordance with the indicator species approach results (Figure 16). It is also worth noting that while oligotrophic species *O. gracilis* disappeared, hypereutrophic *O. tenuicaudis* appeared, the small-sized Cladocera proportion and fluctuations increased, there were still other oligotrophy-mesotrophy indicative species that remained throughout Zone 2. Such species are *M. dispar*, *P. pigra* and *A. elongata* (Figure 16). According to Article III, the macrophyte species *Isoetes lacustris,* which is considered typical of oligotrophic softwater lakes *(*Azella et al., 2024*),* reduces in proportion but does not disappear. Therefore, as such contrasting results are reported from the same lake, it is possible that water quality deterioration in Lake Sekšu resulted in instability of conditions throughout the year, giving a temporal window within the growing season for species with different niches to complete their life cycle, while never truly thriving.

Diatom-inferred TP model of Lake Sekšu predicted TP values between 25 and 50 µg/l in Zone 1 and between 50 and 100 µg/l in Zone 2 (Article III), while Cladocera based models predicted the TP value to be between 10 and 35 µg/l in Zone 1 and between 15 and 55 µg/l in Zone 2 (Figure 18). Both Diatom-inferred TP values and Cladocera-based models predicted the lake to be mesotrophic and eutrophic in Zone 1. However, in Zone 2, the conclusion would be different – based on the Diatom model, the Lake Sekšu should have fully transitioned to highly eutrophic conditions. When comparing the reconstruction results to information from literature, there seems to be strength in both models, Cladocera and Diatom-based models, with the Diatom-based model producing values closer to the extreme events, while the Cladocera-based models present values closer to the baseline.

As Lake Sekšu is part of Riga's drinking water supply system, it could be expected that Lake Sekšu would experience considerable water level fluctuation. There are some reports on the changing water surface area of Lake Sekšu – in 1930, the lake's surface area was 13 ha, in 1992, 7.9 ha, but in 2002, it was 11.9 ha (Latvijas Ezeri, 2010), which most likely could be caused by an increase and decrease of water level. However, precise data on water Depth changes was not available. All of the prediction models overestimated lake Depth, with the BRT model values being slightly closer to the actual value (Figure 18). BRT models estimated a higher water level in Zone 1 than in Zone 2, which seems reasonable, considering the reported results of the lake surface area around this time (Latvijas ezeri, 2010). However, the absolute values of the model prediction seem somewhat unrealistic, with predicted water Depth being as high as 20 m. Considering the gentle slopes of the lake basin, and the current lake Depth estimated as 7 m, this result seems highly unlikely. Pelagic and Macrophyte-associated species, as discussed in chapter 4.2.2, might also respond to water level changes, but there does not seem to be much fluctuation occurring within these groups (Figure 17). In the case of Lake Sekšu, subfossil Cladocera do not seem to respond to water level changes, and while lake Depth in Sekšu may have fluctuated over time (Article III), the lack of observations reported in the literature prevents confirmation.

As indicated by the literature (Jansons, 1997; Pujate, 2003), the ecosystem of Lake Sekšu appears to be highly unstable (Figure 18). This instability complicates model performance evaluation, as it becomes difficult to define a reliable 'true value' against which reconstruction results can be compared. Since low ecosystem stability can reflect poor ecological health (Parparov & Gal, 2017), and the methods tested in this study do not seem to capture such dynamic changes fully, it may be beneficial for future research to investigate how seasonal and annual fluctuations in water chemistry are recorded in lake sediments. This would help avoid drawing overly pessimistic or optimistic conclusions about historical environmental conditions and ensure that reconstructions are not prematurely dismissed due to seemingly contradictory or irregular patterns.

4.5.3 Lake Nakri

Lake Nakri is a small, shallow and relatively undisturbed eutrophic lake in southern Estonia. Based on subfossil Cladocera analysis, there are four distinct zones in the studied sediment section of Lake Nakri. The end of Zone 1 is 11,100 cal. years BP approximately correspond to the beginning of the Holocene (11,700 cal. years BP), Zone 2 (11,000–7,900 cal. years BP) approximately aligns with the Early Holocene period (11,700–8,200 cal. years BP), Zone 3 (7,900–5,300 cal. years BP) lies within the Middle Holocene period (8,200–4,200 cal. years BP), and Zone 4 (5,300 cal. years BP until 2018 CE) include the end of Middle Holocene and all of Late Holocene (Walker et al., 2018).

Six samples were analysed from Zone 1, encompassing a 1000-year period. Therefore, it is no wonder that dominant species vary from sample to sample (Figure 19). Dominant species in this period are *B. (E.) longispina*, *B. (E.) coregoni* and *Daphnia* spp., all of which were identified as indicators of oligotrophic to mesotrophic conditions (Figure 9). During this period, eutrophic condition indicators such as *B. longirostris* and *C. sphaericus* compose approximately 10% each of the species' composition. Species richness in Zone 1 is low (Figure 20), and in the literature, such species composition is sometimes described in relation to oligotrophic lakes (Hessen et al., 2006). Another characteristic of Zone 1 is the lack of Macrophyte-associated species (Figure 20), which could also be connected to higher water levels or nutrient limitation (Figure 6; Hofmann, 1998). The TS evaluation based on indicator species approach is contrasted by the predictions made by the models (Figure 21). All the models predict the TS of Lake Nakri during Zone 1 as eutrophic, while Chl-a BRT models predict the lake to be eutrophic to hypereutrophic. While it is unlikely that Lake Nakri was hypereutrophic during Zone 1 (Kornijów, 2023), there are examples when newly formed lakes can be enriched with nutrients by the animals (such as birds and mammals) that they attract (Kornijów, 2023; Luoto et al., 2015). Other research on lake history during the late glacial period have obtained somewhat similar results and hypothesised that a reason for nutrient enrichment in such lakes is the underdeveloped terrestrial vegetation, which could lead to nutrients from soil being leached into the lake ecosystem (Apolinarska et al., 2012; Tichá et al., 2019; Veski et al., 2010). It is considered that if species response down core is associated with the reconstructed parameter, the trajectories of the reconstruction curves will be similar, even if the absolute values vary (Birks et al., 2012). TSI, Chl-a and TP all showed a decrease in values during Zone 1 and an increase in Zone 2 for all tested BRT and WA-PLS models (Figure 21), which could mean that the late glacial to Early Holocene transition indeed resulted in reduced productivity of the lake ecosystem of Nakri. Among the littoral species present during Zone 1 are oligotrophy-mesotrophy indicators *A. elongata* and *M. dispar.* These species are present in almost every sample of Zone 1, which makes it seem unlikely that Lake Nakri was hypereutrophic during this period, as predicted by the BRT models. It is more likely that Lake Nakri could be described as mesotrophic, as earlier macrofossil research found Characeae remains in Lake Nakri during the late glacial period (Amon et al., 2012). When considering the model results, it must be noted that Zone 1 has the least similarity to the training set from all the lake sediment records analysed (Figure 20). Therefore, the models' predictive power in this situation might be questionable. The same criticism might also be applied to indicator species results, as they, too, are based on modern analogues. While it was identified that *B. (E.) longispina* is indicative of mesotrophic conditions in Article I, in the training set samples, *B. (E.) longispina* relative abundance did not exceed 30%, while in Lake Nakri, relative abundance reaches 80%. Therefore, there is no good modern analogue in the developed training set for comparison with the conditions in the late glacial/Early Holocene period.

Zone 2 (11,000–7,900 cal. years BP) approximately aligns with the Early Holocene period (11,700–8,200 cal. years BP) (Walker et al., 2018). Cladocera composition during this period is dominated by *B. (E.) longispina*, which slowly decreases in relative abundance with the increase of *B. longirostris* towards Zone 3 (Figure 19). During this period, several new Macrophyte-associated species appear, and the summed relative abundance of Macrophyte-associated species increases as well (Figures 19 and 20). This could signify the development of the macrophyte zone in Lake Nakri. As the indicators of oligotrophic conditions are lacking (Figure 19) and the dominant species *B.* (*E.*) *longispina* was classified as the indicator of mesotrophic conditions (Figure 9), it seems that Lake Nakri possibly never was a truly oligotrophic lake. The author would evaluate Lake Nakri as mesotrophic to slightly eutrophic during Zone 2 due to the dominance of *B.* (*E.*) *longispina* and the consequential dominance of medium-sized Cladocera species (Figure 20). In contrast, all of the models evaluated conditions during Zone 2 as eutrophic, and at some points even hypereutrophic (Figure 21). The dissimilarity between core and training set samples for Zone 2 is relatively high but reduces toward Zone 3, which should lead to better environmental estimates.

Zone 3 (7,900–5,330 cal. years BP) lies within the Middle Holocene period (8,200–4,200 years BP) (Walker et al., 2018) and somewhat aligns with the period of Holocene Thermal Maximum (8,000–5,000 years BP). This period is characterised by a temperature approximately 2.5 °C warmer than that of the present day (Renssen et al., 2012; Seppä & Poska, 2004). The increase of *B. longirostris* during this period (Figure 19) suggests an increase in lake productivity (Adamczuk, 2016; Article I). Our results showed that with the increase of TS, an increase of Small-sized species relative abundance can be observed (Figure 6), which can also be seen in the case of Lake Nakri (Figure 20). However, similar results of reduction of Cladocera body size have been observed in relation to warming of the climate (Albini et al., 2025; Beaver et al., 2020), and lake productivity can be influenced by both climate and nutrient limitations (Hao et al., 2018; Meerhoff et al., 2022). Even more, a warmer climate can increase water stratification, which could lead to oxygen depletion in the hypolimnion (Nickus et al., 2010). Under anoxic conditions, P release from sediments occurs (Hupfer & Lewandowski, 2008); therefore, climate could also directly contribute to the TS increase. This makes it challenging to evaluate to what extent the increase of Small-sized Cladocera and *B. longirostris* resulted from climate warming, nutrient enrichment or combined effects of both. None of the models predicted a significant increase in any of the TS descriptive parameters during Zone 3 (Figure 21). This result does not come from a lack of available modern analogues, as the samples of Zone 3 are rather similar to the surface sediment samples (Figure 20). As the model trajectories of the reconstructed TS-related parameters diverge in Zone 3, it is possible that some other parameter was driving subfossil Cladocera assemblages during this period. However, within the current stage of this work, it is not possible to determine if the variation in species composition is a result of climate impact. To solve this problem, a training set with broader geographical coverage would be needed. As the T_{ann} gradient of the training set is only 2.5 °C (Article I), it could be considered that the use of the current training set for TS environmental reconstructions requires an assumption of relatively constant climate.

Zone 4 (5,330 cal. years BP onward) includes the end of the Middle Holocene and all of the Late Holocene. During this period, *B.* (*E.*) *longispina* and *B. longirostris* reach equilibrium, and very little change can be observed until the uppermost sediment layers (Figure 19). Zone 4 mainly differs from other zones in that it has an increased relative abundance of Sediment-associated species (Figure 20) and the appearance of *B. (E.) coregoni*, both characteristic of low TS. These findings somewhat align with the model predictions, as all of the tested TS-related models predict Lake Nakri to be slightly less eutrophic, if compared to the results of Zone 3 (Figure 21).

As the Lake Nakri core covers a comparatively long time period, similar trajectories in environmental parameter reconstructions can be observed across models during certain intervals, but not in others. For instance, the WA-PLS and BRT models generally diverge in their reconstructions of water Depth (Figure 21). However, all models consistently indicate an increase in water Depth during two key periods: the transition from Zone 3 to Zone 4 (around 5,300 cal. years BP) and the Little Ice Age (LIA, 1,500–1,850 CE) (Matthews & Briffa, 2005; Meier et al., 2022; Seppä et al., 2009). The transition between Zones 3 and 4 roughly coincides with the end of the Holocene Thermal Maximum, and this period is also associated with increased precipitation during the Middle Holocene (Mauri et al., 2015; Meier et al., 2022). Similarly, the LIA is characterised by colder winter and summer temperatures alongside heightened precipitation (Wanner et al., 2022). These climatic shifts likely contributed to increased water Depth in Lake Nakri during both periods. Other researchers have also reported an increase in water Depth during LIA (Nevalainen et al., 2013). However, the same time periods are also marked with a decrease of TS, according to most reconstruction models (Figure 21), once again making it difficult to distinguish which parameter has primarily contributed to the changes in subfossil Cladocera assemblages.

Information on water Depth can also be evaluated based on the changes in the relative abundance of Pelagic and Macrophyte-associated species (Figure 6; Hofmann, 1998; Sarmaja-Korjonen, 2001). The steady decrease of Pelagic species and increase in Macrophyte-associated species relative abundances from the bottom of the core towards the top contrasts with the fluctuating patterns of Depth reconstructions by WA-PLS and BRT models (Figures 20 and 21). A decrease in water Depth over time is plausible, as it could result from gradual sediment accumulation filling the lake basin (Kornijów, 2023).

4.6 Evaluation of reconstruction approaches for key environmental parameters

This work aimed to evaluate which subfossil Cladocera assemblage analysis methods (functional groups, indicator species, WA-PLS and BRT models) would be most suitable for reconstructing pH, EC, TS, lake Depth and Area. It was found that subfossil Cladocera species composition in the lakes of Baltic states is primarily driven by pH. Therefore, it is no surprise that all of the developed methods can identify pH-driven changes in subfossil Cladocera assemblages. The author considers quantitative pH reconstructions using BRT and WA-PLS models preferable. The functional groups that displayed some correlation to pH were Macrophyte-associated species and Large-sized Cladocera (Figures 6 and 7). Perhaps combining this knowledge with information on species diversity (Figure 5) might aid in recognising dystrophic and acidic conditions in the past. However, based on the literature, a similar signal of an increase in the relative abundance of Large-sized Cladocera could also be related to lower fish predation pressure, cooler climate or oligotrophic conditions (Beaver et al., 2020; Jeppesen et al., 2001). Furthermore, an increase in Macrophyte-associated species could be related to changes in water Depth (Figure 6; Hofmann, 1998). Indicator species analysis seems to show better results compared to the functional group approach. However, the resolution for distinguishing the change is relatively coarse, as it is only possible to differentiate between lakes with pH < 6 and pH > 6 (Article I). In contrast, WA-PLS and BRT models can assess lake pH changes to high resolution, as shown by the comparisons between the values reported in the literature and reconstructed values (Figures 15 and 18). All of the models within each investigated lake predicted similar pH values (Figures 15, 18, 21), which again could be considered as an argument for why all of the pH models could be regarded as equal.

The only lake with truly significant pH changes within the studied period was Lake Velnezers (Figure 15). The conclusion that the pH was lower in this lake during Zone 1 (before 1920) is supported by the evaluation based on indicator species analysis, functional group analysis, and all of the model reconstructions. However, based on the indicator species analysis, the author would evaluate the pH of Lake Velnezers during Zone 1 to be < 6, but according to the model reconstructions, these values increase from 5.5 to 8 pH units. Partially, the differences in conclusions between these two methods could be connected to pH value distribution within the training set, as there are no lakes with a pH between 6 and 7. In the indicator species analysis the tested groups were pH < 6, pH 6–8 and pH > 8 for gradient continuity, however since the gradient part of lake between 6 and 7 pH points are missing, it is also possible that all the pH < 6 species are capable of living at conditions with pH < 7.

EC was found to be an important explanatory variable for the composition of the subfossil Cladocera species, and it is also somewhat correlated with pH. EC showed reasonable results during the model CV (Figure 12). However, when looking at the lake EC reconstructions, all of the models failed to reconstruct reasonable EC values for Lake Velnezers and Lake Nakri. In Zone 1 of Lake Velnezers, it could be expected that EC values were < 100 µS/cm, as argued from the perspective of indicator species analysis and reported by the models (Figure 15). This result is contrasted by significant underestimation of Velnezers EC by the models in Zones 2-4, when compared to the results of indicator species analysis and observations reported in the literature. For Lake Nakri, only the BRT model (Figure 21) was able to reproduce values similar to the measured EC value (Article I). Nevertheless, the same model predicted an EC value of 1200 µS/cm just one sample below, while WA-PLS models constantly underestimated EC within the core. Therefore, the author does not advise using any of the developed models for the EC reconstructions. This does not mean that EC is not an important parameter influencing Cladocera. As shown by indicator species analysis, species such as *H. gibberum* (Article I) seem more restricted by EC than pH. Several authors have proven that there is a significant connection between lake EC and Cladocera composition (Amsinck et al., 2005; Bjerring et al., 2009; Çakıroğlu et al., 2014). However, some of these studies had better EC gradient coverage, especially for the higher EC values (Bjerring et al., 2009). A potential reason for the failure of EC reconstruction models could be the overlapping influence of pH and EC (Figure 4). Perhaps better EC model results could be achieved if the EC models were developed using the datasets “pH > 6” and “Eubosmina (pH > 6)”, and either by adding more highly conductive lakes to the dataset or by excluding the lakes with the highest EC values. Based on the current results, the indicator species approach appears to be the most suitable method for evaluating EC within the available dataset. This approach allows for the differentiation of lakes into categories such as EC < 100 µS/cm, EC < 200 µS/cm, and EC > 100 µS/cm. EC did not show a correlation to any of the functional groups.

Eutrophication, anthropogenic disturbances, and their effects on freshwater ecosystems have been a focus of limnoecological research for at least the past 50 years (Kornijów, 2024). This research found that lake TS is a highly significant explanatory variable. TS descriptive parameters were effectively reconstructed using functional groups, indicator species, and modelling approaches. Lake Velnezers, which has recently undergone rapid eutrophication, displayed similar trajectories of all TS-related parameters in Zone 4 (Figure 15), suggesting that nutrient enrichment was the main driving force of Cladocera assemblages during this period – in the case of Lake Velnezers, the BRT model reconstructions proved to be the most effective method, as the predicted values closely matched the observations reported in literature(Figure 15), and mirroring trends in sediment chemistry described in Article II. In contrast, while indicator species approach captured the shift of TS towards hypereutrophic conditions, it failed to identify the changing trends of TP, Chl-a and TSI values (Figures 13 and 15).

In contemporary limnology, TS is supposed to be descriptive of lake productivity (Kornijów, 2024). However, there is an issue in this concept that complicates the result interpretation over more extended time periods, as the effects of nutrient availability and climate on productivity are intertwined (Jeppesen et al., 2010; Moss et al., 2011; Visconti et al., 2008). Despite this knowledge, the concept of eutrophication is primarily used as a synonym for nutrient enrichment (Kornijów, 2024; Pannard et al., 2024). Nutrient availability is the main factor influencing lake productivity in the developed training set. However, this might not be the case for Nakri Zone 1 (late glacial period/beginning of the Holocene), as lake productivity might have been limited by temperature. As discussed earlier, in the subfossil Cladocera training set of Baltic countries, TS descriptive parameters such as TSI, Chl-a and TP were identified as significant, while T_{ann} was excluded from the explanatory parameter list as not significant. As a result, the developed reconstruction methods do not provide information necessary to distinguish between the nutrient enrichment and climate influence on the subfossil Cladocera assemblages. This might impair the reconstruction results in such cases as Lake Nakri Zone 1, as the underlying assumption of constant climate is not met (Manuscript I). Another question that needs to be considered in TS environmental reconstructions is whether subfossil Cladocera truly respond to TS-related parameters or do they respond to a more complex "productivity" parameter, which includes temperature. If the limiting parameter for lake "productivity" was climate, it should not accurately represent TSI, Chl-a or TP. As Cladocera feed primarily on algae and bacteria (Ebert, 2005; Smirnov, 2017), their relationship to TP should be indirect, and Chl-a might be a more ecologically relevant parameter to reconstruct. The reconstruction of TS may also be influenced by additional confounding factors, such as lake Depth (Figure 4; Juggins et al., 2013). Nevertheless, in the modern-day situation, all these parameters are so closely related that it seems like an impossible task to draw solid conclusions about modern-day no-analogue situations. This issue could potentially be addressed by expanding the training set to include areas with climatic conditions similar to those inferred from other proxies for the Holocene and late glacial history of the Baltic States.

Subfossil Cladocera are commonly used for lake depth reconstructions (Korhola et al., 2005; Siitonen et al., 2011). In this work, too, Depth was found to have a significant influence on subfossil Cladocera assemblages. However, lake Depth was negatively correlated with lake TS, complicating the distinction between these two parameters and their influences on cladocerans. Cladocera species showed a stronger response to TS, suggesting that lake Depth cannot be reliably reconstructed using BRT or WA-PLS models under the current training set design. Furthermore, evaluating model reliability is challenging due to the lack of observational data from the literature. However, the functional groups Pelagic and Macrophyte-associated Cladocera showed a response to lake Depth, which might help to evaluate periods when water level has increased or decreased, as done by many other authors (Nevalainen et al., 2011; Rudna et al., 2023; Sarmaja-Korjonen, 2001).

Although lake Area was identified as significant explanatory variable, it did not show a clear response to any of the Cladocera species or functional groups. The theoretical basis for lake Area as an explanatory variable includes differences in remaining transportation (Nevalainen, 2011), extinction and colonization dynamics (Arnott et al., 2006), and possibly a number of available niches, which could influence species diversity. However, in this work, no correlation between lake Area and any of the species diversity parameters was found (Figure 5). This aligns with findings from some other studies, which suggest that the species-area relationship in aquatic ecosystems is not always as pronounced as in terrestrial systems (Browne, 1981; Hessen et al., 2006).

4.7 Assumptions and improvements for subfossil Cladocera-based transfer functions

4.7.1 The assumptions linking surface sediments to past environmental conditions

Similarly to many statistical analyses, having assumptions on data structure to function correctly, palaeoecological reconstructions that rely on modern analogues also have some basic fundamental assumptions. The assumptions (based on Lyman, 2017) that would be relevant for this work are listed below:

1. Species ecological tolerance has not changed over time.
2. Each species has a defined ecological niche limited by sensitivity to particular parameters.
3. Species presence suggests that the local environment at that time supported its survival.
4. Changes in species composition reflect changes in environmental conditions.

5. Faunal remains have been identified correctly, and the influence of cryptic species is negligible.
6. Sample size and preservation has not influenced the results.
7. The temporal resolution is sufficient to evaluate the magnitude and the rate of change.

It may be appropriate to add an additional assumption to the list:

8. The surface sediment training set includes a sufficient range of relevant environmental conditions to encompass the ecological optima and tolerances of the species present (Birks et al., 2012; Juggins, 2013).

The use of the *Bosmina/Eubosmina* complex to reconstruct past environmental conditions could lead to violations of assumptions 1 and 5. This is due to the complex taxonomy and relatively short evolutionary history of *Eubosmina* spp. (Faustová et al., 2011; Kotov et al., 2009). It is considered that finer taxonomical resolution could lead to more accurate model outputs, while coarse taxonomical resolution leads to fewer incorrectly identified individuals (Heiri & Lotter, 2010). Nevertheless, no consistent differences could be observed between the CV performance of models built based on datasets "Eubosmina" and "all" or "Eubosmina (pH > 6)" and "pH > 6" (Figure 12). *Eubosmina* spp. taxonomy is famously tangled and confusing already in the literature of contemporary ecology (Kotov et al., 2009; Lieder, 1996), increasing the probability of misidentification. It is even more likely to happen in paleolimnological studies, due to the fragmentation of the individuals. Genetic evidence suggests that radiation of *Eubosmina* species has occurred during the Holocene (Faustová et al., 2011), meaning that transitional forms of these species could be encountered in cores covering the whole Holocene. Only a few researchers have attempted to distinguish *Eubosmina* species and subspecies to high taxonomical resolution in subfossil Cladocera samples (Błędzki & Szeroczyńska, 2015; Zawiska et al., 2025). Most researchers have either combined them under *Eubosmina* spp. or grouped the individuals under species *B. (E.) coregoni* and *B. (E.) longispina*. However, it should be noted that in the most commonly used subfossil Cladocera identification key by Szeroczyńska & Sarmaja-Korjonen (2007), the classification of *B. (E.) coregoni* includes wider variability of characteristics than would be descriptive of this species in contemporary limnology (Błędzki & Rybak, 2016). Therefore, as there are inconsistencies in defining the species *B. (E.) coregoni* and *B. (E.) longispina* between paleolimnology and contemporary limnology, the transfer of knowledge between these fields regarding *Eubosmina* spp. should be approached with caution. Importantly, this issue might not be limited to *Eubosmina*; indicator species and transfer functions broadly rely on modern ecological relationships, and similar uncertainties could potentially affect other taxa, though this has not been systematically investigated.

Assumption 6 also presents challenges. It is well known that not all taxa preserve equally well in lake sediments. For example, *Daphnia* species are often poorly preserved in sediments, but the specific conditions under which preservation quality improves or deteriorates are not well understood (Leppänen & Weckström, 2016; Sarmaja-Korjonen, 2007). The sample preservation in general could have significant implications for both the training set and the sediment records. For example, the training set sample from Lake Vööla meri exhibited relatively poor preservation, potentially leading to non-representative species assemblages. Similarly, in the sediment cores, poor preservation was observed in Zone 1 (late glacial period) of Lake Nakri, which could also result in biased or incomplete faunal records. Such preservation biases may ultimately limit the reliability of ecological interpretations, particularly in cases where key taxa are underrepresented or entirely absent from the sediment record.

Assumption 7, “the temporal resolution is sufficient to evaluate the magnitude and the rate of change,” is particularly relevant for the record of Lake Sekšu and Zone 1 of Lake Nakri. Lake Nakri Zone 1 contains information from 6 sediment samples that cover approximately 1000-year period. As dominant species differ from sample to sample, the full magnitude, direction, and timing of changes are not possible to evaluate (Figure 19). Therefore, a more dense sampling of subfossil Cladocera during Nakri Zone 1 would be necessary. The ecosystem of Lake Sekšu appears to be highly unstable, as reported by the literature on TS-related parameters (Figure 18), and the methods applied in this study do not seem to fully capture such dynamic changes. However, it would not be fair to say that the sampling effort for Lake Sekšu was insufficient, as the sediment core was sampled in 1 cm intervals, and every sub-sample was analysed.

4.7.2 Future directions for improvement of subfossil Cladocera based environmental reconstructions in Baltic states

The models developed in this study produced good results for reconstructing pH and TS-related parameters. However, the surface sediment training set for the Baltic States could be improved by enhancing data distribution, expanding gradient coverage, including additional environmental parameters, and applying better validation methods to better understand Cladocera sensitivity and responses to environmental change. The proposed improvements include:

1. Increasing the number of observations for lakes with pH < 6.
2. Extending the training set coverage to areas that are representative of the full range of Holocene climatic conditions in the Baltic states.
3. Using datasets “Eubosmina (pH > 6)” or “pH > 6”, and either by excluding the extreme EC values from the existing training set or by additional sampling of high EC lakes, could potentially improve the EC model.
4. Developing subsets of data filtered for constant Depth or TS conditions could improve Depth and TS reconstructions by reducing the interference between these variables. For instance, separate TS models could be created for deep and shallow lakes. However, applying such models would require independent estimates of past Depth or TS values from other proxies.
5. Obtaining more precise lake environment measurements, especially for lake Depth.
6. Including observations of fish, macrophytes, catchment, land cover, and land use in the analysis.
7. Increasing the total number of observations for improved BRT model performance.
8. Surface sediment dating to better account for variability in sedimentation rate and consequential differences in temporal coverage.
9. Testing the reconstruction models on well-dated sediment records from lakes with long-term monitoring data.

Implementing these improvements could lead to more reliable paleoenvironmental reconstructions and a deeper understanding of past ecological changes in lake ecosystems across different temporal scales.

5 Conclusions

The thesis focuses on subfossil Cladocera assemblages as a potential tool for environmental reconstructions of the past conditions in lakes of the Baltic states. Functional group, indicator species, WA-PLS, and BRT reconstruction methods were developed based on the 78-lake surface sediment training set of Estonia, Latvia, and Lithuania. It was found that the subfossil Cladocera assemblages could be used to reconstruct pH, EC, TS, and lake Depth. However, the precision of the reconstruction varies from parameter to parameter and between methods.

- pH is the main driving factor in the subfossil Cladocera species assemblages, and can be successfully quantitatively reconstructed using WA-PLS and BRT models. It is also possible to approximately evaluate pH using indicator species approach; however, quantitative reconstruction models are preferable as they are capable of assessing pH values more accurately.
- TS can be reconstructed using the indicator species approach, and changes in TS can be approximated using the functional group approach. Quantitative reconstructions of TSI, TP, and Chl-a are possible. However, certain assumptions must be met. That is, pH in the analyzed period must have been neutral or alkaline, and other driving factors, such as climate, do not have a significant impact during the studied time period.
- EC can be approximated using the indicator species approach. Other methods do not seem to be able to consistently reconstruct EC. This is due to the high correlation between EC and pH.
- Changes in lake Depth can be assessed using the functional group approach. Depth and TS are closely linked parameters, and for further development of the Depth and TS models, a more targeted training set development for these parameters would be necessary.
- Considering the development of the training set data subsets, exclusion of the sites with pH < 6 significantly improved the BRT and WA-PLS model performances for TSI, TP, Chl-a, and Depth reconstructions. Separating species *Bosmina* (*Eubosmina*) *coregoni* and *B.* (*E.*) *longispina* or combining them under *Eubosmina* spp. did not have a consistent impact on the model cross-validation results or the conclusions drawn from the WA-PLS, BRT, or indicator species-based environmental reconstructions for cores of Lake Velnezers, Lake Sekšu, and Lake Nakri.
- The functional group approach is helpful in observing changes in pH, TS, and Depth, but it does not provide numerical approximations of past environmental conditions. The indicator species approach allows for simple approximations of pH, TS, and EC. BRT models provide reasonable absolute value estimates for pH, TSI, TP, and Chl-a if results are averaged between samples with LOESS smoothing. However, the sample-to-sample value estimations are relatively unstable. WA-PLS estimations provided reasonable pH absolute value estimations and might be useful to capture overall trends in the changes of the conditions of TSI, TP, and Chl-a, but sometimes underestimate the absolute values. It might be useful to apply these models together, as they showed similar trends in cases where nutrient enrichment could be considered the main driving factor of the lake ecosystem. Using these methods together might provide insights into

whether nutrient input was the main driving force of the changes in the ecosystem, or could it be a more complex combination of environmental factors.

- Lake Velnezers has undergone changes in pH and TS over the last 200 years. In the earlier periods characterized by the transition from forested to agricultural lands, there was an increase in pH, which changed the composition of Cladocera species. In the time period from 1950 onwards, Lake Velnezers was primarily influenced by eutrophication and reached its peak nutrient levels between the years 1990 and 2010, when it became highly eutrophic to hypereutrophic.
- Lake Sekšu has become more eutrophic during the last 100 years. The baseline conditions have changed little, as Lake Sekšu has transitioned from a mesotrophic to a slightly eutrophic TS. However, the lake ecosystem might have undergone periods of high seasonal nutrient-level fluctuations that occasionally might have reached hypereutrophic conditions.
- Lake Nakri, in the last 12,000 years, has changed from a mesotrophic lake to an eutrophic lake, becoming shallower but has not undergone significant changes in pH or EC. Most of the past changes in Lake Nakri have been climate-driven; therefore, precise estimations of the TSI, TP, and Chl-a values throughout the Holocene are impossible.

List of Figures

References

Adamczuk, M. (2016). Past, present, and future roles of small cladoceran Bosmina longirostris (OF Müller, 1785) in aquatic ecosystems. *Hydrobiologia*, *767*, 1-11. https://doi.org/10.1007/s10750-015-2495-7

Adamowicz, S.J., & Purvis, A. (2005). How many branchiopod crustacean species are there? Quantifying the components of underestimation. *Global Ecology and Biogeography*, *14*(5), 455-468. https://doi.org/10.1111/j.1466-822X.2005.00164.x

Agasild, H., Blank, K., Haberman, J., Tuvikene, L., Zingel, P., Nõges, P., Olli, K., Bernotas, P., & Cremona, F. (2025). Interactive effects shape the dynamics of Chydorus sphaericus (OF Müller, 1776) population in a shallow eutrophic lake. *Hydrobiologia*, *852*(2), 341-357. https://doi.org/10.1007/s10750-024-05612-4

Albini, D., Ransome, E., Dumbrell, A.J., Pawar, S., O'Gorman, E.J., Smith, T.P., Bell, T., Jackson, M.C., & Woodward, G. (2025). Warming alters plankton body-size distributions in a large field experiment. *Communications Biology*, *8*(1), 162. https://doi.org/10.1038/s42003-024-07380-2

Alexander, T.J., Vonlanthen, P., & Seehausen, O. (2017). Does eutrophication-driven evolution change aquatic ecosystems?. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *372*(1712), 20160041. doi: 10.1098/rstb.2016.0041

Amoatey, P., & Baawain, M.S. (2019). Effects of pollution on freshwater aquatic organisms. Water Environment Research, 91(10), 1272-1287. https://doi.org/10.1002/wer.1221

Amon, L., Veski, S., Heinsalu, A., & Saarse, L. (2012). Timing of Lateglacial vegetation dynamics and respective palaeoenvironmental conditions in southern Estonia: evidence from the sediment record of Lake Nakri. *Journal of Quaternary Science*, *27*(2), 169-180. https://doi.org/10.1002/jqs.1530

Amon, L., Veski, S., & Vassiljev, J. (2014). Tree taxa immigration to the eastern Baltic region, southeastern sector of Scandinavian glaciation during the Late-glacial period (14,500–11,700 cal. BP). *Vegetation History and Archaeobotany*, *23*, 207-216. https://doi.org/10.1007/s00334-014-0442-6

Amsinck, S.L., Jeppesen, E., & Landkildehus, F. (2005). Relationships between environmental variables and zooplankton subfossils in the surface sediments of 36 shallow coastal brackish lakes with special emphasis on the role of fish. *Journal of Paleolimnology*, *33*, 39-51. https://doi.org/10.1007/s10933-004-0504-3

Anderson, L.I., Crighton, W.R., & Hass, H. (2003). A new univalve crustacean from the Early Devonian Rhynie chert hot-spring complex. *Earth and Environmental Science Transactions of The Royal Society of Edinburgh*, *94*(4), 355-369. doi:10.1017/S0263593300000742

Anderson, N.J., Bugmann, H., Dearing, J.A., & Gaillard, M.J. (2006). Linking palaeoenvironmental data and models to understand the past and to predict the future. *Trends in ecology & evolution*, *21*(12), 696-704. 10.1016/j.tree.2006.09.005

Aplinkos Apsaugos Agentūra (2024). Ežerų ir tvenkinių monitoringo rezultatai. URL: https://aaa.lrv.lt/lt/veiklos-sritys/vanduo/upes-ezerai-ir-tvenkiniai/valstybinis-upiu-ezeru-ir-tvenkiniu-monitoringas/ezeru-ir-tvenkiniu-monitoringo-rezultatai/?fbclid=IwAR1Ab_0aJCnEdACdxKXQEouFIckTmfZrbmoYHuLejCsLZSvpOH2FboTuoJ4 (accessed 24.05.2024)

Apolinarska, K., Woszczyk, M., & Obremska, M. (2012). Late Weichselian and Holocene palaeoenvironmental changes in northern Poland based on the Lake Skrzynka record. *Boreas*, *41*(2), 292-307. https://doi.org/10.1111/j.1502-3885.2011.00235.x

Apsīte, E., Elferts, D., Zubaničs, A., & Latkovska, I. (2014). Long-term changes in hydrological regime of the lakes in Latvia. *Hydrology Research*, *45*(3), 308-321. https://doi.org/10.2166/nh.2013.435

Arnott, S. E., Magnuson, J. J., Dodson, S. I., & Colby, A. C. (2006). Lakes as islands: biodiversity, invasion, and extinction. *Longterm dynamics of lakes in the landscape. Edited by JJ Magnuson, TK Kratz, and BJ Benson. Oxford Press, Oxford, UK*, 67-88.

Azzella, M.M., Vecchia, A.D., Abeli, T., Alahuhta, J., Amoroso, V.B., Ballesteros, E., Bertrin, V., Brunton, D., Bobrov, A.A., Caldeira, C., Ceschin, S., Chemeris, E.V., Čtvrtlíková, M., de Winton, M., Gacia, E., Grishutkin, O.G., Hofstra, D., Ivanova, D., Ivanova, M.O., … , Bolpagni, R. (2024). Global assessment of aquatic Isoëtes species ecology. *Freshwater Biology*, *69*(10), 1420-1437. https://doi.org/10.1111/fwb.14316

Barnett, A., & Beisner, B.E. (2007). Zooplankton biodiversity and lake trophic state: explanations invoking resource abundance and distribution. *Ecology*, *88*(7), 1675-1686. https://doi.org/10.1890/06-1056.1

Barone, M., Dimante-Deimantovica, I., Busmane, S., Koistinen, A., Poikane, R., Saarni, S., Stivrins, N., Tylmann, W., Uurasjärvi, E., & Viksna, A. (2024). What to monitor? Microplastics in a freshwater lake–From seasonal surface water to bottom sediments. *Environmental Advances*, *17*, 100577. https://doi.org/10.1016/j.envadv.2024.100577

Battarbee, R.W. (1990). The causes of lake acidification, with special reference to the role of acid deposition. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, *327*(1240), 339-347. https://doi.org/10.1098/rstb.1990.0071

Bauze-Krastiņš, M.G. (2009). Garkalnes novada teritorijas plānojums 2009.-2021. gadam. I sējums. Paskaidrojuma raksts, Garkalnes novads.

Beaver, J.R., Tausz, C.E., Black, K.M., & Bolam, B.A. (2020). Cladoceran body size distributions along temperature and trophic gradients in the conterminous USA. *Journal of Plankton Research*, *42*(6), 613-629. https://doi.org/10.1093/plankt/fbaa053

Bennion, H., Battarbee, R.W., Sayer, C.D., Simpson, G.L., & Davidson, T.A. (2011). Defining reference conditions and restoration targets for lake ecosystems using palaeolimnology: a synthesis. *Journal of Paleolimnology*, *45*, 533-544. https://doi.org/10.1007/s10933-010-9419-3

Berman, J.J. (2016). Chapter 4—Understanding your data. *Data simplification*, 135-187.

Bērzinš, B., & Bertilsson, J. (1990). Occurrence of limnic micro-crustaceans in relation to pH and humic content in Swedish water bodies. *Hydrobiologia*, *199*(1), 65-71. https://doi.org/10.1007/BF00007834

Birks, H.J.B., Lotter, A.F., Juggins, S., Smol, J.P. (2012) *Tracking environmental change using lake sediments, Data handling and numerical techniques*. Springers.

Bjerring, R., Nykänen, M., Sarmaja-Korjonen, K., Sinev, A., Jensen, K., Nevalainen, L., Szeroczyńska, K. & Zawisza, E. (2008). Description of the subfossil head shield of Alona protzi Hartwig 1900 (Anomopoda, Chydoridae) and the environmental characteristics of its finding sites. *Studia Quaternaria*, 47-53.

Bjerring, R., Becares, E., Declerck, S., Gross, E.M., Hansson, L.A., Kairesalo, T., Nykänen, M., Halkiewicz, A., Kornijów, R., Conde-Porcuna, J.M., Seferlis, M., Nõges, T., Moss, B., Amsinck., S.L., Odgaards, B.V., & Jeppesen, E. (2009). Subfossil Cladocera in relation to contemporary environmental variables in 54 Pan-European lakes. *Freshwater Biology*, *54*(11), 2401-2417. https://doi.org/10.1111/j.1365-2427.2009.02252.x

Blaauw, M., & Christen, J.A. (2011). Flexible paleoclimate age-depth models using an autoregressive gamma process. DOI: 10.1214/11-BA618

Black, A.R., & Dodson, S.I. (1990). Demographic costs of Chaoborus-induced phenotypic plasticity in Daphnia pulex. *Oecologia*, *83*, 117-122. https://doi.org/10.1007/BF00324642

Błędzki, L.A., & Szeroczyńska, K. (2015). Palaeolimnological evidence of Bosmina morphotypes appearance in the late Holocene. *The Holocene*, *25*(3), 557-561. https://doi.org/10.1177/0959683614562433

Błędzki, L.A., & Rybak, J.I. (2016). Freshwater Crustacean Zooplankton of Europe: Cladocera & Copepoda (Calanoida, Cyclopoida) Key to species identification, with notes on ecology, distribution, methods and introduction to data analysis. Springer.

Boronat, L., Miracle, M.R. & Armengol, X. (2001). Cladoceran assemblages in a mineralization gradient. *Hydrobiologia*, *442*, 75-88. https://doi.org/10.1023/A:1017522004975

Bos, D.G., Cumming, B.F., & Smol, J.P. (1999). Cladocera and Anostraca from the Interior Plateau of British Columbia, Canada, as paleolimnological indicators of salinity and lake level. *Hydrobiologia*, *392*, 129-141. https://doi.org/10.1023/A:1003542709450

Brancelj, A., & Dumont, H.J. (2007). A review of the diversity, adaptations and groundwater colonization pathways in Cladocera and Calanoida (Crustacea), two rare and contrasting groups of stygobionts. *Fundamental and Applied Limnology/ Archiv fuer Hydrobiologie*, *168*(1), 3-17.

Branco, C.W.C., Fintelman-Oliveira, E., & dos Santos Miranda, V.B. (2023). A review of functional approaches for the study of freshwater communities with a focus on zooplankton. *Hydrobiologia*, *850*(21), 4719-4744. https://doi.org/10.1007/s10750-023-05227-1

Brezonik, P. L. (1984). Trophic state indices: rationale for multivariate approaches. *Lake and Reservoir Management*, *1*(1), 441-445. https://doi.org/10.1080/07438148409354553

Briede, A. (1996). Fosfora un smago metālu akumulācija Latvijas ūdenstilpēs [Accumulation of phosphorus and heavy metals in the water bodies of Latvia] [Doctoral dissertation, University of Latvia]. DSpace. https://dspace.lu.lv/dspace/handle/7/213

Brodersen, K.P., Whiteside, M.C., & Lindegaard, C. (1998). Reconstruction of trophic state in Danish lakes using subfossil chydorid (Cladocera) assemblages. *Canadian Journal of Fisheries and Aquatic Sciences*, *55*(5), 1093-1103. https://doi.org/10.1139/f98-008

Browman, H.I., Kruse, S., & O'Brien, W.J. (1989). Foraging behavior of the predaceous cladoceran, Leptodora kindti, and escape responses of their prey. *Journal of Plankton Research*, *11*(5), 1075-1088. https://doi.org/10.1093/plankt/11.5.1075

Brown, K.A., Bunting, M.J., Carvalho, F., de Bello, F., Mander, L., Marcisz, K., Mottl, O., Reitalu, T., & Svenning, J.C. (2023). Trait-based approaches as ecological time machines: Developing tools for reconstructing long-term variation in ecosystems. *Functional Ecology*, *37*(10), 2552-2569. https://doi.org/10.1111/1365-2435.14415

Browne, R.A. (1981). Lakes as islands: biogeographic distribution, turnover rates, and species composition in the lakes of central New York. *Journal of Biogeography*, 75-83. https://www.jstor.org/stable/2844594

Buren, S., & Arnott, S.E. (2025). The effect of calcium on acute sodium chloride toxicity in Daphnia species. *Environmental Toxicology and Chemistry*. doi: 10.1093/etojnl/vgae066

Burge, D.R., Edlund, M.B., & Frisch, D. (2018). Paleolimnology and resurrection ecology: The future of reconstructing the past. Evolutionary Applications, 11(1), 42-59. https://doi.org/10.1111/eva.12556

Burks, R.L., Lodge, D.M., Jeppesen, E., & Lauridsen, T.L. (2002). Diel horizontal migration of zooplankton: costs and benefits of inhabiting the littoral. *Freshwater biology*, *47*(3), 343-365. https://doi.org/10.1046/j.1365-2427.2002.00824.x

Butler, S.J., Freckleton, R.P., Renwick, A.R., & Norris, K. (2012). An objective, niche-based approach to indicator species selection. *Methods in Ecology and Evolution*, *3*(2), 317-326. https://doi.org/10.1111/j.2041-210X.2011.00173.x

Cáceres, M.D., & Legendre, P. (2009). Associations between species and groups of sites: indices and statistical inference. *Ecology*, *90*(12), 3566-3574. https://doi.org/10.1890/08-1823.1

Cáceres, M., Legendre, P., & Moretti, M. (2010). Improving indicator species analysis by combining groups of sites. *Oikos*, *119*(10), 1674-1684.

Çakıroğlu, A.İ., Tavşanoğlu, Ü.N., Levi, E.E., Davidson, T.A., Bucak, T., Özen, A., Akyıldız, G.K., Jeppesen, E., & Beklioğlu, M. (2014). Relatedness between contemporary and subfossil cladoceran assemblages in Turkish lakes. *Journal of Paleolimnology*, *52*, 367-383. https://doi.org/10.1007/s10933-014-9799-x

Carlson, R.E. (1977). A trophic state index for lakes 1. *Limnology and oceanography*, *22*(2), 361-369. https://doi.org/10.4319/lo.1977.22.2.0361

Carlson, R.E. (2007). Estimating trophic state. *Lakeline*, *27*(1), 25-28.

Catalan, J., Pla-Rabés, S., Wolfe, A.P., Smol, J.P., Rühland, K.M., Anderson, N.J., Kopáček, J., Stuchlík, E., Schmidt, R., Koinig, K.A., & Camarero, L. (2013). Global change revealed by palaeolimnological records from remote lakes: a review. *Journal of Paleolimnology*, *49*, 513-535. https://doi.org/10.1007/s10933-013-9681-2

Cavaletto, J. F., Vanderploeg, H.A., Pichlová-Ptáčníková, R., Pothoven, S.A., Liebig, J.R., & Fahnenstiel, G.L. (2010). Temporal and spatial separation allow coexistence of predatory cladocerans: Leptodora kindtii, Bythotrephes longimanus and Cercopagis pengoi, in southeastern Lake Michigan. *Journal of Great Lakes Research 36*, 65-73. https://doi.org/10.1016/j.jglr.2010.04.006

Česonienė, L., Šileikienė, D., & Dapkienė, M. (2020). Relationship between the water quality elements of water bodies and the hydrometric parameters: Case study in Lithuania. *Water*, *12*(2), 500. https://doi.org/10.3390/w12020500

Chen, G., Dalton, C., & Taylor, D. (2010). Cladocera as indicators of trophic state in Irish lakes. *Journal of Paleolimnology*, *44*, 465-481. https://doi.org/10.1007/s10933-010-9428-2

Cole, J.J., Carpenter, S.R., Pace, M.L., Van de Bogert, M.C., Kitchell, J.L., & Hodgson, J.R. (2006). Differential support of lake food webs by three types of terrestrial organic carbon. *Ecology Letters*, *9*(5), 558-568. https://doi.org/10.1111/j.1461-0248.2006.00898.x

Daubarien, J., Valiuškevičius, G., & Asijavičiūt, V. (2011). The structure of the landscape of Lithuanian lake shores of various sizes. *APLINKOS APSAUGOS INŽINERIJA,14-osios Lietuvos jaunųjų mokslininkų konferencijos „Mokslas – Lietuvos ateitis“, straipsnių rinkinys*, 100-106.

Daufresne, M., Lengfellner, K., & Sommer, U. (2009). Global warming benefits the small in aquatic ecosystems. *Proceedings of the National Academy of Sciences*, *106*(31), 12788-12793. https://doi.org/10.1073/pnas.0902080106

Davidson, T.A., Sayer, C.D., Perrow, M., Bramm, M., & Jeppesen, E. (2010). The simultaneous inference of zooplanktivorous fish and macrophyte density from sub-fossil cladoceran assemblages: a multivariate regression tree approach. *Freshwater Biology*, *55*(3), 546-564. https://doi.org/10.1111/j.1365-2427.2008.02124.x

Davidson, T.A., Bennion, H., Jeppesen, E., Clarke, G.H., Sayer, C.D., Morley, D., Odgaard, B.V., Rasmussen, P., Rawcliffe, R., Salgado, J., & Simpson, G.L. (2011a). The role of cladocerans in tracking long-term change in shallow lake trophic status. *Hydrobiologia*, *676*, 299-315. https://doi.org/10.1007/s10750-011-0851-9

Davidson, T.A., Amsinck, S.L., Bennike, O., Christoffersen, K.S., Landkildehus, F., Lauridsen, T.L., & Jeppesen, E. (2011b). Inferring a single variable from an assemblage with multiple controls: getting into deep water with cladoceran lake-depth transfer functions. *Hydrobiologia*, *676*, 129-142. https://doi.org/10.1007/s10750-011-0901-3

Davidson, T.A., & Jeppesen, E. (2013). The role of palaeolimnology in assessing eutrophication and its impact on lakes. *Journal of Paleolimnology*, *49*, 391-410. https://doi.org/10.1007/s10933-012-9651-0

de Eyto, E. (2001). Chydorus sphaericus as a biological indicator of water quality in lakes. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, *27*(6), 3358-3362.

De Schamphelaere, K.A., Baken, S., Cardwell, A., Du Laing, G., Nys, C., Stubblefield, W., Viaene, K., & Weighman, K. (2025). The effect of pH on chronic copper toxicity to Ceriodaphnia dubia within its natural pH niche. *Environmental Toxicology and Chemistry*, *44*(2), 484-496. https://doi.org/10.1093/etojnl/vgae039

Decaestecker, E., Declerck, S., De Meester, L., & Ebert, D. (2005). Ecological implications of parasites in natural Daphnia populations. *Oecologia*, *144*, 382-390. https://doi.org/10.1007/s00442-005-0083-7

Decaestecker, E., De Meester, L., & Mergeay, J. (2009). Cyclical parthenogenesis in Daphnia: sexual versus asexual reproduction. In I. Schön & K. Martens (Eds.) *Lost sex: The evolutionary biology of parthenogenesis* (pp. 295-316). Springer.

Deevey, E. S. (1942). Studies on Connecticut lake sediments; 3, The biostratonomy of Linsley Pond. *American Journal of Science*, *240*(4), 233–264. https://doi.org/10.2475/ajs.240.4.233

Deneke, R. (2000). Review of rotifers and crustaceans in highly acidic environments of pH values≤ 3. *Hydrobiologia*, *433*(1), 167-172. https://doi.org/10.1023/A:1004047510602

Dodson, S. (1990). Predicting diel vertical migration of zooplankton. *Limnology and Oceanography*, *35*(5), 1195-1200. https://doi.org/10.4319/lo.1990.35.5.1195

Dong, X., Kattel, G., & Jeppesen, E. (2020). Subfossil cladocerans as quantitative indicators of past ecological conditions in Yangtze River Basin lakes, China. *Science of the Total Environment*, *728*, 138794. https://doi.org/10.1016/j.scitotenv.2020.138794

Doubek, J.P., Campbell, K.L., Doubek, K.M., Hamre, K.D., Lofton, M.E., McClure, R.P., Ward, N.K., & Carey, C.C. (2018). The effects of hypolimnetic anoxia on the diel vertical migration of freshwater crustacean zooplankton. *Ecosphere*, *9*(7). https://doi.org/10.1002/ecs2.2332

Dručka, A. (2014). Antropogēnās ietekmes liecības Rīgas Velnezera nogulumos [Evidence of anthropogenic influence in the sediments of The Riga Velnezers] [Bachelor thesis, University of Latvia]. DSpace. http://dspace.lu.lv/dspace/handle/7/23966

Duffy, M.A., James, T.Y., & Longworth, A. (2015). Ecology, virulence, and phylogeny of Blastulidium paedophthorum, a widespread brood parasite of Daphnia spp. *Applied and Environmental Microbiology*, *81*(16), 5486-5496.

Dufrêne, M., & Legendre, P. (1997). Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological monographs*, *67*(3), 345-366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2

Dziļuma, M. (2003). Riga Water and the Riga Water Supply Museum. Riga Water.

Ebert, D. (2005). *Ecology, epidemiology, and evolution of parasitism in Daphnia*. National Library of Medicine, e-book.

Elias, S. (2025). *Encyclopedia of Quaternary science, 3rd Edition*. Volume 4. UK: Elsevier.

Ellis, E. C., & Ramankutty, N. (2008). Putting people in the map: anthropogenic biomes of the world. *Frontiers in Ecology and the Environment*, *6*(8), 439-447. https://doi.org/10.1890/070062

Ellis, E. C., Kaplan, J. O., Fuller, D. Q., Vavrus, S., Klein Goldewijk, K., & Verburg, P. H. (2013). Used planet: A global history. *Proceedings of the National Academy of Sciences*, *110*(20), 7978-7985. https://doi.org/10.1073/pnas.1217241110

Elith, J., Leathwick, J.R., & Hastie, T. (2008). A working guide to boosted regression trees. *Journal of animal ecology*, *77*(4), 802-813. https://doi.org/10.1111/j.1365-2656.2008.01390.x

Enache, M., & Prairie, Y.T. (2002). WA-PLS diatom-based pH, TP and DOC inference models from 42 lakes in the Abitibi clay belt area (Quebec, Canada). *Journal of Paleolimnology*, *27*, 151-171. https://doi.org/10.1023/A:1014281128544

Eņģele, L., & Sniedze-Kretalova, R. (2013). Saldūdeņu biotoopi. In A. Auniņš (Ed.) *Eiropas Savienības aizsargājamie biotopi Latvijā, Noteikšanas rokasgrāmata, 2. precizētais izdevums* (pp. 105-130). Latvijas Dabas fonds un Vides aizsardzības un reģionālās attīstības ministrija.

Erlandsson, M., Folster, J., Laudon, H., Weyhenmeyer, G.A., & Bishop, K. (2008). Natural variability in lake pH on seasonal, interannual and decadal time scales: Implications for assessment of human impact. *Environmental science & technology*, *42*(15), 5594-5599.

Estonian ministry of climate (2025) https://loodusveeb.ee/en/themes/inland-waters/distribution-inland-waters

Evtimova, V.V., & Donohue, I. (2016). Water-level fluctuations regulate the structure and functioning of natural lakes. *Freshwater Biology*, *61*(2), 251-264. https://doi.org/10.1111/fwb.12699

Faith, D.P., Minchin, P.R., & Belbin, L. (1987). Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio*, *69*, 57-68. https://doi.org/10.1007/BF00038687

Faustová, M., Sacherová, V., Svensson, J.E., & Taylor, D.J. (2011). Radiation of European Eubosmina (Cladocera) from Bosmina (E.) longispina—concordance of multipopulation molecular data with paleolimnology. *Limnology and Oceanography*, *56*(2), 440-450. https://doi.org/10.4319/lo.2011.56.2.0440

Flössner, D. (2000). *Die Haplopoda unde Cladocera Mitteleuropas.* Backhuys Publishers, Leiden, Netherlands.

Forró, L., Korovchinsky, N.M., Kotov, A.A., & Petrusek, A. (2008). Global diversity of cladocerans (Cladocera; Crustacea) in freshwater. *Freshwater animal diversity assessment*, 177-184. https://doi.org/10.1007/978-1-4020-8259-7_19

Fryer, G. (1968). Evolution and adaptive radiation in the Chydoridae (Crustacea: Cladocera): a study in comparative functional morphology and ecology. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *254*(795), 221-385. https://doi.org/10.1098/rstb.1968.0017

Fryer, G. (1987). Morphology and the classification of the so-called Cladocera. In *Cladocera: Proceedings of the Cladocera Symposium, Budapest 1985* (pp. 19-28). Springer Netherlands.

Gao, H., Liu, X., & Ban, S. (2022). Effect of acute acidic stress on survival and metabolic activity of zooplankton from Lake Biwa, Japan. *Inland Waters*, *12*(4), 488-498. https://doi.org/10.1080/20442041.2022.2058861

García-Girón, J., Fernández-Aláez, C., Fernández-Aláez, M., & Luis, B. (2018). Subfossil Cladocera from surface sediment reflect contemporary assemblages and their environmental controls in Iberian flatland ponds. *Ecological Indicators*, *87*, 33-42. https://doi.org/10.1016/j.ecolind.2017.12.007

Gąsiorowski, M., & Hercman, H. (2005). Recent sedimentation and eutrophication of Kruklin Lake after artificial drop in water-level in the middle of 19th century. *Studia Quaternaria*, *22*, 17-25.

Geller, W., & Müller, H. (1981). The filtration apparatus of Cladocera: filter mesh-sizes and their implications on food selectivity. *Oecologia*, *49*, 316-321. https://doi.org/10.1007/BF00347591

Gleason, H.A. (1922). On the relation between species and area. *Ecology*, *3*(2), 158-162. https://doi.org/10.2307/1929150

Glime, J.M. (2017). Arthropods: Crustacea – Copepoda and Cladocera. Chapter 10-1. In J.M. Glime (Ed.) *Bryophyte ecology, Volume 2. Biological interaction*. Michigan Technological University, e-book.

Gliwicz, Z.M. (1990). Food thresholds and body size in cladocerans. *Nature*, *343*(6259), 638-640. https://doi.org/10.1038/343638a0

Gliwicz, Z.M., & Umana, G. (1994). Cladoceran body size and vulnerability to copepod predation. *Limnology and Oceanography*, *39*(2), 419-424. https://doi.org/10.4319/lo.1994.39.2.0419

Gomes, L.F., Pereira, H.R., Gomes, A.C.A.M., Vieira, M.C., Martins, P.R., Roitman, I., & Vieira, L.C.G. (2019). Zooplankton functional-approach studies in continental aquatic environments: a systematic review. *Aquatic Ecology*, *53*, 191-203. https://doi.org/10.1007/s10452-019-09682-8

Goren, L., & Ben-Ami, F. (2013). Ecological correlates between cladocerans and their endoparasites from permanent and rain pools: patterns in community composition and diversity. *Hydrobiologia*, *701*, 13-23. https://doi.org/10.1007/s10750-012-1243-5

Gray, E., Cappelli, G., Gammell, M.P., Roden, C.M., & Lally, H.T. (2022). A review of dystrophic lake and pool habitat in Europe: an Irish perspective. *Journal for Nature Conservation*, *68*, 126189. https://doi.org/10.1016/j.jnc.2022.126189

Grimm, E.C. (1987). CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers & geosciences*, *13*(1), 13-35. https://doi.org/10.1016/0098-3004(87)90022-7

Grimm, E.C. (2011). TILIA 1.7.16 software. Illinois State Museum,Research and Collection Center, Springfield.

Gyllström, M., & Hansson, L.A. (2004). Dormancy in freshwater zooplankton: induction, termination and the importance of benthic-pelagic coupling. *Aquatic Sciences*, *66*, 274-295. https://doi.org/10.1007/s00027-004-0712-y

Hakanson, L., & Jansson, M. (1983). *Principles of lake sedimentology*. Caldwell, The Blackburn press.

Hammer, Ø., Harper, D.A.T., & Ryan, P.D. (2001). PAST: Paleontological Statistics software package for education and data analysis. *Paleontologia Electronica 4(1),* 9.

Hao, B., Roejkjaer, A.F., Wu, H., Cao, Y., Jeppesen, E., & Li, W. (2018). Responses of primary producers in shallow lakes to elevated temperature: a mesocosm experiment during the growing season of Potamogeton crispus. *Aquatic Sciences*, *80*, 1-10. https://doi.org/10.1007/s00027-018-0585-0

Heinsalu, A., & Alliksaar, T. (2009). Palaeolimnological assessment of environmental change over the last two centuries in oligotrophic Lake Nohipalu Valgjärv, southern Estonia. *Estonian Journal of Earth Sciences*, *58*(2). doi:10.3176/earth.2009.2.03

Heiri, O., & Lotter, A.F. (2010). How does taxonomic resolution affect chironomid-based temperature reconstruction?. *Journal of Paleolimnology*, *44*, pp. 589-601. https://doi.org/10.1007/s10933-010-9439-z

Heiri, O., Brooks, S.J., Birks, H.J.B., & Lotter, A.F. (2011). A 274-lake calibration data-set and inference model for chironomid-based summer air temperature reconstruction in Europe. Quaternary Science Reviews, 30(23-24), 3445-3456. https://doi.org/10.1016/j.quascirev.2011.09.006

Henrikson, B. I. (1993). Sphagnum mosses as a microhabitat for invertebrates in acidified lakes and the colour adaptation and substrate preference in Leucorrhinia dubia (Odonata, Anisoptera). *Ecography*, *16*(2), 143-153.

Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers, D., Simmons, A., Soci, C., Abdalla, S., Abellan, X., Balsamo, G., Bechtold, P., Biavati, G., Bidlot, G., Bonavita, M., …, Thépaut, J.N. (2020). The ERA5 global reanalysis. *Quarterly journal of the royal meteorological society*, *146*(730), 1999-2049.

Herzog, Q., Tittgen, C., & Laforsch, C. (2016). Predator-specific reversibility of morphological defenses in Daphnia barbata. *Journal of Plankton Research*, *38*(4), 771-780. https://doi.org/10.1093/plankt/fbw045

Hessen, D. O., Faafeng, B.A., & Andersen, T. (1995) "Competition or niche segregation between Holopedium and Daphnia; empirical light on abiotic key parameters." In *Cladocera as Model Organisms in Biology: Proceedings of the Third International Symposium on Cladocera, held in Bergen, Norway, 9–16 August 1993* (pp. 253-261). Springer Netherlands.

Hessen, D.O., Faafeng, B.A., Smith, V.H., Bakkestuen, V., & Walseng, B. (2006). Extrinsic and intrinsic controls of zooplankton diversity in lakes. *Ecology*, *87*(2), 433-443. https://doi.org/10.1890/05-0352

Hiiemäe, R. (2024). Environmental folklore as a vernacular code of sustainability: the case of Estonian lakes. *Journal of Environmental Studies and Sciences*, 1-12. https://doi.org/10.1007/s13412-024-00974-6

Hofmann, W. (1998). Cladocerans and chironomids as indicators of lake level changes in north temperate lakes. *Journal of Paleolimnology*, *19*, 55-62. https://doi.org/10.1023/A:1007999419765

Hupfer, M., & Lewandowski, J. (2008). Oxygen controls the phosphorus release from lake sediments–a long-lasting paradigm in limnology. *International Review of Hydrobiology*, *93*(4-5), 415-432. https://doi.org/10.1002/iroh.200711054

Jackson, D.A. (1993). Stopping rules in principal components analysis: a comparison of heuristical and statistical approaches. Ecology, 74(8), 2204-2214. https://doi.org/10.2307/1939574

Jansons, E. (1997), Rīgas dzeramais ūdens un tā resursu aizsardzība. Baltezeru un to apkaimes izpēte. Pārskats par 1995., 1996. un 1997. pirmajā pusgadā veikto pētījumu atskaitēm. Rīgas Ūdens.

Jensen, T.C., Zawiska, I., Oksman, M., Słowiński, M., Woszczyk, M., Luoto, T.P., Tylmann, W., Nevalainen, L., Obremska, M., Schartau, A.K., & Walseng, B. (2020). Historical human impact on productivity and biodiversity in a subalpine oligotrophic lake in Scandinavia. *Journal of Paleolimnology*, *63*, 1-20. https://doi.org/10.1007/s10933-019-00100-5

Jeppesen, E., Madsen, E.A., Jensen, J.P., & Anderson, N. (1996). Reconstructing the past density of planktivorous fish and trophic structure from sedimentary zooplankton fossils: a surface sediment calibration data set from shallow lakes. *Freshwater Biology*, *36*(1), 115-127. https://doi.org/10.1046/j.1365-2427.1996.00085.x

Jeppesen, E., Søndergaard, M., Jensen, J.P., Mortensen, E., Hansen, A.M., & Jørgensen, T. (1998). Cascading trophic interactions from fish to bacteria and nutrients after reduced sewage loading: an 18-year study of a shallow hypertrophic lake. *Ecosystems*, *1*(3), 250-267. https://doi.org/10.1007/s100219900020

Jeppesen, E., Peder Jensen, J., SØndergaard, M., Lauridsen, T., & Landkildehus, F., (2000). Trophic structure, species richness and biodiversity in Danish lakes: changes along a phosphorus gradient. *Freshwater biology*, *45*(2), 201-218. https://doi.org/10.1046/j.1365-2427.2000.00675.x

Jeppesen, E., Leavitt, P., De Meester, L. & Jensen, J.P. (2001). Functional ecology and palaeolimnology: using cladoceran remains to reconstruct anthropogenic impact. *Trends in Ecology & Evolution*, *16*(4), 191-198.

Jeppesen, E., Moss, B., Bennion, H., Carvalho, L., DeMeester, L., Feuchtmayr, H., Friberg, N., Gessner, M.O., Hefting, M., Lauridsen, T.L., & Liboriussen, L., (2010). Interaction of climate change and eutrophication. In M. Kernan, R.W. Battarbee & B.R. Moss (Eds.) *Climate change impacts on freshwater ecosystems* (pp. 119-151). Blackwell Publishing Ltd.

Jeziorski, A., Tanentzap, A.J., Yan, N.D., Paterson, A.M., Palmer, M.E., Korosi, J.B., Rusak, J.A., Arts, M.T., Keller, W., Ingram, R., Cairns, A., & Smol, J.P. (2015). The jellification of north temperate lakes. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1798), 20142449. https://doi.org/10.1098/rspb.2014.2449

Jeziorski, A., & Smol, J.P. (2017). The ecological impacts of lakewater calcium decline on softwater boreal ecosystems. *Environmental Reviews*, *25*(2), 245-253. https://doi.org/10.1139/er-2016-0054

Johnsen, G.H., & Raddum, G.G. (1987). A morphological study of two populations of Bosmina longispina exposed to different predation. *Journal of plankton research*, *9*(2), 297-304. https://doi.org/10.1093/plankt/9.2.297

Jones, R.I. (1992). The influence of humic substances on lacustrine planktonic food chains. *Hydrobiologia*, *229*, 73-91. https://doi.org/10.1007/BF00006992

Jones, I.D., & Smol, J.P. (2024). *Wetzel's limnology, lake and river ecosystems*. Elsevier.

Juggins, S. (2013). Quantitative reconstructions in palaeolimnology: new paradigm or sick science?. *Quaternary Science Reviews*, *64*, 20-32. https://doi.org/10.1016/j.quascirev.2012.12.014

Juggins, S., Anderson, N.J., Hobbs, J.M.R., & Heathcote, A.J. (2013). Reconstructing epilimnetic total phosphorus using diatoms: statistical and ecological constraints. *Journal of Paleolimnology*, *49*, 373-390. https://doi.org/10.1007/s10933-013-9678-x

Juggins, S. (2022). "rioja: Analysis of Quaternary Science Data." R package version 1.0-5. https://cran.r-project.org/package=rioja.

Kalinowska, K., & Karpowicz, M. (2020). Ice-on and ice-off dynamics of ciliates and metazooplankton in the Łuczański Canal (Poland). *Aquatic Ecology*, *54*(4), 1121-1134. https://doi.org/10.1007/s10452-020-09797-3

Kamenik, C., Szeroczyńska, K., & Schmidt, R. (2007). Relationships among recent Alpine Cladocera remains and their environment: implications for climate-change studies. *Hydrobiologia*, *594*, 33-46.

Karpowicz, M., Ejsmont-Karabin, J., Kozłowska, J., Feniova, I., & Dzialowski, A.R. (2020). Zooplankton community responses to oxygen stress. *Water*, *12*(3), 706. https://doi.org/10.3390/w12030706

Karpowicz, M., & Ejsmont-Karabin, J. (2021). Diversity and structure of pelagic zooplankton (Crustacea, Rotifera) in NE Poland. Water, 13(4), 456. https://doi.org/10.3390/w13040456

Karpowicz, M., Grabowska, M., Ejsmont-Karabin, J., & Ochocka, A. (2023). Humic lakes with inefficient and efficient transfer of matter in planktonic food webs. *Scientific Reports*, *13*(1), 7913.

Kattel, G.R., Battarbee, R.W., Mackay, A.W., & Birks, H.J.B. (2008). Recent ecological change in a remote Scottish mountain loch: an evaluation of a Cladocera-based temperature transfer-function. Palaeogeography, Palaeoclimatology, Palaeoecology, 259(1), 51-76. https://doi.org/10.1016/j.palaeo.2007.03.052

Kaushal, S.S., Likens, G.E., Pace, M.L., Reimer, J.E., Maas, C.M., Galella, J.G., Utz, R.M., Duan, S., Kryger, J.R., Yaculak, A.M., Boger, W.L., Bailey, N.V., Haq, S., Wood, K.L., Wessel, B.M., Park, C.E., Collison, D.C., Aisin, B.Y.I., …, Woglo, S.A. (2021). Freshwater salinization syndrome: from emerging global problem to managing risks. *Biogeochemistry*, *154*, 255-292.

Keskkonnainvesteeringute keskus (2024). https://register.metsad.ee/#/

Keskkonnaseire infosüsteem (2024). Programm: Väikejärvede seire. https://kese.envir.ee/kese/listParameterValueNew.action (accessed: 24.05.2024)

Kleiven, O.T., Larsson, P., & Hobæk, A. (1992). Sexual reproduction in Daphnia magna requires three stimuli. *Oikos*, 197-206. https://doi.org/10.2307/3545010

Klemetsen, A., Aase, B.M., & Amundsen, P.A. (2020). Diversity, abundance, and life histories of littoral chydorids (Cladocera: Chydoridae) in a subarctic European lake. *The Journal of Crustacean Biology*, *40*(5), 534-543. https://doi.org/10.1093/jcbiol/ruaa048

Koch, U., Von Elert, E., & Straile, D. (2009). Food quality triggers the reproductive mode in the cyclical parthenogen Daphnia (Cladocera). *Oecologia*, *159*, 317-324. https://doi.org/10.1007/s00442-008-1216-6

Kolar, C.S., & Wahl, D.H. (1998). Daphnid morphology deters fish predators. *Oecologia*, *116*, 556-564. https://doi.org/10.1007/s004420050621

Korhola, A., Olander, H., & Blom, T. (2000). Cladoceran and chironomid assemblages as qualitative indicators of water depth in subarctic Fennoscandian lakes. *Journal of Paleolimnology*, *24*, 43-54. https://doi.org/10.1023/A:1008165732542

Korhola, A., & Rautio M. (2001). Cladocera and other branchiopod crustaceans. In J. P. Smol, H.J.B. Birks & W.M. Last (Eds.)*Tracking environmental change using lake sediments, Volume 4, Zoological indicators* (pp. 5-42). Kluwer academic Publishers.

Korhola, A., Tikkanen, M., & Weckström, J. (2005). Quantification of Holocene lake-level changes in Finnish Lapland using a cladocera–lake depth transfer model. *Journal of Paleolimnology*, *34*, 175-190. https://doi.org/10.1007/s10933-005-1839-0

Kornijów, R. (2023). Lake aging concept revisited: alternative comprehensive approach to lake ontogeny. *Canadian Journal of Fisheries and Aquatic Sciences*, *80*(8), 1385-1393. https://doi.org/10.1139/cjfas-2023-0027

Kornijów, R. (2024). Eutrophication and derivative concepts. Origins, compatibility and unresolved issues. *Ecohydrology & Hydrobiology*, *24*(2), 289-298. https://doi.org/10.1016/j.ecohyd.2023.07.001

Korosi, J.B., & Smol, J.P. (2012). Contrasts between dystrophic and clearwater lakes in the long-term effects of acidification on cladoceran assemblages. *Freshwater Biology*, *57*(12), 2449-2464. https://doi.org/10.1111/fwb.12012

Korosi, J.B., Kurek, J., & Smol, J.P. (2013). A review on utilizing Bosmina size structure archived in lake sediments to infer historic shifts in predation regimes. *Journal of plankton research*, *35*(2), 444-460. https://doi.org/10.1093/plankt/fbt007

Korponai, J. L., Kövér, C., López-Blanco, C., Gyulai, I., Forró, L., Katalinic, A., Ketola, M., Nevalainen, L., Luoto, T.P., Sarmaja-Korjonen, K., Magyar, E.K., Weckström, J., Urák, I., Vadkerti, E. & Buczkó, K. (2020). Effect of temperature on the size of sedimentary remains of littoral chydorids. *Water*, *12*(5), 1309.

Köster, D., & Pienitz, R. (2006). Seasonal diatom variability and paleolimnological inferences–a case study. *Journal of Paleolimnology*, *35*, 395-416. https://doi.org/10.1007/s10933-005-1334-7

Kotov, A.A. (2007). Jurassic Cladocera (Crustacea, Branchiopoda) with a description of an extinct Mesozoic order. *Journal of Natural History*, *41*(1-4), 13-37. https://doi.org/10.1080/00222930601164445

Kotov, A.A., Ishida, S., & Taylor, D.J. (2009). Revision of the genus Bosmina (Cladocera: Bosminidae), based on evidence from male morphological characters and molecular phylogenies. *Zoological Journal of the Linnean Society*, *156*(1), 1-51. https://doi.org/10.1111/j.1096-3642.2008.00475.x

Krause-Dellin, D., & Steinberg, C. (1986). Cladoceran remains as indicators of lake acidification. *Hydrobiologia*, *143*(1), 129-134. https://doi.org/10.1007/BF00026655

Krutofala, T., & Levins, I. (2006). Pazemes ūdeņu Atradnes “Baltezers”, Iecirkņa “Akoti” Pase. Pazemes ūdeņu Ekspluatācijas Krājumu Novērtējums. Atradne “Baltezers”, iecirknis “Akoti”. Gruntsūdens Horizonts; Latvijas Vides, ģeoloģijas un Meteoroloģijas Aģentūra: Rīga, Latvija.

Krztoń, W., & Kosiba, J. (2020). Variations in zooplankton functional groups density in freshwater ecosystems exposed to cyanobacterial blooms. *Science of the Total Environment*, *730*, 139044. https://doi.org/10.1016/j.scitotenv.2020.139044

Kuczyńska-Kippen, N.M., & Nagengast, B. (2006). The influence of the spatial structure of hydromacrophytes and differentiating habitat on the structure of rotifer and cladoceran communities. *Hydrobiologia*, *559*, 203-212. https://doi.org/10.1007/s10750-005-0867-0

Kuczyńska-Kippen, N. (2008). Spatial distribution of zooplankton communities between the Sphagnum mat and open water in a dystrophic lake. *Polish Journal of Ecology*, *56*(1), 57.

Kultti, S., Nevalainen, L., Luoto, T.P., & Sarmaja-Korjonen, K. (2011). Subfossil chydorid (Cladocera, Chydoridae) ephippia as paleoenvironmental proxies: evidence from boreal and subarctic lakes in Finland. *Hydrobiologia*, *676*, 23-37. https://doi.org/10.1007/s10750-011-0869-z

Kuptsch, P (1927) Die Cladoceren der Umgegend von Riga. *Arch. Hydrobiol.*, *18*, 273–315.

Kurbatova, S.A., & Yershov, I.Y. (2009). Crustaceans and rotifers in the predatory feeding of Utricularia. *Inland Water Biology*, *2*, 271-275. https://doi.org/10.1134/S1995082909030122

Kurek, J., Korosi, J.B., Jeziorski, A., & Smol, J.P. (2010). Establishing reliable minimum count sizes for cladoceran subfossils sampled from lake sediments. *Journal of Paleolimnology*, *44*, 603-612. https://doi.org/10.1007/s10933-010-9440-6

Latvijas Ezeri (2010). https://www.ezeri.lv/database/

Laureto, L.M.O., Cianciaruso, M.V., & Samia, D.S.M. (2015). Functional diversity: an overview of its history and applicability. *Natureza & Conservação*, *13*(2), 112-116. https://doi.org/10.1016/j.ncon.2015.11.001

Le Moal, M., Gascuel-Odoux, C., Ménesguen, A., Souchon, Y., Étrillard, C., Levain, A., Moatar, F., Pannard, A., Souchu, P., Lefebvre, A., & Pinay, G (2019). Eutrophication: a new wine in an old bottle?. *Science of the total environment*, 651, 1-11. https://doi.org/10.1016/j.scitotenv.2018.09.139

Lemke, M. A., Lemke, M.J., & Benke, A.C. (2007). Importance of detrital algae, bacteria, and organic matter to littoral microcrustacean growth and reproduction. *Limnology and Oceanography*, *52*(5), 2164-2176.

Leppänen, J.J., & Weckström, J. (2016). Varying degradation of subfossil Daphnia longispina during the past 250 years and the discovery of fossil helmet-type head shields: preliminary results. *Advances in Oceanography and Limnology*, *7*(2). https://doi.org/10.4081/aiol.2016.6293

Lewis, J.L., Mattes, B.M., Yates, E.K., Palmer, E., Johansen, J.R., & Relyea, R.A. (2025). Nutrient inputs in mesocosms of an oligotrophic lake fail to sustain an algal bloom. *Ecosphere*, *16*(2). https://doi.org/10.1002/ecs2.70175

Līcīte, V. (2017a). ES nozīmes ūdeņu biotopu inventarizācijas anketa, Velnezers. 4 September 2017. 17VL008_59_1, Dabas Aizsardzības Pārvalde, Sigulda.

Līcīte, V. (2017b). ES nozīmes ūdeņu biotopu inventarizācijas anketa, Sekšu ezers. 16 September 2017. 17VL008_73_1, Dabas Aizsardzības Pārvalde, Sigulda.

Lieder, U. (1996). *Crustacea, Cladocera/Bosminidae*. Germany, Gustav Fischer Verlag.

Liiv, M., Alliksaar, T., Freiberg, R., Heinsalu, A., Ott, I., Reitalu, T., Tõnno, I., Vassiljev, J., & Veski, S. (2018). Drastic changes in lake ecosystem development as a consequence of flax retting: a multiproxy palaeolimnological study of Lake Kooraste Linajärv, Estonia. *Vegetation History and Archaeobotany*, *27*, 437-451. https://doi.org/10.1007/s00334-017-0650-y

Locke, A., & Sprules, W. G. (2000). Effects of acidic pH and phytoplankton on survival and condition of Bosmina longirostris and Daphnia pulex. *Hydrobiologia*, *437*, 187-196.

López, M.O.A., Montesinos López, M.A., & Crossa, J. (2022). *Multivariate statistical machine learning methods for genomic prediction*. Springer Nature.

Loreau, M., & De Mazancourt, C. (2013). Biodiversity and ecosystem stability: a synthesis of underlying mechanisms. *Ecology letters*, *16*, 106-115. https://doi.org/10.1111/ele.12073

Lotter, A.F., Birks, H.J.B., Hofmann, & W., Marchetto, A. (1997). Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. I. Climate. *Journal of Paleolimnology* 18, 395-420. https://doi.org/10.1023/A:1007982008956

Lotter, A.F., Birks, H.J.B., Hofmann, W., & Marchetto, A. (1998). Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. *Journal of Paleolimnology*, *19*, 443-463. https://doi.org/10.1023/A:1007994206432

Luoto, T.P., Oksman, M., & Ojala, A.E. (2015). Climate change and bird impact as drivers of High Arctic pond deterioration. *Polar Biology*, *38*, 357-368. https://doi.org/10.1007/s00300-014-1592-9

LVĢMC (2015). Daugavas upju baseinu apgabala apsaimniekošanas plāns 2016.-2021. gadam. Rīga, 218 pp.

LVĢMC (2022). Virszemes ūdeņu tipi, references apstākļi, ūdensobjektu grupēšana [WWW document]. URL:https://videscentrs.lvgmc.lv/files/Udens/UBA_2022_2027/Daugavas%20UBAP%202022-2027%20pielikumi/II%20nodalas%20pielikumi/2.4.1.a%20piel.%20Udenu%20tipologija.pdf (accessed 08.05.2025).

Lyman, R.L. (2017). Paleoenvironmental reconstruction from faunal remains: ecological basics and analytical assumptions. *Journal of Archaeological Research*, *25*, 315-371. https://doi.org/10.1007/s10814-017-9102-6

Maberly, S.C. (1996). Diel, episodic and seasonal changes in pH and concentrations of inorganic carbon in a productive lake. *Freshwater Biology*, *35*(3), 579-598. https://doi.org/10.1111/j.1365-2427.1996.tb01770.x

Makohonienko, M., Płóciennik, M., Papiernik, P., Kittel, P., Gałka, M., Mroczkowska, A., Apolinarska, K., Okupny, D., Panfil, M., Kotrys, B., Luoto, T.P., Krąpiec, M., & Tyszkowski, S. (2023). Environmental changes during mesolithic-neolithic transition in kuyavia lakeland, central poland. *Quaternary International*, *644*, 196-221. https://doi.org/10.1016/j.quaint.2021.11.020

Martinsen, K.T., Zak, N.B., Baastrup-Spohr, L., Kragh, T., & Sand-Jensen, K. (2022). Ecosystem metabolism and gradients of temperature, oxygen and dissolved inorganic carbon in the littoral zone of a macrophyte-dominated lake. *Journal of Geophysical Research: Biogeosciences*, *127*(12).

Matthews, J.A., & Briffa, K.R. (2005). The 'Little Ice Age': re-evaluation of an evolving concept. *Geografiska Annaler: Series A, Physical Geography*, *87*(1), pp.17-36.

Mauri, A., Davis, B.A., Collins, P.M., & Kaplan, J.O. (2015). The climate of Europe during the Holocene: a gridded pollen-based reconstruction and its multi-proxy evaluation. *Quaternary Science Reviews*, *112*, 109-127. https://doi.org/10.1016/j.quascirev.2015.01.013

McGill, B.J., Enquist, B.J., Weiher, E., & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends in ecology & evolution*, *21*(4), 178-185.

Meadows, J., & Zunde, M. (2014). A lake fortress, a floating chronology, and an atmospheric anomaly: the surprising results of a radiocarbon wiggle-match from Āraiši, Latvia. *Geochronometria*, *41*, 223-233.

Meerhoff, M., Audet, J., Davidson, T.A., De Meester, L., Hilt, S., Kosten, S., Liu, Z., Mazzeo, N., Paerl, H., Scheffer, M., & Jeppesen, E. (2022). Feedback between climate change and eutrophication: revisiting the allied attack concept and how to strike back. *Inland Waters*, *12*(2), 187-204. https://doi.org/10.1080/20442041.2022.2029317

Meier, H.M., Kniebusch, M., Dieterich, C., Gröger, M., Zorita, E., Elmgren, R., Myrberg, K., Ahola, M.P., Bartosova, A., Bonsdorff, E., Börgel, F., Capell, R., Carlén, I., Carlund, T., Carstensen, J., Christensen, O.B., Dierschke, V., Frauen, C., Frederiksen, M., ..., Zhang, W. (2022). Climate change in the Baltic Sea region: a summary. *Earth System Dynamics*, *13*(1), 457-593.

Mikalauskienė, R., Mažeika, J., Jefanova, O., & Szwarczewski, P. (2015). Investigation of the recent sediment mass acumulation rates in the Baltic upland lakes. Proceedings of the 3rd international conference on Po and radioactive Pb isotopes. 11-14 October. Kusadasi/Turkey.

Military topographic map (1908). Военно-топографическая карта 1908 (1 verst) [map] URL〈https://vesture.dodies.lv/#m=15/56.97800/24.25077&l=O/7〉 (Accessed 14 March 2024).

Moss, B., Kosten, S., Meerhoff, M., Battarbee, R.W., Jeppesen, E., Mazzeo, N., Havens, K., Lacerot, G., Liu, Z., De Meester, L., Paerl, H., & Scheffer, M. (2011). Allied attack: climate change and eutrophication. *Inland waters*, *1*(2), 101-105.

Murphy, K.J. (2002). Plant communities and plant diversity in softwater lakes of northern Europe. *Aquatic botany*, *73*(4), 287-324. https://doi.org/10.1016/S0304-3770(02)00028-1

Mustonen, T., & Huusari, N. (2020). How to know about waters? Finnish traditional knowledge related to waters and implications for management reforms. *Reviews in Fish Biology and Fisheries*, *30*(4), 699-718. https://doi.org/10.1007/s11160-020-09619-7

Naderian, D., Noori, R., Kim, D., Jun, C., Bateni, S.M., Woolway, R.I., Sharma, S., Shi, K., Qin, B., Zhang, Y., Jeppesen, E., & Maberly, S.C. (2025). Environmental controls on the conversion of nutrients to chlorophyll in lakes. *Water Research*, *274*, 123094. https://doi.org/10.1016/j.watres.2025.123094

NARA, 1940. 1940 NARA Aerophoto. [map] URL https://vesture.dodies.lv/#m=15/56.97800/24.25077&l=O/N (accessed 3.14.24)

Nevalainen, L. (2010). Evaluation of microcrustacean (Cladocera, Chydoridae) biodiversity based on sweep net and surface sediment samples. *Ecoscience*, *17*(4), 356-364. https://doi.org/10.2980/17-4-3364

Nevalainen, L. (2011). Intra-lake heterogeneity of sedimentary cladoceran (Crustacea) assemblages forced by local hydrology. *Hydrobiologia*, *676*(1), 9-22. https://doi.org/10.1007/s10750-011-0707-3

Nevalainen, L., Sarmaja-Korjonen, K., & Luoto, T.P. (2011). Sedimentary Cladocera as indicators of past water-level changes in shallow northern lakes. *Quaternary Research*, *75*(3), 430-437. https://doi.org/10.1016/j.yqres.2011.02.007

Nevalainen, L., Helama, S., & Luoto, T.P. (2013). Hydroclimatic variations over the last millennium in eastern Finland disentangled by fossil Cladocera. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *378*, 13-21. https://doi.org/10.1016/j.palaeo.2013.03.016

Nevalainen, L., & Rautio, M. (2014). Spectral absorbance of benthic cladoceran carapaces as a new method for inferring past UV exposure of aquatic biota. *Quaternary Science Reviews*, *84*, 109-115. https://doi.org/10.1016/j.quascirev.2013.11.020

Nevalainen, L., & Luoto, T.P. (2017). Relationship between cladoceran (Crustacea) functional diversity and lake trophic gradients. *Functional Ecology*, *31*(2), 488-498. https://doi.org/10.1111/1365-2435.12737

Nickus, U., Bishop, K., Erlandsson, M., Evans, C.D., Forsius, M., Laudon, H., Livingstone, D.M., Monteith, D., & Thies, H. (2010). Direct impacts of climate change on freshwater ecosystems. in Kernan, M., Battarbee, R. W., Moss, B. R. (ed.) *Climate change impacts on freshwater ecosystems* (pp. 119-151). Chichester: Blackwell Publishing Ltd.

Nikodemus, O., Kļaviņš, M., Krišjāne, Z., & Zelčs, V.(2018). Latvija, zeme, daba, tauta. Latvijas Universitātes akadēmiskais apgāds.

Nock, C.A., Vogt, R.J., & Beisner, B.E. (2016). Functional traits. *eLS*, *1*, 1-8.

Nürnberg, G. K. (1996). Trophic state of clear and colored, soft-and hardwater lakes with special consideration of nutrients, anoxia, phytoplankton and fish. *Lake and Reservoir Management*, *12*(4), 432-447. https://doi.org/10.1080/07438149609354283

Nürnberg, G. K., & Shaw, M. (1998). Productivity of clear and humic lakes: nutrients, phytoplankton, bacteria. *Hydrobiologia*, *382*, 97-112. https://doi.org/10.1023/A:1003445406964

O'Sullivan, P.E., & Reynolds, C.S. (2004). *The lakes handbook, Volume I, Limnology and limnetic ecology*. Blackwell publishing.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., & Weedon, J. (2022). _vegan: Community Ecology Package_. R package version 2.6-4, https://CRAN.R-project.org/package=vegan

Packard, A.T. (2001). Clearance rates and prey selectivity of the predaceous cladoceran Polyphemus pediculus. *Hydrobiologia*, *442*, 177-184. https://doi.org/10.1023/A:1017582323631

Padhye, S., & Kotov, A.A. (2010). Cladocera (Crustacea: Branchiopoda) in Indian hot water springs. *Invertebrate Zoology*, *7*(1), 155-158.

Pannard, A., Souchu, P., Chauvin, C., Delabuis, M., Gascuel-Odoux, C., Jeppesen, E., Le Moal, M., Ménesguen, A., Pinay, G., Rabalais, N.N., & Souchon, Y. (2024). Why are there so many definitions of eutrophication?. *Ecological monographs*, *94*(3). https://doi.org/10.1002/ecm.1616

Parparov, A., & Gal, G. (2017). Quantifying ecological stability: from community to the lake ecosystem. *Ecosystems*, *20*(5), 1015-1028. https://doi.org/10.1007/s10021-016-0090-z

Pawlikiewicz, P., & Jurasz, W. (2017), November. Ecological drivers of cladoceran diversity in the central European city (Łódź, Poland): effects of urbanisation and size of the waterbody. In *Annales Zoologici Fennici 54(5-6),* 315-333. https://doi.org/10.5735/086.054.0504

Pijanowska, J. (1990). Cyclomorphosis in Daphnia: an adaptation to avoid invertebrate predation. *Hydrobiologia*, *198*, 41-50. https://doi.org/10.1007/BF00048621

Pijanowska, J., & Kowalczewski, A. (1997.) Predators can induce swarming behaviour and locomotory responses in Daphnia. *Freshwater Biology*, *37*(3), 649-656. https://doi.org/10.1046/j.1365-2427.1997.00192.x

Pinel-Alloul, B., Patoine, A., & Marty, J. (2021). Multi-scale and multi-system perspectives of zooplankton structure and function in Canadian freshwaters. *Canadian Journal of Fisheries and Aquatic Sciences*, *78*(10), 1543-1562. https://doi.org/10.1139/cjfas-2020-0474

Punning, J.M., Boyle, J.F., Terasmaa, J., Vaasma, T., & Mikomägi, A. (2007). Changes in lake-sediment structure and composition caused by human impact: repeated studies of Lake Martiska, Estonia. *The Holocene*, *17*(1), 145-151.

Pujate, A., 2015. Vides apstākļu izmaiņu un cilvēka darbības pēdas Rīgas līča piekrastes ezeru nogulumos [Traces of environmental change and human impact in the sediments of lakes along the coast of the gulf of Riga]. Doctoral thesis. University of Latvia.

Qin, B., Zhou, J., Elser, J.J., Gardner, W.S., Deng, J., & Brookes, J.D. (2020). Water depth underpins the relative roles and fates of nitrogen and phosphorus in lakes. *Environmental Science & Technology*, *54*(6), 3191-3198. https://doi.org/10.1021/acs.est.9b05858

Radosavljevic, J., Slowinski, S., Shafii, M., Akbarzadeh, Z., Rezanezhad, F., Parsons, C.T., Withers, W., & Van Cappellen, P. (2022). Salinization as a driver of eutrophication symptoms in an urban lake (Lake Wilcox, Ontario, Canada). *Science of the Total Environment*, *846*, 157336.

Rattray, M.R., Howard-Williams, C., & Brown, J.M.A. (1991). Sediment and water as sources of nitrogen and phosphorus for submerged rooted aquatic macrophytes. *Aquatic Botany*, *40*(3), 225-237. https://doi.org/10.1016/0304-3770(91)90060-I

Rautio, M., & Nevalainen, L. (2025). Cladocera. In S. Elias (Ed.) *Encyclopedia of Quaternary science, 3rd Edition* (pp. 280-291). Volume 4, Elsevier. https://doi.org/10.1016/B978-0-323-99931-1.00256-7

Renssen, H., Seppä, H., Crosta, X., Goosse, H., & Roche, D.M. (2012). Global characterization of the Holocene thermal maximum. *Quaternary Science Reviews*, *48*, 7-19. https://doi.org/10.1016/j.quascirev.2012.05.022

Reynaud, A., & Lanzanova, D. (2017). A global meta-analysis of the value of ecosystem services provided by lakes. *Ecological Economics*, *137*, 184-194. https://doi.org/10.1016/j.ecolecon.2017.03.001

Reynolds, C., & Cumming, G.S. (2015). The role of waterbirds in the dispersal of freshwater cladocera and bryozoa in southern Africa. *African Zoology*, *50*(4), 307-311. https://doi.org/10.1080/15627020.2015.1108164

Reynolds, S.A., & Aldridge, D.C. (2021). Global impacts of invasive species on the tipping points of shallow lakes. *Global Change Biology*, *27*(23), 6129-6138. https://doi.org/10.1111/gcb.15893

Rhode, S.C., Pawlowski, M., & Tollrian, R. (2001). The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus Daphnia. *Nature*, *412*(6842), 69-72. https://doi.org/10.1038/35083567

Richter, G., & Baszio, S. (2001). First proof of planctivory/insectivory in a fossil fish: Thaumaturus intermedius from the Eocene Lake Messel (FRG). *Palaeogeography, Palaeoclimatology, Palaeoecology*, *173*(1-2), 75-85. https://doi.org/10.1016/S0031-0182(01)00318-2

Ridgeway, G., & Developers, G. (2024). _gbm: Generalized Boosted Regression Models_. R package version 2.2.2, https://CRAN.R-project.org/package=gbm

Rose, N.L. (1990). A method for the selective removal of inorganic ash particles from lake sediments. *Journal of Paleolimnology*, *4*, 61-67. https://doi.org/10.1007/BF00208299

Rose, K.C. (2024). Light in inland waters. In I.D. Jones & J.P. Smol (Eds.) *Wetzel's limnology, lake and river ecosystems* (pp. 75-94). Elsevier.

Rother, A., Pitsch, M., & Huelsmann, S. (2010). The importance of hatching from resting eggs for population dynamics and genetic composition of Daphnia in a deep reservoir. *Freshwater biology*, *55*(11), 2319-2331. https://doi.org/10.1111/j.1365-2427.2010.02441.x

Rõuk, A.M. (1992). Laminated sediments in Estonian Lakes – preliminary data. Geological survey of Finland. Special paper 14, 105-107.

Różańska-Boczula, M., & Sender, J. (2025). Exploring the relationships between macrophyte groups and environmental conditions in lake ecosystems. *Scientific Reports*, *15*(1), 11162. https://doi.org/10.1038/s41598-024-80553-5

Ruddiman, W.F., He, F., Vavrus, S.J., & Kutzbach, J.E., 2020. The early anthropogenic hypothesis: A review. *Quaternary Science Reviews*, *240*, 106386. https://doi.org/10.1016/j.quascirev.2020.106386

Rudna, M., Wojewódka-Przybył, M., Forysiak, J., Milecka, K., & Okupny, D. (2023). Cladocera Responses to the Climate-Forced Abrupt Environmental Changes Related to the Late Glacial/Holocene Transition. *Water*, *15*(2), 348. https://doi.org/10.3390/w15020348

Salonen, J.S., Luoto, M., Alenius, T., Heikkilä, M., Seppä, H., Telford, R.J., & Birks, H.J.B. (2014). Reconstructing palaeoclimatic variables from fossil pollen using boosted regression trees: comparison and synthesis with other quantitative reconstruction methods. *Quaternary Science Reviews*, *88*, 69-81. https://doi.org/10.1016/j.quascirev.2014.01.011

Sarmaja-Korjonen, K. (2001). Correlation of fluctuations in cladoceran planktonic: littoral ratio between three cores from a small lake in southern Finland: Holocene water-level changes. *The Holocene*, *11*(1), 53-63. https://doi.org/10.1191/095968301677071335

Sarmaja-Korjonen, K. (2007). Subfossil shell margins and tail spines of Daphnia in Finnish lake sediments-is Daphnia underrepresented in cladocera analysis?. *Studia Quaternaria*, 61-64.

Seidl, M.D., Paul, R.J., & Pirow, R. (2005). Effects of hypoxia acclimation on morpho-physiological traits over three generations of Daphnia magna. *Journal of experimental biology*, *208*(11), 2165-2175. https://doi.org/10.1242/jeb.01614

Seppä, H., & Poska, A. (2004). Holocene annual mean temperature changes in Estonia and their relationship to solar insolation and atmospheric circulation patterns. *Quaternary Research*, *61*(1), 22-31. https://doi.org/10.1016/j.yqres.2003.08.005

Seppä, H., Bjune, A.E., Telford, R.J., Birks, H.J.B., & Veski, S. (2009). Last nine-thousand years of temperature variability in Northern Europe. *Climate of the Past*, *5*(3), 523-535.

Shapiera, M., Jeziorski, A., Yan, N.D., & Smol, J.P. (2011). Calcium content of littoral Cladocera in three softwater lakes of the Canadian Shield. *Hydrobiologia*, *678*, 77-83. https://doi.org/10.1007/s10750-011-0824-z

Shapiro, S.S., & Wilk, M.B. (1965). An analysis of variance test for normality (complete samples). *Biometrika*, *52*(3-4), 591-611. https://www.jstor.org/stable/2333709

Siitonen, S., Väliranta, M., Weckström, J., Juutinen, S., & Korhola, A. (2011). Comparison of Cladocera-based water-depth reconstruction against other types of proxy data in Finnish Lapland. *Hydrobiologia*, *676*, 155-172. https://doi.org/10.1007/s10750-011-0885-z

Sinev, A.Y., & Gavrilko, D.E. (2021). Longitudinal gradient in the Camptocercus lilljeborgi Schoedler, 1862 species group (Cladocera: Anomopoda: Chydoridae). *Zootaxa*, *5047*(2), 123-138.

Smirnov, N.N. (2017). *Physiology of the Cladocera*. Elsevier Academic Press.

Smol, J.P., Cumming, B.F., Dixit, A.S., & Dixit, S.S. (1998). Tracking recovery patterns in acidified lakes: a paleolimnological perspective. *Restoration Ecology*, *6*(4), 318-326. https://doi.org/10.1046/j.1526-100X.1998.06402.x

Smol, J.P. (2010). The power of the past: using sediments to track the effects of multiple stressors on lake ecosystems. *Freshwater biology*, *55*, 43-59. https://doi.org/10.1111/j.1365-2427.2009.02373.x

Smol, J.P. (2019). Under the radar: long-term perspectives on ecological changes in lakes. *Proceedings of the Royal Society B*, *286*(1906), 20190834. https://doi.org/10.1098/rspb.2019.0834

Šolcová, A., Alahuhta, J., Gałka, M., Kolada, A., & Hájková, P. (2024). Developing a European aquatic macrophyte transfer function for reconstructing past lake-water chemistry. *Science of the Total Environment*, *954*, 176613. https://doi.org/10.1016/j.scitotenv.2024.176613

St. Pierre, J.I., & Kovalenko, K.E. (2014). Effect of habitat complexity attributes on species richness. *Ecosphere*, *5*(2), 1-10. https://doi.org/10.1890/ES13-00323.1

Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O. and Ludwig, C., 2015. The trajectory of the Anthropocene: the great acceleration. *The anthropocene review*, *2*(1), pp.81-98. https://doi.org/10.1177/2053019614564785

Stenert, C., Wüsth, R., Pires, M.M., Freiry, R.F., Nielsen, D., & Maltchik, L. (2017). Composition of cladoceran dormant stages in intermittent ponds with different hydroperiod lengths. *Ecological research*, *32*, 921-930. https://doi.org/10.1007/s11284-017-1498-4

Sterner, R.W., Elser, J.J., & Hessen, D.O. (1992). Stoichiometric relationships among producers, consumers and nutrient cycling in pelagic ecosystems. *Biogeochemistry*, *17*, 49-67. https://doi.org/10.1007/BF00002759

Stivrins, N., Grudzinska, I., Elmi, K., Heinsalu, A., & Veski, S. (2018). Determining reference conditions of hemiboreal lakes in Latvia, NE Europe: a palaeolimnological approach. In *Annales de Limnologie-International Journal of Limnology 54*, 22.

Stivrins, N., Trasune, L., Jasiunas, N., Kalnina, L., Briede, A., Maksims, A., Steinberga, D., Jeskins, J., Rendenieks, Z., Bikse, J., Kalvans, A., Lanka, A., Ozola, I., & Veski, S. (2022). Indicative value and training set of freshwater organic-walled algal palynomorphs (non-pollen palynomorphs). *Quaternary Science Reviews*, *282*, 107450. https://doi.org/10.1016/j.quascirev.2022.107450

Stivrins, N. (2023). Non-pollen palynomorphs from 78 surface sediment samples reveal spatial distribution of phytoplankton in Latvian lakes and ponds. *Estonian Journal of Earth Sciences*, *72*(2), 226-235. https://doi.org/10.3176/earth.2023.87

Suchora, M., Bober, A., Kultys, K., Zalat, A.A., Terpiłowski, S., Komadowska, K., Żarski, M., Boczkowska, J., Standzikowski, K., & Pidek, I.A. (2025). A comparative analysis of the palaeoecological and palaeohydrological records of two neighbouring Eemian lakes: Implications for palaeolake evolution in Central Poland. *CATENA*, *251*, 108814. https://doi.org/10.1016/j.catena.2025.108814

Sun, X.Y., Xia, X., & Yang, Q. (2016). Dating the origin of the major lineages of Branchiopoda. *Palaeoworld*, *25*(2), pp. 303-317.

Sun, P., Holden, P.B., & Birks, H.J.B. (2024). Can machine learning algorithms improve upon classical palaeoenvironmental reconstruction models?. *Climate of the Past Discussions*, *2024*, 1-27.

Suursaar, Ü., Torn, K., Mäemets, H., & Rosentau, A. (2024). Overview and evolutionary path of Estonian coastal lagoons. *Estuarine, Coastal and Shelf Science*, *303*, 108811. https://doi.org/10.1016/j.ecss.2024.108811

Sysoev, V.V., Ibragimova, A.G., Gololobova, M.A., Medeiros, A., Smol, J.P., & Kotov, A.A. (2025). Changes in size of key indicators used in palaeolimnological studies: A critical review. *Earth-Science Reviews*, 104995. https://doi.org/10.1016/j.earscirev.2024.104995

Szeroczyńska, K. (2002). Human impact on lakes recorded in the remains of Cladocera (Crustacea). *Quaternary International*, *95*, 165-174. https://doi.org/10.1016/S1040-6182(02)00037-X

Szeroczyńska, K., & Sarmaja-Korjonen, K. (2007). Atlas of subfossil Cladocera from central and northern Europe. Friends of the Lower Vistula Society.

Szpakowska, B., Świerk, D., Pajchrowska, M., & Gołdyn, R. (2021). Verifying the usefulness of macrophytes as an indicator of the status of small waterbodies. *Science of the Total Environment*, *798*, 149279. https://doi.org/10.1016/j.scitotenv.2021.149279

Taminskas, J., Pileckas, M., Šimanauskienė, R., & Linkevičienė, R. (2012). Wetland classification and inventory in Lithuania. *Baltica*, *25*(1), 33-44.

Tammeorg, O., Haldna, M., Nõges, P., Appleby, P., Möls, T., Niemistö, J., Tammeorg, P., & Horppila, J. (2018). Factors behind the variability of phosphorus accumulation in Finnish lakes. *Journal of Soils and Sediments*, *18*, 2117-2129. https://doi.org/10.1007/s11368-018-1973-8

Ter Braak, C. J. F., Juggins, S., Birks, H. J. B., & Van der Voet, H. (1993). Weighted averaging partial least squares regression (WA-PLS): definition and comparison with other methods for species-environment calibration. In *Multivariate environmental statistics* (No. 6, pp. 525-560). Elsevier.

Ter Braak, C.J.F., & Juggins, S. (1993). Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. Hydrobiologia, 269/270, 485-502.

Terasmaa, J. (2018). Estonia, the land of lakes. *Dynamiques environnementales. Journal international de géosciences et de l'environnement*, (42), 358-366. https://doi.org/10.4000/dynenviron.2504

Tessier, A.J. (1986). Comparative population regulation of two planktonic cladocera (Holopedium gibberum and Daphnia catawba). *Ecology*, *67*(2), 285-302. https://doi.org/10.2307/1938573

Tichá, A., Bešta, T., Vondrák, D., Houfková, P., & Jankovská, V. (2019). Nutrient availability affected shallow-lake ecosystem response along the Late-Glacial/Holocene transition. *Hydrobiologia*, *846*, 87-108. https://doi.org/10.1007/s10750-019-04054-7

Tollrian, R. (1995). Chaoborus crystallinus predation on Daphnia pulex: can induced morphological changes balance effects of body size on vulnerability?. *Oecologia*, *101*, 151-155. https://doi.org/10.1007/BF00317278

Tollrian, R., & Heibl, C. (2004). Phenotypic plasticity in pigmentation in Daphnia induced by UV radiation and fish kairomones. *Functional ecology*, *18*(4), 497-502. https://doi.org/10.1111/j.0269-8463.2004.00870.x

Tõnno, I., Agasild, H., Kõiv, T., Freiberg, R., Nõges, P., & Nõges, T. (2016). Algal diet of small-bodied crustacean zooplankton in a cyanobacteria-dominated eutrophic lake. *PloS one*, *11*(4), p.e0154526. https://doi.org/10.1371/journal.pone.0154526

Tóth, M., Van Hardenbroek, M., Bleicher, N., & Heiri, O. (2019). Pronounced early human impact on lakeshore environments documented by aquatic invertebrate remains in waterlogged Neolithic settlement deposits. *Quaternary Science Reviews*, *205*, 126-142. https://doi.org/10.1016/j.quascirev.2018.12.015

Tumurtogoo, U., Figler, A., Korponai, J., Sajtos, Z., Grigorszky, I., Berta, C., & Gyulai, I. (2022). Density and diversity differences of contemporary and subfossil cladocera assemblages: a case study in an oxbow lake. Water, 14(14), 2149. https://doi.org/10.3390/w14142149

Turner, M.G., Wei, D., Prentice, I.C., & Harrison, S.P. (2021). The impact of methodological decisions on climate reconstructions using WA-PLS. Quaternary Research, 99, 341-356. https://doi.org/10.1017/qua.2020.44

Tylmann, W., Bonk, A., Goslar, T., Wulf, S., & Grosjean, M. (2016). Calibrating 210Pb dating results with varve chronology and independent chronostratigraphic markers: problems and implications. *Quaternary Geochronology*, *32*, 1-10. https://doi.org/10.1016/j.quageo.2015.11.004

Üheverstane kaart (1911). [Map] URL: https://xgis.maaamet.ee/xgis2/page/app/ajalooline

Väliranta, M., Salonen, J.S., Heikkilä, M., Amon, L., Helmens, K., Klimaschewski, A., Kuhry, P., Kultti, S., Poska, A., Shala, S., Veski, S., & Birks, H.H (2015). Plant macrofossil evidence for an early onset of the Holocene summer thermal maximum in northernmost Europe. *Nature communications*, *6*(1), 6809. https://doi.org/10.1038/ncomms7809

Van Damme, K., & Kotov, A.A. (2016). The fossil record of the Cladocera (Crustacea: Branchiopoda): Evidence and hypotheses. *Earth-Science Reviews*, *163*, 162-189. https://doi.org/10.1016/j.earscirev.2016.10.009

Van Damme, K., & Nevalainen, L. (2019). The most latent cladoceran in the Holarctic revealed—sinking Unapertura Sarmaja-Korjonen, Hakojärvi & Korhola, 2000 into the genus Rhynchotalona Norman, 1903 (Branchiopoda: Cladocera: Chydoridae). Zootaxa 4613. https://doi.org/10.11646/zootaxa.4613.3.3

Vanderploeg, H.A., Ludsin, S.A., Cavaletto, J.F., Höök, T.O., Pothoven, S.A., Brandt, S.B., Liebig, J.R., & Lang, G.A. (2009). Hypoxic zones as habitat for zooplankton in Lake Erie: refuges from predation or exclusion zones?. *Journal of Experimental Marine Biology and Ecology*, *381*. https://doi.org/10.1016/j.jembe.2009.07.015

Velle, G., Brodersen, K.P., Birks, H.J.B., & Willassen, E. (2012). Inconsistent results should not be overlooked: A reply to Brooks et al.(2012). *The Holocene*, *22*(12), 1501-1508. https://doi.org/10.1177/0959683612449765

Veski, S., Heinsalu, A., Lang, V., Kestlane, Ü., & Possnert, G. (2004). The age of the Kaali meteorite craters and the effect of the impact on the environment and man: evidence from inside the Kaali craters, island of Saaremaa, Estonia. *Vegetation History and Archaeobotany*, *13*, 197-206. https://doi.org/10.1007/s00334-004-0043-x

Veski, S., Koppel, K., & Poska, A. (2005). Integrated palaeoecological and historical data in the service of fine-resolution land use and ecological change assessment during the last 1000 years in Rõuge, southern Estonia. *Journal of Biogeography*, *32*(8), 1473-1488. https://doi.org/10.1111/j.1365-2699.2005.01290.x

Veski, S., Heinsalu, A., Poska, A., & Seppä, H. (2010). Annually laminated lake sediment record from Rõuge Tõugjärv, southern Estonia − implications for paleoclimatic and palaeoenvironmental reconstructions. First workshop of the PAGES Varves working group, April 7-9, Palmse-Estonia, Programme and Abstracts.

Veski, S., Seppä, H., Stančikaitė, M., Zernitskaya, V., Reitalu, T., Gryguc, G., Heinsalu, A., Stivrins, N., Amon, L., Vassiljev, J., & Heiri, O. (2015). Quantitative summer and winter temperature reconstructions from pollen and chironomid data between 15 and 8 ka BP in the Baltic–Belarus area. *Quaternary International*, *388*, 4-11. https://doi.org/10.1016/j.quaint.2014.10.059

Visconti, A., Manca, M., & De Bernardi, R. (2008). Eutrophication-like response to climate warming: an analysis of Lago Maggiore (N. Italy) zooplankton in contrasting years. *Journal of Limnology*, *67*(2), 87.

Vogt, R.J., Matthews, B., Cobb, T.P., Graham, M.D., & Leavitt, P.R. (2013). Food web consequences of size-based predation and vertical migration of an invertebrate predator (Leptodora kindtii). *Limnology and Oceanography*, *58*(5), 1790-1801. https://doi.org/10.4319/lo.2013.58.5.1790

Walker, M., Head, M.J., Berkelhammer, M., Björck, S., Cheng, H., Cwynar, L., Fisher, D., Gkinis, V., Long, A., Lowe, J., Newnham, R., Rasmussen, S.O., & Weiss, G. (2018). "Formal ratification of the subdivision of the Holocene Series/Epoch (Quaternary System/Period): two new Global Boundary Stratotype Sections and Points (GSSPs) and three new stages/subseries." *Episodes Journal of International Geoscience* 41 (4), 213-223.

Walther, A., & Linderholm, H.W. (2006). A comparison of growing season indices for the Greater Baltic Area. *International Journal of Biometeorology*, *51*, 107-118. https://doi.org/10.1007/s00484-006-0048-5

Wang, S.C., Liu, X., Liu, Y., & Wang, H. (2020). Benthic-pelagic coupling in lake energetic food webs. *Ecological Modelling*, *417*, 108928. https://doi.org/10.1016/j.ecolmodel.2019.108928

Wang, Q., Hamilton, P.B., Xu, M., & Kattel, G. (2021). Comparison of boosted regression trees vs WA-PLS regression on diatom-inferred glacial-interglacial climate reconstruction in Lake Tiancai (southwest China). *Quaternary International*, *580*, 53-66.

Wang, W., Xiang, L., Li, Y., Suo, Q., Song, X., Zhang, Y., Huang, C., Muhammad, F., Wang, T., Ren, X., Chen, S., Chen, G., & Huang, X. (2024). Modern distribution of Cladocera in lakes of northern China and western Mongolia and its environmental implications. *Fundamental Research*. https://doi.org/10.1016/j.fmre.2024.09.004

Wanner, H., Pfister, C., & Neukom, R. (2022). The variable European little ice age. *Quaternary Science Reviews*, *287*, 107531. https://doi.org/10.1016/j.quascirev.2022.107531

Whiteside, M.C., & Harmsworth, R.V. (1967). Species diversity in chydorid (Cladocera) communities. *Ecology*, *48*(4), 664-667. https://doi.org/10.2307/1936514

Wilkinson, G. M., Carpenter, S. R., Cole, J. J., Pace, M. L., & Yang, C. (2013). Terrestrial support of pelagic consumers: patterns and variability revealed by a multilake study. *Freshwater Biology*, *58*(10), 2037-2049. https://doi.org/10.1111/fwb.12189

Williamson, C.E., Overholt, E.P., Pilla, R.M., Leach, T.H., Brentrup, J.A., Knoll, L.B., Mette, E.M., & Moeller, R.E. (2016). Ecological consequences of long-term browning in lakes. *Scientific reports*, *5*(1), 18666.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., & NCEAS Predicting Species Distributions Working Group (2008). Effects of sample size on the performance of species distribution models. *Diversity and distributions*, *14*(5), 763-773. https://doi.org/10.1111/j.1472-4642.2008.00482.x

Wojtal-Frankiewicz, A., Frankiewicz, P., Jurczak, T., Grennan, J., & McCarthy, T.K. (2010). Comparison of fish and phantom midge influence on cladocerans diel vertical migration in a dual basin lake. *Aquatic Ecology*, *44*, 243-254. https://doi.org/10.1007/s10452-009-9280-5

Womack, T., Slater, B.J., Stevens, L.G., Anderson, L.I., & Hilton, J. (2012). First cladoceran fossils from the Carboniferous: palaeoenvironmental and evolutionary implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *344*, 39-48. https://doi.org/10.1016/j.palaeo.2012.05.012

Woolway, R.I., Kraemer, B.M., Lenters, J.D., Merchant, C.J., O'Reilly, C.M., & Sharma, S. (2020). Global lake responses to climate change. *Nature Reviews Earth & Environment*, *1*(8), 388-403. https://doi.org/10.1038/s43017-020-0067-5

Wrzesiński, D., & Ptak, M. (2016). Water level changes in Polish lakes during 1976–2010. *Journal of Geographical Sciences*, *26*, 83-101. https://doi.org/10.1007/s11442-016-1256-5

Xu, X., Li, W., Fujibayashi, M., Nomura, M., Nishimura, O., & Li, X. (2015). Asymmetric response of sedimentary pool to surface water in organics from a shallow hypereutrophic lake: the role of animal consumption and microbial utilization. *Ecological Indicators*, *58*, 346-355. https://doi.org/10.1016/j.ecolind.2015.06.009

Yatigammana, S.K., & Cumming, B.F. (2017). Cladocera assemblages from reservoirs in Sri Lanka and their relationship to measured limnological variables. *Lakes & Reservoirs: Research & Management*, *22*(3), 247-261. https://doi.org/10.1111/lre.12183

Yıldız, D., Yalçın, G., Calderó-Pascual, M., Metin, M., Kavak, P., Dede, C., Spoljar, M., Gottstein, S., McCarthy, V., Nejstgaard, J.C., Jeppesen, E., Ger, K.A., & Beklioğlu, M. (2025). Allochthonous matter quality regulates functionality of lake zooplankton. *Hydrobiologia*, 1-23. https://doi.org/10.1007/s10750-024-05774-1

Young, S., & Taylor, V.A. (1988). Visually guided chases in Polyphemus pediculus. *Journal of Experimental Biology*, *137*(1), 387-398.

Zagars, M., Christoffersen, K.S., & Cremona, F. (2025). Lake food web structure in Teici Nature reserve, Latvia: fish presence shapes functioning of pristine bog lake food webs. *Hydrobiologia*, *852*(2), 323-339. https://doi.org/10.1007/s10750-024-05525-2

Zaret, T.M. (1972). Predators, invisible prey, and the nature of polymorphism in the cladocera (class Crustacea) 1. *Limnology and Oceanography*, *17*(2), 171-184. https://doi.org/10.4319/lo.1972.17.2.0171

Zawiska, I., Correa-Metrio, A., Rzodkiewicz, M., & Wolski, J. (2025). Cladocera assemblages indicate environmental gradients of lake productivity and morphometry in central Europe. *Boreas, 54*(2), 179-280. https://doi.org/10.1111/bor.70001

Zawisza, E., Zawiska, I., & Correa-Metrio, A. (2016). Cladocera community composition as a function of physicochemical and morphological parameters of dystrophic lakes in NE Poland. *Wetlands*, *36*, 1131-1142. https://doi.org/10.1007/s13157-016-0832-x

Zeileis, A., & Hothorn, T. (2002). Diagnostic Checking in Regression Relationships. R News 2(3), 7-10. URL https://CRAN.R-project.org/doc/Rnews/

Zhou, J., Leavitt, P.R., Zhang, Y., & Qin, B. (2022). Anthropogenic eutrophication of shallow lakes: is it occasional?. *Water Research*, *221*, p.118728. https://doi.org/10.1016/j.watres.2022.118728

Zohary, T., & Ostrovsky, I. (2011). Ecological impacts of excessive water level fluctuations in stratified freshwater lakes. *Inland waters*, *1*(1), 47-59. https://doi.org/10.5268/IW-1.1.406

Acknowledgements

Like most scientific works nowadays, my PhD thesis was not created in a vacuum of knowledge. Rather, it was built on the foundations of previously published works and the support of friends, colleagues, and strangers. For parts of my work, I must thank the help of countless people who spend hours developing open source software, creating tutorials, and helping other “people on the internet” with their code issues. Nevertheless, my greatest gratitude must be expressed to my support network of supervisors, colleagues (technical, data, moral, and knowledge support), friends, and financing providers. All of this would not have been possible without you. I appreciate every second you invested in my PhD journey.

I would like to thank all of my supervisors for their time, the knowledge and wisdom, the materials, and the technical expertise they have shared with me. I would like to thank my supervisor, Prof. Siim Veski, for providing me with the opportunity to pursue this PhD, his almost inexhaustible support and patience throughout my journey, not only in helping me complete my PhD but also in enabling me to make the most of the entire experience. Thank you for all the guidance during these last five years. You truly helped me to identify and focus on the most important aspects of this work. I would also like to thank my co-supervisor, Dr. Inta Dimante-Deimantoviča, who has supported me since the very start of my career as a paleolimnologist. Your detail-oriented perspective elevated the quality of every aspect of the work you were involved in, and your dedication to scientific excellence has inspired my growth as a researcher. I would also like to express my deep appreciation to my co-supervisor, Dr. Anneli Poska, for her support and dedication. The countless hours of video calls we had, the detailed feedback, and thoughtful advice you provided have been helping me advance my thesis and publications with an efficiency I never imagined possible. I often wonder how you manage to find time for our meetings, suggestions, discussions, and your own research, especially knowing I’m not your only PhD student. Thank you for going above and beyond at every step of the way.

I would like to thank Kalle Olli for the useful comments on the content of the thesis.

I am grateful to all of the people who helped support the technical aspects of this research. I would like to thank Kati Lind for teaching me how to analyse Chlorophyll-*a* samples, Enn Kaup for instructions in TP analysis. I would like to thank Merlin Liiv and Tiiu Alliksaar for teaching me how to operate the spectrophotometer and for helping with the LOI analysis. I would also like to thank Tiiu for helping with purchasing all the necessary equipment for the Chlorophyll-*a* and Cladocera analysis. I am thankful to Helen Tammert, Anu Kisand, and Teet Jäetma for supporting me with technical equipment. I must also acknowledge the help of Jolanta Jēkabsone, Dabas Aizsardzības pārvalde, Vahanas Grigorianas, University of Latvia team (Ilga Kokorīte, Laura Grīnberga, Dāvis Ozoliņš, Agnija Skuja), and Ingmar Ott for their help with monitoring data and information on lakes from Latvia, Lithuania, and Estonia. I would also like to thank Liisa Nevalainen, Kay Van Damme, Izabel Zawiska, and Edyta Zawisza, who helped me with species determination. Triin Reitalu, Varvara Bakumenko and Suprosanna Shit for help with programming and statistical analysis. I am thankful to Jüri Vassiljev, Sophie Graul, Ivan Krivokorin and Zane Rekšņa for their help with data visualization. I greatly enjoyed the fieldwork that was necessary to make this thesis a reality. And I am thankful to all those who were involved in the sediment and water parameter sampling process. Thank you, Ivan, Atko, Varvara, James, Merlin, Normunds, Matīss Žagars, the University of

Acknowledgements

Like most scientific works nowadays, my PhD thesis was not created in a vacuum of knowledge. Rather, it was built on the foundations of previously published works and the support of friends, colleagues, and strangers. For parts of my work, I must thank the help of countless people who spend hours developing open source software, creating tutorials, and helping other “people on the internet” with their code issues. Nevertheless, my greatest gratitude must be expressed to my support network of supervisors, colleagues (technical, data, moral, and knowledge support), friends, and financing providers. All of this would not have been possible without you. I appreciate every second you invested in my PhD journey.

I would like to thank all of my supervisors for their time, the knowledge and wisdom, the materials, and the technical expertise they have shared with me. I would like to thank my supervisor, Prof. Siim Veski, for providing me with the opportunity to pursue this PhD, his almost inexhaustible support and patience throughout my journey, not only in helping me complete my PhD but also in enabling me to make the most of the entire experience. Thank you for all the guidance during these last five years. You truly helped me to identify and focus on the most important aspects of this work. I would also like to thank my co-supervisor, Dr. Inta Dimante-Deimantoviča, who has supported me since the very start of my career as a paleolimnologist. Your detail-oriented perspective elevated the quality of every aspect of the work you were involved in, and your dedication to scientific excellence has inspired my growth as a researcher. I would also like to express my deep appreciation to my co-supervisor, Dr. Anneli Poska, for her support and dedication. The countless hours of video calls we had, the detailed feedback, and thoughtful advice you provided have been helping me advance my thesis and publications with an efficiency I never imagined possible. I often wonder how you manage to find time for our meetings, suggestions, discussions, and your own research, especially knowing I’m not your only PhD student. Thank you for going above and beyond at every step of the way.

I would like to thank Kalle Olli for the useful comments on the content of the thesis.

I am grateful to all of the people who helped support the technical aspects of this research. I would like to thank Kati Lind for teaching me how to analyse Chlorophyll-*a* samples, Enn Kaup for instructions in TP analysis. I would like to thank Merlin Liiv and Tiiu Alliksaar for teaching me how to operate the spectrophotometer and for helping with the LOI analysis. I would also like to thank Tiiu for helping with purchasing all the necessary equipment for the Chlorophyll-*a* and Cladocera analysis. I am thankful to Helen Tammert, Anu Kisand, and Teet Jäetma for supporting me with technical equipment. I must also acknowledge the help of Jolanta Jēkabsone, Dabas Aizsardzības pārvalde, Vahanas Grigorianas, University of Latvia team (Ilga Kokorīte, Laura Grīnberga, Dāvis Ozoliņš, Agnija Skuja), and Ingmar Ott for their help with monitoring data and information on lakes from Latvia, Lithuania, and Estonia. I would also like to thank Liisa Nevalainen, Kay Van Damme, Izabel Zawiska, and Edyta Zawisza, who helped me with species determination. Triin Reitalu, Varvara Bakumenko and Suprosanna Shit for help with programming and statistical analysis. I am thankful to Jüri Vassiljev, Sophie Graul, Ivan Krivokorin and Zane Rekšņa for their help with data visualization. I greatly enjoyed the fieldwork that was necessary to make this thesis a reality. And I am thankful to all those who were involved in the sediment and water parameter sampling process. Thank you, Ivan, Atko, Varvara, James, Merlin, Normunds, Matīss Žagars, the University of

Latvia, and the Supervisors teams. Beautiful nature and good company truly made the fieldworks to be a magical experience.

I would also like to thank all of my co-authors, each of whom had their own unique perspective. I am grateful for the support of Helle Pohl-Raidla, who always knows what is going on. I must not forget to acknowledge my moral support team of fellow PhD students and ex-PhD students, Eliise, Varvara, Ivan, Sophie, Thibaud, Nata-Ly, Ogechukwu, Nthati, Mawo, Mark, Renee, Tatiana, and Ansis. I also thank Jaak, who always has an interesting story to tell. I am completely sure that I have forgotten someone in this list of amazing people of TalTech colleagues, so if it is You, please forgive me! I truly appreciate the whole team of the TalTech Department of Geology. Working with you all has really been a pleasure.

I thank my family and friends, who were always there for me and ready to listen, even in cases where they had no idea what I was talking about. I would also like to thank all the fellow professionals I have met at conferences, summer schools, workshops, and other occasions. I have gained much from your scientific work and from your feedback. I would also like to thank those colleagues who provided me with information and materials that could not be included in this dissertation. I still intend to utilize these materials in my future articles and am looking forward to our collaboration.

Lastly, I would like to thank the financial support of projects DAR 16024, PRG 323, PRG 1993, TK 215, TF 24023 as well as Dora + scholarship.

Abstract

Model-Based Reconstructions of Lake Environments in the Baltic States Using Subfossil Cladocera

Paleolimnology offers a valuable tool for evaluating historical lake conditions. This includes periods before human disturbance, varying climate conditions, and the impacts of specific human activities on lake ecosystems, some of which may not have been thoroughly studied or documented at the time due to differing societal priorities or the early stage of ecological science during those periods. Knowledge of lake history is a basis for more effective restoration strategies and goals, and supports predictions about lake development under future climate change and ongoing anthropogenic impact. Nevertheless, reconstructing historical lake environments becomes increasingly challenging, as multiple stressors can influence lake ecosystems simultaneously.

One of the key proxies for evaluating historical changes in lakes is subfossil Cladocera. Cladocera are microscopic crustaceans that spend their entire life cycle within the lake and are widely used to reconstruct environmental parameters such as trophic state, pH, electrical conductivity, and water depth. However, species' responses to environmental factors can vary between regions, and until now, such an evaluation for subfossil Cladocera in the Baltic States has been lacking. Furthermore, although various qualitative and quantitative approaches are used globally to reconstruct past environmental conditions using subfossil Cladocera, comparisons between these methods and their relative suitability are rare.

A surface sediment training set comprising 78 lakes across the Baltic States was developed to address this research gap. The lakes were selected to represent a wide gradient of environmental parameters known to affect the Cladocera assemblages, such as pH, electrical conductivity, trophic state, depth, and surface area – all of which were found to significantly influence subfossil Cladocera species assemblages as revealed by redundancy analysis (RDA). The connection between environment and subfossil Cladocera species assemblages was further analyzed using functional groups and indicator species approaches. Weighted averaging partial least squares (WA-PLS) and boosted regression tree (BRT) models were developed for the quantitative reconstruction of past lake environments. WA-PLS was selected as it is one of the most robust and widely used methods for transfer function development in paleolimnology, while BRT represents a more recent machine-learning-based approach capable of handling complex, nonlinear relationships between species assemblages and environmental variables. Although BRT has been applied in other ecological contexts, its use in subfossil Cladocera studies remains rare, and to date, no direct comparison between WA-PLS and BRT has been conducted in this context. Observations of water pH, electrical conductivity, trophic state descriptive parameters (total phosphorus, total nitrogen, chlorophyll-a, transparency), and water depth, where available, were compared to the reconstructed values and used as a part of the reconstruction method and model evaluations. Although this study focuses on subfossil Cladocera, the results were also compared with conclusions drawn from other proxies, as reported in the articles that are a part of this work.

The analysis revealed that pH is the most significant factor influencing subfossil Cladocera assemblages and can be reliably reconstructed using both WA-PLS and BRT modeling approaches. In contrast, electrical conductivity could not be quantitatively reconstructed; however, it could be qualitatively approximated using the indicator

species approach. Trophic state can be reconstructed using BRT models, particularly when changes are primarily driven by nutrient enrichment. However, this approach becomes unreliable when other major drivers, such as pH shifts or climate variability, are present. Trophic state can also be assessed using functional group composition and indicator species analysis. Quantitative reconstructions of lake depth produced less reliable results. Based on the current data, shifts in the proportions of pelagic versus macrophyte-associated Cladocera species are recommended as a more robust proxy for evaluating depth-related changes. Although the lake surface area was found to significantly influence Cladocera assemblages, it could not be reliably reconstructed.

All above-mentioned reconstruction methods were applied to sediment cores from three small eutrophic lakes, each representing a different time period and level of human disturbance. The core from Lake Velnezers spans from before 1850 to 2018 CE and was the site most severely impacted by human activity. Its catchment has undergone a transition from forested to agrarian land and, most recently, to an urbanized area. Reconstructions from Lake Velnezers indicate a rise in pH associated with agricultural development in its catchment, followed by severe eutrophication driven by urbanization. The sediment core from Lake Sekšu covers the period from 1935 to 2018 CE. This lake is located in a forested area and forms part of the drinking water supply system for the city of Riga. In Lake Sekšu, model results, along with functional group and indicator species analysis, suggest a slight increase in pH and moderate eutrophication. Lake Nakri is located in a forested area and has experienced minimal human impact. The sediment record of Lake Nakri covers a long-term period, extending from the Late Glacial (12,100 calibrated years BP) to 2017 CE. Lake Nakri experienced some eutrophication between 7900 and 5600 calibrated years BP, but has remained relatively stable since. However, changes during the Late Glacial and Early Holocene periods remain difficult to interpret due to the absence of modern analogues and climatic conditions that differ from those represented in the training set.

These findings highlight the value of subfossil Cladocera for reconstructing historical lake conditions such as pH, electrical conductivity, trophic state, and water depth. They also demonstrate the potential of combining or selectively applying functional group analysis, indicator species, and quantitative modeling approaches, depending on the most suitable method for each parameter. The findings contribute to the development of regionally appropriate approaches for assessing lake history and informing potential lake management strategies.

Lühikokkuvõte

Subfossiilsete vesikirbuliste põhised järvekeskkonna mudelrekonstruktsioonid Läänemeremaades

Paleolimnoloogia meetod järvede mineviku keskkonnatingimuste hindamiseks võimaldab uurida perioode enne inimtegevuse mõju, selgitada erinevaid kliimatingimusi ning eelajaloolise inimeste tegevuste mõju järvede ökosüsteemidele, Järvesetetes kajastunud teadmised järvede minevikust on aluseks tõhusamate järvede taastamisstrateegiate ja -eesmärkide kujundamisel ning toetavad järvede arenguprognoose tulevaste kliimamuutuste ja jätkuva inimtegevuse tingimustes. Siiski on järvede mineviku keskkonnatingimuste rekonstrueerimine keeruline, kuna järvede ökosüsteeme mõjutavad sageli mitmed tegurid samaaegselt.

Üheks oluliseks indikaatoriks mineviku keskkonnamuutuste hindamisel järvedes on subfossiilsed vesikirbulised (Cladocera). Vesikirbulised on mikroskoopilised koorikloomad, kes veedavad kogu oma elutsükli järves ning leiavad laialdast kasutust veekeskkonna parameetrite nagu troofiline seisund, pH, elektrijuhtivus ja veesügavus, rekonstrueerimisel. Siiski võivad liikide reageeringud keskkonnateguritele piirkonniti erineda ning seni pole Balti riikides subfossiilseid vesikirbulisi sellisteks uuringuteks kasutatud. Lisaks kasutatakse maailmas erinevaid kvalitatiivseid ja kvantitatiivseid lähenemisviise mineviku keskkonnatingimuste rekonstrueerimiseks, kuid nende meetodite võrdlusi ja sobivuse hindamisi on vähe.

Selle uurimislünga täitmiseks koguti Balti riikide 78 järve pinnasesette andmebaas. Valitud järved esindavad laia vesikirbuliste kooslusi mõjutavate keskkonnaparameetrite vahemikku, nagu pH, elektrijuhtivus, troofiline seisund, sügavus ja pindala. Kõik need osutusid redundantsusanalüüsiga (redundancy analysis – RDA) olulisteks teguriteks subfossiilsete vesikirbuliste koosluste kujunemisel. Keskkonna ja vesikirbuliste koosluste seoseid analüüsiti funktsionaalsete rühmade ja indikaatorliikide abil. Kvantitatiivseks rekonstruktsioonideks töötati välja kaalutud keskmiste osaliste vähimruutude meetodil (weighted averaging partial least squares - WA-PLS) ja võimendatud regressioonipuudel (boosted regression tree - BRT) põhinevad mudelid. WA-PLS valiti, kuna see on üks kõige usaldusväärsemaid ja laialdasemalt kasutatavaid ülekandefunktsiooni meetodeid paleolimnoloogias, samas kui BRT esindab uuema põlvkonna masinõppepõhist lähenemist, mis suudab käsitleda keerukaid, mittelineaarseid seoseid organismide koosluste ja keskkonnamuutujate vahel. Kuigi BRT-d on rakendatud muudes ökoloogilistes uuringutes, on selle kasutamine subfossiilsete vesikirbuliste uurimisel harv ning seni pole WA-PLS-i ja BRT otsest võrdlust tehtud. Vaatlustel mõõdetud järve vee pH, elektrijuhtivuse, troofilise seisundi (kogufosfor, kogulämmastik, klorofüll-a, läbipaistvus) ja veekogu sügavuse andmeid võrreldi modelleeritud väärtustega ning kasutati mudelite usaldusväärsuse hindamisel. Kuigi uuring keskendub subfossiilsetele vesikirbulistele, võrreldi tulemusi ka teiste andmete põhjal tehtud järeldustega mida on kirjeldatud töö osaks olevates artiklites.

Tulemused näitavad, et pH on kõige olulisem tegur, mis mõjutab subfossiilsete vesikirbuliste kooslusi, ning seda saab usaldusväärselt rekonstrueerida nii WA-PLS kui ka BRT mudelite abil. Elektrijuhtivust ei olnud võimalik kvantitatiivselt rekonstrueerida, kuid seda saab kvalitatiivselt hinnata indikaatorliikide abil. Troofilist seisundit saab rekonstrueerida BRT mudelite abil, juhul kui muutuste peamiseks põhjuseks veekeskkonna toitainetega rikastumine. Kui aga kaasnevad teised olulised mõjutajad, näiteks pH- või kliimamuutused, on see lähenemine ebausaldusväärne. Troofilist seisundit saab hinnata ka funktsionaalsete rühmade ja indikaatorliikide analüüsi abil. Järve sügavuse kvantitatiivne rekonstrueerimine oli vähem usaldusväärne. Käesolevate andmete põhjal oleks soovituslik veesügavuse muutuste hindamiseks kasutada pelagiaalse ja makrofüütidega seotud vesikirbuliste liikide osakaalu muutusi. Kuigi järve pindala mõjutas vesikirbuliste kooslusi oluliselt, ei olnud seda võimalik usaldusväärselt rekonstrueerida.

Kõiki eespool mainitud rekonstrueerimismeetodeid rakendati kolme väikese eutrofeerunud järve setteläbilõigetele, millest igaüks esindab erinevat ajaperioodi ja inimtegevuse taset. Velnezersi järve setteläbilõige hõlmab ajavahemikku 1850–2018 ning see oli kõige tugevama inimtegevuse mõjuga järv. Selle järve valgala on esialgsest metsasest piirkonnast muutunud põllumajanduslikuks ja hiljem linnastunud alaks. Velnezersi rekonstruktsioonid näitavad pH tõusu seoses põllumajanduse arenguga ning sellele järgnenud tugevat eutrofeerumist linnastumise tõttu. Sekšu järve setteläbilõige hõlmab ajavahemikku 1935–2018. See järv asub ka metsases piirkonnas ja kuulub Riia linna joogivee varustussüsteemi. Sekšu järve modelleerimistulemused ja funktsionaalsete rühmade ning indikaatorliikide analüüs viitavad kergelt suurenenud pH-le ja mõõdukale eutrofeerumisele. Nakri järv asub vähese inimtegevuse mõjuga metsases piirkonnas. Selle setteläbilõige hõlmab pikaajalist perioodi, ulatudes hilisjääajast (12000 kalibreeritud aastat tagasi) kuni tänapäevani. Nakri järves esines suurenenud eutrofeerumist ajavahemikus 7900–5600 kalibreeritud aastat tagasi, kuid sellest ajast alates on järve seisund püsinud suhteliselt stabiilsena. Samas, hilisjääajal ja varaholotseenis toimunud muutusi on raske tõlgendada, kuna puuduvad tänapäevased kliima- ja keskkonnatingimuste analoogid.

Antud töö tulemused rõhutavad subfossiilsete vesikirbuliste väärtust mineviku järvede keskkonnatingimuste, nagu pH, elektrijuhtivus, troofiline seisund ja veesügavus, rekonstrueerimisel. Samuti näitavad need, kui oluline on kombineerida või valida sobivaim meetod (funktsionaalsete rühmade analüüs, indikaatorliigid või kvantitatiivne modelleerimine) sõltuvalt hinnatavast parameetrist. Tulemused aitavad arendada piirkonnale sobivaid lähenemisviise järvede mineviku keskkonnatingimuste hindamiseks ja järvede võimalike haldusstrateegiate kujundamiseks.

Appendix 1

Article I

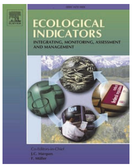
Lanka, A., Poska, A., Bakumenko, V., Dimante-Deimantovica, I., Liiv, M., Stivrins, N., Zagars, M. and Veski, S., (2024). Subfossil Cladocera as indicators of pH, trophic state and conductivity: Separate and combined effects in hemi boreal freshwater lakes. *Ecological Indicators*, *167*, p.112592. https://doi.org/10.1016/j.ecolind.2024.112592

Ecological Indicators 167 (2024) 112592

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



Original Articles

Subfossil Cladocera as indicators of pH, trophic state and conductivity: Separate and combined effects in hemi boreal freshwater lakes

Anna Lanka [a], Anneli Poska [a,b,*], Varvara Bakumenko [a], Inta Dimante-Deimantovica [c], Merlin Liiv [a], Normunds Stivrins [a,d], Matiss Zagars [c], Siim Veski [a]

[a] *Department of Geology, Tallinn University of Technology, Ehitajate Tee 5, 19086 Tallinn, Estonia*
[b] *Department of Physical Geography and Ecosystem Science, Lund University, Sölvegatan 12, S-223 62, Sweden*
[c] *Latvian Institute of Aquatic Ecology, Voleru 4, Riga LV-1007, Latvia*
[d] *Department of Geography, University of Latvia, Jelgavas 1, Riga LV-1004, Latvia*

ARTICLE INFO

Keywords:
Baltic states
Cladocera
Environmental indicators
IndVal
(paleo)limnology
Reference conditions
Sediments

ABSTRACT

Identifying lake reference conditions is a crucial task for successful lake restoration. A common method is the paleolimnological approach. However, lakes can be influenced by multiple stressors over time, making it necessary to consider possible combined effects.

In this study, we aimed to untangle the interpretation of subfossil Cladocera in relation to different environmental parameters in lakes of Baltic states. To determine indicator species that could be used for reconstructing past environmental conditions, we developed a 78-lake surface sediment training set. Lakes were selected to cover gradients of different lake sizes, depths, electrical conductivity (EC), pH, and trophic states. Redundancy analysis (RDA) identified pH, trophic state and EC as significant parameters influencing subfossil Cladocera species composition. Using IndVal.g analysis, we distinguished species that are indicative of a combination of parameters such as pH<6 and EC<100 μS/cm (*Alonella excisa*, *Alona rustica*, *Polyphemus pediculus*, *Holopedium gibberum, Drepanothrix dentata)*, pH>6 and EC>100 μS/cm (*Disparalona rostrata*, *Leydigia leydigi*, *Pleuroxus uncinatus, Pleuroxus trigonellus*), pH>6 and oligotrophic/mesotrophic conditions(*Monospilus dispar*). We identified species that can be indicative of several parameters that do not necessarily combine (for example, *Alonopsis elongata* for pH<6 or oligotrophic/mesotrophic conditions or EC<200 μS/cm), or were indicative of only one parameter (for example *Paralona pigra*, *Ophryoxus gracilis* – oligotrophy; *Bosmina longispina*- mesotrophy; *Bosmina longirostris* – eutrophy; *Chidorus sphaericus*, *Oxyurella tenuicaudis*–hypereutrophy; *Leptodora kindtii* pH>6; *Pleuroxus aduncus* EC>100 μS/cm). These findings add to the understanding of subfossil Cladocera species interpretation in paleolimnological samples, enabling better assessment of anthropogenic influence and reference conditions of lake ecosystems.

1. Introduction

Lake ecosystems around the world have been influenced by multiple stressors, such as warming (Meerhoff et al., 2012; Woolway et al., 2020), eutrophication (Le Moal et al., 2019; Abell et al., 2022), brownification (Klante et al., 2021; Blanchet et al., 2022; Tichá et al., 2023), acidification (Battarbee, 1990; Farmer, 1990), salinization (Kaushal et al., 2021), as well as pollution from different anthropogenic sources (Dauvalter, 1997; Grizzetti et al., 2017; Amoatey and Baawain, 2019). These stressors can interact in complex ways, often having similar, opposing, or additive effects on water ecosystems (Moss et al., 2011; Gutiérrez-Cánovas et al., 2022; Radosavljevic et al., 2022). The responses may vary based on the specific climate region and species community involved (Adrian et al., 2009).

To stop the deterioration of aquatic ecosystems and ensure good water quality in European Union (EU) member states, the European Commission developed the Water Framework Directive (WFD) (European Commission, 2014). As a part of the evaluation for lake water quality status, WFD requires the identification of lake-type specific reference conditions, which can be defined as lake conditions before substantial human impact. In areas with considerable anthropogenic pressure undisturbed lakes that could have preserved type-specific

---

[*] Corresponding author at: Department of Geology, Tallinn University of Technology, Ehitajate Tee 5, 19086 Tallinn, Estonia.
E-mail address: anneli.poska@nateko.lu.se (A. Poska).

https://doi.org/10.1016/j.ecolind.2024.112592
Received 11 July 2024; Received in revised form 2 September 2024; Accepted 8 September 2024

reference conditions might be lacking. In these areas, paleolimnology arguably provides the only technique for establishing reference conditions with any confidence (Bennion et al., 2011; Stivrins et al., 2018). Determining the reference conditions is becoming an increasingly difficult task, considering the long list of stressors and the differences in their timespans and effects on lake ecosystems. Furthermore, it is essential for successful lake restoration to consider that the ecosystem might have undergone several consecutive or simultaneous changes brought by different stressors.

Since direct measurements often cannot be used to acquire information on lake reference biological and physicochemical quality elements as per WFD, the indicator species approach and various independent paleolimnological proxies are employed to investigate lake history and establish reference conditions. (Lindenmayer and Linkens, 2010; Bennion et al., 2011). One such proxy is subfossil Cladocera. Cladocera are a group of planktonic microscopic crustaceans which can be found in a variety of water bodies. However, the highest species richness is reported from freshwater aquatic ecosystems. Cladocerans spend their entire life cycle in water and due to their central position in the food web they are considered to reflect information of both top down and bottom-up food web structuring mechanisms (Korhola and Rautio, 2001; Forró et al., 2008). This makes Cladocera an excellent organism to reflect the changes within lake ecosystems. This crustacean group can be utilized to study contemporary and historical changes in trophic status (Hofmann, 1996; Alliksaar et al., 2005; Chen et al., 2010; Gąsiorowski et al., 2021), pH (Krause-Dellin and Steinberg, 1986; Bērziņš and Bertilsson, 1990), conductivity, climate, fish predation (Bjerring et al., 2009; Çakıroğlu et al., 2014; Nevalainen et al., 2015; Korponai et al., 2020) and water level (Hofmann, 1998; Korhola et al.,2000; Nevalainen et al, 2011).

Modern surface sediment training set is the most used approach to interpret subfossil Cladocera assemblages. In cases where the region lacks a subfossil Cladocera training set, information on species ecology from live Cladocera can be used (Milan et al., 2017). However, this approach could have its limitations since subfossil Cladocera samples often show higher Cladocera species diversity than contemporary ones, especially concerning littoral taxa (Çakıroğlu et al., 2014; García-Girón et al., 2018; Tumurtogoo et al., 2022).

Many surface sediment training sets focus on capturing only one environmental parameter (Brodersen et al., 1998; Chen et al., 2010), which may not account for the natural variability of lakes and the complexity of factors influencing Cladocera. This could lead to misinterpretation of the results (Velle et al., 2012; Zettler et al., 2013) since studies that utilize multiproxy paleolimnological assessments of lake ecosystems or long-term monitoring data show that lakes often experience changes in several parameters (such as pH, conductivity, transparency, water color, trophic state) simultaneously (Eilers et al., 1989; Heinsalu and Alliksaar, 2009; Baastrup-Spohr et al., 2017; Zawisza et al., 2019).

Baltic states (Estonia, Latvia, Lithuania) are rich in lakes with large natural variability in size, depth, alkalinity, conductivity, water color, pH and tropic state (Ott, 2005; LVĢMC, 2022). These variations in standing water bodies can arise due to different origins (glacial, glaciokarst, bog, coastal lakes) and catchment-related characteristics (bedrock: sand, silt, clay, limestone; land cover: forested, bog, agricultural, urban areas) as well as intensity of anthropogenic impact (Cimdiņš, 2001; ÓSullivan and Reynolds, 2004; Liiv et al., 2018; Nikodemus et al., 2018; Terasmaa, 2018). Thus far research on Cladocera and other zooplankton organisms' indicative value in the Baltic states has been focused on contemporary material (Mäemets, 1983; Urtāne, 1998; Čeirāns, 2007; Haberman and Haldna, 2014) with a few recent paleolimnological studies using subfossil Cladocera as a proxy for water quality (Alliksaar et al., 2005; Błędzki et al, 2013; Koff et al., 2016; Marzecová et al., 2017; Zawiska et al.,2020; Lanka et al., 2024).

To determine the sensitivity of Cladocera communities to various environmental parameters and to address the issues with environmental reconstructions based on training sets with a single explanatory gradient, we have developed a surface sediment training set. We used lakes, ponds, and bog pools along gradients of pH, conductivity, trophic state, lake depth and area, and analyzed the subfossil Cladocera assemblages with a focus on the indicator species approach in the Baltics for the first time. We hypothesize that it is possible to use subfossil Cladocera indicator species to distinguish between lakes of different pH, trophic state, and electrical conductivity (EC).

2. Materials and methods

2.1. Study site selection

We selected 78 lakes and artificial water bodies in Estonia, Latvia, and Lithuania (Fig. 1), representing wide size, depth, trophic status, pH, and electric conductivity gradients (Appendix A). For 39 of the studied sites, information on trophic state related parameters, pH, and conductivity was available from monitoring data of Lithuania (Aplinkos Apsaugos Agentūra, 2024), Latvia (LVĢMC, shared upon request), Estonia (Keskkonnaseire infosüsteem, 2024). The rest of the environmental data is a combination of published (Stivrins et al., 2022; Zagars et al., 2024) and unpublished data collected bythe authors of this publication. Since the environmental variables were collected from different sources, not all lakes have all the measurements, resulting in some methodological differences and gaps in the dataset (Appendix B).

2.2. Lake water descriptive parameters

We measured lake water descriptive parameters (pH, EC, total phosphorous (TP), Chlorophyll-*a* (Chl-*a*), Secchi depth, dissolved oxygen (DO), total nitrogen (TN)) for each lake that had no monitoring data available one to four times during the years 2021 and 2022 between

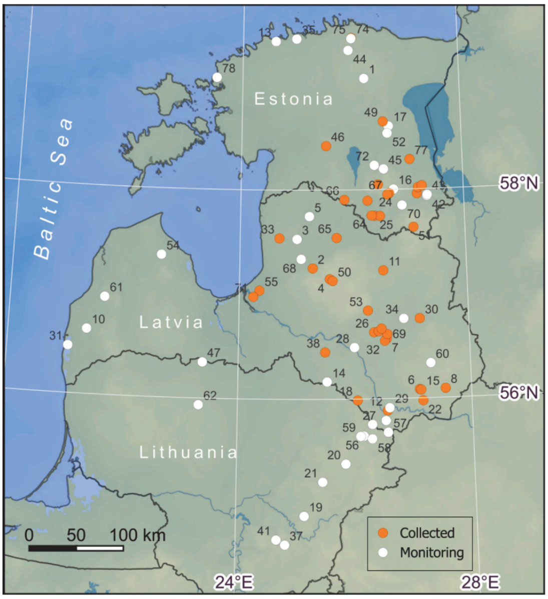


Fig. 1. The geographic location of 78 selected study lakes from the Baltic states. Orange dots in the map represent lakes for which authors collected the environmental data; white dots represent lakes with data from national monitoring programs. More information on sites, their coordinates and collected environmental data can be found in Appendix A. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

April and October, as these months are descriptive of the growing season in the Baltic countries (Walther and Linderholm, 2006).

We measured water pH, EC, and DO in the field using a ProDSS probe for the top water layer (30 cm below the water surface) and bottom water layer (approximately 50 cm above sediments). Further in the text, we refer to the measurements of the top water layer as pH and EC and of the bottom water layer as pH_{bot}, EC_{bot}, and DO_{bot}.

We determined water transparency (Secchi depth) using a white Secchi disc.

We measured Chl-*a* and TP in laboratory conditions using water samples collected during the above-described field campaigns.

We collected water samples for Chl-*a* at 30 cm water depth in 1.5-liter plastic bottles and transported them to the laboratory in a cold box until further processing. We filtered the samples in a darkened laboratory no later than 24 h after using Whatman 47 mm GF/F filters with a Vacuum pump Laboport N816. Samples were filtered either until the filter clogged or until approximately one liter of water was filtered. We measured the amount of filtered water after filtration using a measuring cylinder (500 ± 5 ml) and froze the filters until further analysis. We thawed the filters and kept them in 10 ml of 96 % ethanol in darkness for 24 h before the analysis. Thereafter, Chl-*a* samples were analyzed in 665 and 750 nm spectrum using 10 mm wide glass cuvettes and Analytik Jena Specord 250 spectrophotometer. We collected water samples for TP analysis in sealable 14 ml plastic containers and froze them until further analysis. We determined TP concentration in the laboratory using the HACH LKC349 analysis kit and Hach Lange DR 2800 spectrophotometer. In some lakes (Appendix A), we also measured TN according to standard protocol (e.g., Grasshof et al., 1983). Analysis was performed at an accredited laboratory (ISO/IEC/17025).

Monitoring data was available for 39 of the lakes (Appendix A). We selected the data available for the months between April and October up to five years before sediment collection. Monitoring data had different observation frequencies; therefore, we used the mean value of these measurements.

2.3. Auxiliary parameters

We compiled a 30-year (1991-2020) mean annual temperature (T_{ann}) dataset based on monthly mean temperatures obtained from the ERA5 dataset (Copernicus Climate Data Store), which contains gridded extrapolated climate data with hourly temporal and $0.25^{\circ} \times 0.25^{\circ}$ spatial resolution (Hersbach et al., 2020).

We sourced information regarding the maximum depth ($Depth_{max}$), average depth ($Depth_{ave}$), and area of the lakes from various references. For lakes in Estonia, from kalapeedia.ee; for lakes in Latvia, data was obtained from the database ezeri.lv; and for lakes in Lithuania, from zvejogidas.lt.

2.4. Surface sediment analysis

We collected surface sediments from the selected lakes using a Willner-type gravity corer in the deepest part of the lake, if possible, during 2021 and 2022. The upper two cm of each sediment core was collected and preserved for further analysis. This amount of surface sediments could accumulate in approximately 5–20 years (Stivrins et al. 2018, Zawiska et al., 2020), therefore representing the modern-day situation while avoiding bias that could appear due to one year extreme conditions.

2.4.1. Cladocera analysis

We took 1–2 cm^3 subsamples for Cladocera analysis. We prepared the subsamples in the laboratory according to a standard procedure described by Frey (1986). Heated in 10 % KOH in an 85 °C water bath for 30 min, filtered through a sieve with a mesh size 40 µm, and then diluted with 10 ml of water and colored with Safranin O.

We prepared slides for microscopy from 100 µl of homogenized subsample and examined them under a light microscope at 100x, 200x, and 400x magnification. Slides were scanned fully to avoid counting bias due to uneven remain distribution. We continued the microscopy until at least 70 individuals were counted and examined one extra slide for each lake to identify any previously undetected species (Kurek et al., 2010).

Subfossil Cladocera species identification was based on the identification key by Szeroczyńska and Sarmaja-Korjonen (2007). Due to difficulties in distinguishing between the remains of *Daphnia* and *Cereodaphnia*, we merged these two taxa into *Daphnia* spp. group. Similarly, there were difficulties distinguishing between *Corontella rectangula* and *Alona guttata* head shiels and shells. According to the identification key (Szeroczyńska and Sarmaja-Korjonen, 2007), species present in the sample should be determined based on post abdomen. In most of our samples, postabdomens were not present, and sometimes, the postabdomens of both taxa were present in the same sample. Therefore, regarding head shields and shells, we merged them under the group *Corontella rectangula/Alona guttata.*

2.4.2. Sediment analysis

We performed loss on ignition (LOI) analysis using the standard methodology for all collected sediment samples (Heiri et al., 2001). Dried samples were heated at 550 °C for four hours to obtain values of sediment organic content (LOI_{org}) and 950 °C for two hours for carbonate (LOI_{carb}) and minerogenic matter (LOI_{min}) content. To measure the carbonates in the CO_3^{2-} form, we multiplied the carbonate results by a coefficient of 1,36 (Heiri et al., 2001).

We analyzed sediment samples from 56 lakes for total organic carbon and total nitrogen content through combustion in a FLASH 2000 Organic Elemental Analyzer. Based on organic matter content, 2–8 mg of dried powdered sediment was put into silver capsules. Samples in capsules were pre-treated with 10 % HCl to remove inorganic C and dried on a hotplate at 70 °C for 5 h. Once dry, the silver capsules were left to cool and carefully wrapped to form granules. Thereafter, the obtained granules were packed into tin containers to facilitate combustion. Cystine or BBOT ($C26H26N2O2S$) was used as a standard (ThermoFisher Scientific), and organic matter-rich sediment or the algae *Spirulina* was used as a reference material (IVA Analysentechnik e. K). Analyses were done in triplicate, and the average was calculated by selecting the two measurements that had the most similar results. The C/N values are expressed as atomic ratios (Meyers and Teranes, 2001).

2.5. Data analysis

We performed data analysis in program R 4.3.3. We used the average values of the obtained water descriptive parameters, to reduce the bias originating from one year/season extremes. Exception is r DO_{bot}, for which we calculated the average values of July and August to see if any of the Cladocera species could be sensitive to summer anoxia. Cladocera data was analyzed in the form of relative abundances. To normalize the data distribution, we used natural logarithmic transformation for the environmental variables and square root transformation for Cladocera relative abundances. The Cladocera species that were present in less than five samples (*Diaphanosoma brachyurum*, *Scrapholeberis* sp., *Acantholeberis curvirostris*, *Camptocercus lilljeborgi*, *Phreathalona protzi*, *Rhyncatalona latens*, *Pseudochydorus globosus*, *Anchystropus emarginatus*, *Macrothrix* sp.) were excluded from further analysis (Appendix C).

We calculated the trophic state index (TSI: Carlson, 1977, 2007) using Secchi depth, Chl-*a*, TP, and TN (where available) for each lake (Carlson, 2007). We excluded Secchi depth as a parameter for calculations of TSI for dystrophic lakes since one of the characteristics of dystrophic lakes is their dark water color (Gray et al., 2022), which could bias the results (Brezonik et al., 2019). Lakes were classified as dystrophic based on literature (Nature Conservation Agency Republic of Latvia, 2020).

We tested the relationships between collected environmental parameters (pH, pH$_{\mathrm{bot}}$, EC, EC$_{\mathrm{bot}}$, TSI, Secchi depth, Chl-*a*, TP, TN, DO$_{\mathrm{bot}}$, T$_{\mathrm{ann}}$, area, maximum depth (Depth $_{\mathrm{max}}$, average depth (Depth$_{\mathrm{ave}}$), C/N, LOI organic (LOI$_{\mathrm{org}}$), LOI carbonate (LOI$_{\mathrm{carb}}$), LOI mineral (LOI$_{\mathrm{min}}$) using Pearson's correlation coefficient (Berman, 2016). This was done to assess whether the tested parameters are independent. We employed multivariate analysis to select the environmental parameters suitable for further study. To determine the most appropriate ordination methods for our dataset, we started with Cladocera composition-based Detrended Correspondence Analysis (DCA: Hill and Gauch, 1980). The DCA axis 1 and 2 lengths were less than 3 (2,24 and 1,73), in which case Euclidean distance-based ordination methods are suggested (Birks, 1998; Lepš and Šmilauer, 2003). We used Redundancy analysis (RDA: Wollenberg, 1977) to determine which environmental parameters explain the species composition best. RDA analysis is sensitive to missing values. Therefore, we kept only the environmental variables with less than 5 % missing values (pH, EC, TSI, Secchi depth, Chl-*a*, TP, T$_{\mathrm{ann}}$, area, Depth$_{\mathrm{max}}$, LOI$_{\mathrm{org}}$, LOI$_{\mathrm{carb}}$, LOI$_{\mathrm{min}}$). For the purpose of RDA analysis, the few missing values of these environmental parameters were substituted using the data imputation by the "missForest" package (Stekhoven and Buehlmann, 2012). We used a forward selection algorithm to reduce the number of explanatory variables in RDA analysis and only kept the statistically significant variables ($p < 0.05$). To test the significance of the variables and the model, we used an ANOVA-like permutation test available in the library "vegan" (Oksanen et al., 2022). To further explore Cladocera species composition and how it relates to environmental parameters, we used Principal Component Analysis (PCA) (Jolliffe and Cadima, 2016).

To determine species indicative of specific environmental conditions, we calculated the IndVal.g value (Cáceres and Legendre, 2009), which is a variation of the IndVal method initially described by Dufrene and Legendre (1997). IndVal is one of the most commonly used methods for indicator species evaluation (Podani and Csányi, 2010). IndVal value is designed to account for the specificity of species for the selected environmental group (index A) and the observation frequency within the group (index B) (Dufrêne and Legendre, 1997). The difference between IndVal and IndVal.g is that IndVal.g takes into account the differences in group size. We calculated IndVal.g using the R package "indicspecies" (Cáceres and Legendre, 2009). As the method requires division of samples into groups, we categorized lakes based on water pH (acidic < 6, circum-neutral 6–8, alkaline > 8), EC (0–100, 100–200, 200–300, 300–400, >400) and into trophic state groups (TSG) based on their TSI (oligotrophic, mesotrophic, eutrophic, and hypereutrophic) (Table 1) and dystrophic based on literature. This was done because dystrophic lakes are usually viewed separately from clearwater lakes since the particular environmental conditions in these ecosystems can override the influence of nutrient concentrations (Korosi and Smol, 2012; Gray et al., 2022), and their classification criteria rely less on the nutrient levels and more on the lake catchment characteristics (Górniak et al., 1999; Gray et al., 2022).

Since significant changes in the lake morphometry are not common, the IndVal.g method was not used to analyze Cladocera species for different lake size and depth classes.

We used IndVal.g function from the "indicspecies" package in R to analyze for pH, TSG, and EC two times – once allowing for all the combinations of the groups (IndVal.g$^{\mathrm{all}}$) and the second time restricting each species to just one group (IndVal.g^{1}) of the chosen parameter (Cáceres et al., 2010). IndVal.g$^{\mathrm{all}}$ allows the inclusion of species with broader ecological niches in the assessment of lake conditions (De Cáceres et al., 2010), while the more traditional approach of assigning species to only one group (IndVal.g^{1}) could be more successful in finding the optimal conditions of the indicator species. Thus, we hope to improve the interpretation of the subfossil Cladocera assemblages in sedimentary records by analyzing species using both methods. IndVal.g analysis was done with 999 permutations.

Additionally, we tested the relationship between potential Cladocera indicator species and pH, pH$_{\mathrm{bot}}$, EC, EC$_{\mathrm{bot}}$, TSI, Secchi depth, Chl-*a*, TP, TN, DO$_{\mathrm{bot}}$, T$_{\mathrm{ann}}$, area, Depth$_{\mathrm{max}}$, Depth$_{\mathrm{ave}}$, C/N, LOI$_{\mathrm{org}}$, LOI$_{\mathrm{carb}}$, LOI$_{\mathrm{min}}$ using Pearson's correlation coefficient (Berman, 2016). This was done, to determine if any of the indicator species had stronger correlation with other measured parameters than those identified by the RDA analysis.

3. Results

3.1. Water chemistry

Our environmental data covers lakes with a wide range of pH, TSI, EC, area, Depth$_{\mathrm{max}}$, sediment LOI$_{\mathrm{org}}$, LOI$_{\mathrm{carb}}$, and LOI$_{\mathrm{min}}$ composition (Table 2). The gradient of T$_{\mathrm{ann}}$ for our data set is short (approximately 2.5 °C). Most of the lakes are alkaline (pH>8), eutrophic, and experience summer anoxia at the bottom water layer (Table 2). Lakes in the acidic group (pH<6) are also dystrophic, except for lake Nr 43, which is a mesotrophic lake. There are eight oligotrophic and six hypereutrophic lakes in our data set. The dataset contains 22 lakes with EC below 100 µS/cm. The least represented EC group is lakes with EC between 100 and 200 µS/cm (seven lakes). There are nine lakes with EC above 400 µS/cm and the variability of measurements within this group is large.

Correlation analysis showed that DO$_{\mathrm{bot}}$, T$_{\mathrm{ann}}$ had no significant

Table 2

Summary of the environmental parameters. pH, pH$_{\mathrm{bot}}$, electrical conductivity (EC and EC$_{\mathrm{bot}}$; µS/cm), trophic state index (TSI), Secchi depth (m), chlorophyll-*a* (Chl-*a*; µg/l), total phosphorous (TP; µg/l), total nitrogen (TN; µg/l), dissolved oxygen at the bottom layer (DO$_{\mathrm{bot}}$;mg/l), annual temperature (T$_{\mathrm{ann}}$°C), area (ha), maximum depth (Depth$_{\mathrm{max}}$;m), average depth (Depth$_{\mathrm{ave}}$; m), sediment C/N ratio, LOI$_{\mathrm{org}}$ (%), LOI$_{\mathrm{carb}}$ (%), LOI$_{\mathrm{min}}$ (%).

	Number of lakes with measurement	minimum	maximum	mean	median
pH	78	4,02	9,25	7,77	8,14
pH$_{\mathrm{bot}}$	39	3,80	8,65	7,42	7,60
EC	76	6	10,808	423	270
EC$_{\mathrm{bot}}$	39	9	474	215	229
TSI	78	34	90	55	55
Secchi	78	0,15	8,83	2,01	1,46
Chl-*a*	78	1	375	30	14
TP	78	8	1757	88	41
TN	49	288	3291	1019	828
DO$_{\mathrm{bot}}$	45	0,00	9,87	2,32	0,65
T$_{\mathrm{ann}}$	78	5,72	8,03	6,54	6,47
Area	78	1	8210	299	46
Depth$_{\mathrm{max}}$	78	1,00	33,00	9,60	6,85
Depth$_{\mathrm{ave}}$	60	0,50	10,90	4,25	3,90
C/N	56	6,99	44,40	13,27	11,76
LOI$_{\mathrm{org}}$	76	1,97	91,21	45,06	42,38
LOI$_{\mathrm{carb}}$	76	0,00	44,99	10,08	5,89
LOI$_{\mathrm{min}}$	76	7,30	97,74	45,18	45,29

Table 1

Trophic state descriptive water parameters and the threshold values between different trophic states according to Nürnberg 1996, Carlson 2007.

Trophic state	Trophic State Index	Secchi depth (m)	Total Phosphorous (µg/l)	Total Nitrogen(µg/l)	Chlorophyll-*a* (µg/l)
Oligotrophic	<40	>4	<10	<350	<3.5
Mesotrophic	40–50	2–4	10–30	350–650	3.5–9
Eutrophic	50–70	1–2	30–100	650–1200	9–25
Hypereutrophic	>70	<1	>100	>1200	>25

correlation with other measured parameters (Fig. 2). EC values correlated between the top and bottom water layers, and so did pH values. We found a positive correlation between EC and pH ($r = 0.53$). EC and pH values had a significant correlation with sediment descriptive parameters, such as C/N ratio and LOI$_{org}$, LOI$_{min}$, and LOI$_{carb}$ content of the sediments. Trophic state descriptive parameters (TSI, Secchi depth, Chl-*a*, TP, TN) showed a correlation between themselves. In addition, these parameters are correlated with Depth$_{max}$ (with TSI $r = -0.66$) and Depth$_{ave}$ (with TSI $r = -0.63$). Trophic state descriptive parameters showed no correlation with pH and EC in our data set.

3.2. Multivariate analysis

Forward selection in environmental analysis identified the parameters with statistically significant explanatory power for the RDA model as pH ($p < 0.001$), TSI ($p < 0.001$), area ($p < 0.001$), EC ($p = 0.022$), and Depth$_{max}$ ($p = 0.011$). When performing RDA analysis with all the environmental parameters, the constrained axis explained about 48 % of all data variation. After reducing the number of explanatory environmental parameters, this proportion was reduced to 38 % (Fig. 3), of which the first two axes accounted for 87 % of the explainable variation. From the explanatory variables, pH and EC had the strongest association with the RDA 1 axis, TSI and Depth$_{max}$ to the RDA 2 axis, and area to the RDA 3 axis (Table 3).

Cladocera species composition based PCA analysis revealed that our lakes cluster along the PC1 axis according to their TSG and pH. The two most clearly distinguishable groups were dystrophic/acidic (pH$<$6) and hypereutrophic lakes (Fig. 4). Regarding species composition, the group closest to dystrophic lakes was the oligotrophic lake group. The transition from oligotrophy to hypereutrophy forms a gradient along the PC1 and PC2 axes.

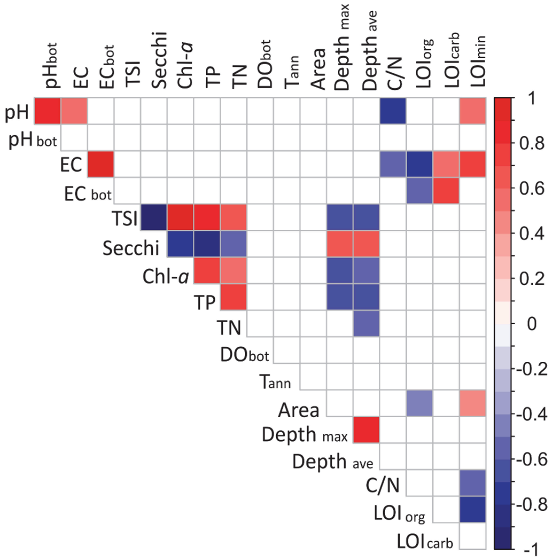


Fig. 2. Correlations between environmental variables (see details in Table 2, Appendix A). Only statistically significant correlations are shown ($p < 0.05$). Positive correlations between parameters are depicted in red, and negative correlations in blue. The strength of the correlation is indicated by color intensity. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Indicator species analysis

There were no significant differences between the pH and EC groups regarding TSI values (Fig. 5). However, hypereutrophic lakes had a pH median between 8.5 and 9.0, which is slightly more alkaline than the oligotrophic, mesotrophic and eutrophic lakes (median between 8 and 8.5). All acidic lakes (pH$<$6) had low EC values, but not all lakes with low EC had a low pH (Fig. 5). In our data set, the only EC group that did not contain oligotrophic lakes was EC 100–200 µS/cm (Appendix A). However, the EC median values increased with increasing trophic degree, and most of the lakes of the EC group $>$ 400 µS/cm belonged to the eutrophic lake group (Fig. 5).

We found 30 species with indicator species potential for pH, TSG and/or EC based on IndVal.g results. There were only three species that were indicative of only one of the environmental groups. These were *Oxyurella tenuicaudis* for hypereutrophy, and *Ophryoxus gracilis* and *Paralona pigra* for oligotrophy (Fig. 6). Other species that had a clear preference for a group within pH, TS, or EC were always indicative of more than one parameter. Such species were *Aonopsis elongata*, *Alonella excisa*, *Drepanothrix dentata*, *Alona rustica, Polyphemus pediculus*, *Holopedium gibberum* and *Coronatella rectangula*. Most Cladocera species were indicative of more than one parameter, and the group they were indicative of can depend on the selection criteria (IndVal.g^{all} or IndVal.g^{1}) (Fig. 6).

The only species indicative of acidic conditions (pH$<$6) that had its full distribution (except one outlier) within the pH range below six was *H. gibberum* (Fig. 7). *D. dentata* and *P. pediculus* had their occurrence median within pH$<$6. Species with their occurrence median within the pH 6–8 range were *Alona intermedia*, *A. rustica,* and *O. gracilis*. The rest of the species had a median pH of $>$ 8. While common in pH 6–8 and pH$>$8 conditions, some species were completely absent in pH$<$6. Such species were *Leptodora kindtii* (present in 0 % of pH$<$6, 47 % of pH 6–8, 63 % of pH$>$8 sites), *Monospilus dispar* (present in 0 % of pH$<$6, 41 % of pH 6–8, 45 % of pH$>$8 sites) (Appendix E). Some species (*Leydigia acanthocercoides*, *Pleuroxus aduncus*, *Bosmina theresites*, *Chydorus gibbus*, *Simpcephalus* sp.) were not observed in sites with pH$<$6. However, they could not be considered as common in any other pH group either.

Regarding the TSG, most species had their occurrence median in the TSI range descriptive of eutrophic conditions (Fig. 7). Exceptions were *A. elongata* and *P. pigra*, with their median in the mesotrophic TSI value range (40–50). Species that we did not find in oligotrophic conditions were *A. rustica*, *P. aduncus*, *P. pediculus,* and *Kurtzia latissima* (Appendix E). Species absent from eutrophic and hypereutrophic lakes were *Bythotrephes longimanus* and *H. gibberum*. Species listed as potential indicators in Fig. 6 that did not occur in the hypereutrophic lakes are *H. gibberum*, *O. gracilis*, *D. dentata*, *A. intermedia*, *A. rustica*, *Ilyocryptus sp.*, *M. dispar*, and *P. pigra*. Several species were absent from hypereutrophic lakes but were not identified as significant indicators by the IndVal.g analysis. Such species were *B. longimanus*, *C. gibbus*, *Rhyncathalona falcata*, *Simocephalus* sp. and *Latona setifera* (Appendix E).

Species strictly limited to lakes with EC 0–100 µS/cm were *H. gibberum* and *D. dentata* (Fig. 7). *A. elongata* and *A. rustica* occurrence medians were within the EC range of 0–100 µS/cm. However, they could occasionally appear in lakes with EC up to 300 µS/cm. The only species we did not find in the softwater lakes are *P. aduncus* and *Simoocephalus* sp.

9 out of 30 potential indicator species reached relative abundance above 10 %. We observed an increase of relative abundance with an increase of pH for *A. elongata*, *A. excisa*, *Acroperus harpae*, *Daphnia* spp. (Fig. 8). An opposite trend could be observed for *C. rectangula/ A. guttata*. We observed an increase in relative abundance with decreasing TSI in *Bosmina coregoni*, *Camptocercus rectirostris*, *D. dentata,* and *O. gracilis*. Species such as *Bosmina longirostris* and *Chydorus sphaericus* reached their maximum relative abundance in eutrophic conditions. *C. rectangula*, *C.rectangula/ A. guttata*, and *O. tenuicaudis* relative abundance increased with the increase of TSI values. *Binapertura*

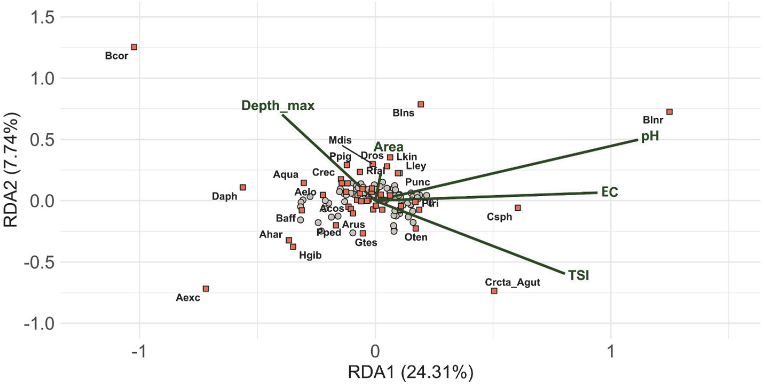


Fig. 3. Redundancy analysis (RDA) on studied lakes. The ordination plot is scaled by species, with the statistically significant explanatory variables portrayed on the green arrows. Red squares – species, gray circles – sites. Statistical significance of the RDA model $p < 0.001$. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 3
Biplot scores of the constraining variables for each of the three statistically significant RDA axes.

	RDA1	RDA2	RDA3
pH	0.752	0.650	−0.414
TSI	0.546	−0.762	−0.158
EC	0.638	0.164	−0.414
Area	0.015	0.410	−0.900
$\text{Detph}_{\text{max}}$	−0.265	0.842	−0.321

affinis, *C. sphaericus*, and P. aduncus relative abundance increased with the increase of EC.

The strongest correlations were observed between *A. excisa* ($r = -0.78$), *H. gibberum* ($r = -0.72$), *P. pediculus* ($r = -0{,}59$), *B. longirostris* ($r = 0.57$) and pH (Fig. 9). Some of the potential acidity indicators showed a stronger correlation with pH_{bot} than pH, such as *D. dentata* (pH $r = -0.43$, pH_{bot} $r = -0.86$), *H. gibberum* (pH $r = -0.72$, pH_{bot} $r = -0.88$), *A. elongata* (pH $r = -0.43$, pH_{bot} $r = -0.55$). Species indicative of more than one pH group (Fig. 6) generally showed weaker but still significant correlation with pH. Most of the species were correlated to several environmental parameters. An exception could be *Ilyocryptus sp.*, which only showed correlation with EC and EC_{bot}. Most species that correlated with pH also correlated with the C/N values. Regarding trophic state, *B. coregoni* had the strongest correlation with TSI values ($r = -0.61$).

4. Discussion

This study aims to identify species for environmental reconstruction based on sediment cores which are most often taken from the deepest part of the lake (Smol, 2008). However, these types of samples usually do not provide the spatial resolution to fully encompass different lake habitats, and temporal resolution of different months within one growing season. Therefore the results of this study might not at all cases be representative of full ecological spectrum of individual species as it is known that environment within microhabitats might differ, littoral taxa have higher accumulation closer to their original habitat (Nevalainen, 2011) and the conditions within lake can differ from month to month (Søndergaard et al., 2002). We found that subfossil Cladocera assemblages were primarily influenced by pH and TSI, with EC, lake area, and $\text{Depth}_{\text{max}}$ also being significant (Fig. 3). Since this study aims to reconstruct environmental parameters crucial for lake restoration, we analyzed subfossil Cladocera assemblages in Eastern Baltic lakes in relation to pH, trophic state, and EC gradients.

4.1. Waterbody environmental gradients

Our dataset does not fully support the common claim that dystrophic lakes are in general poor in nutrients and unproductive (Arsenault et al., 2018; Górniak, 2017; Cappelli et al., 2023). Two of the studied dystrophic lakes could be classified as relatively nutrient poor–Lakes Liepsalas (Nr 32) and Tolkājas (Nr 63) have a TSI value < 50 corresponding to

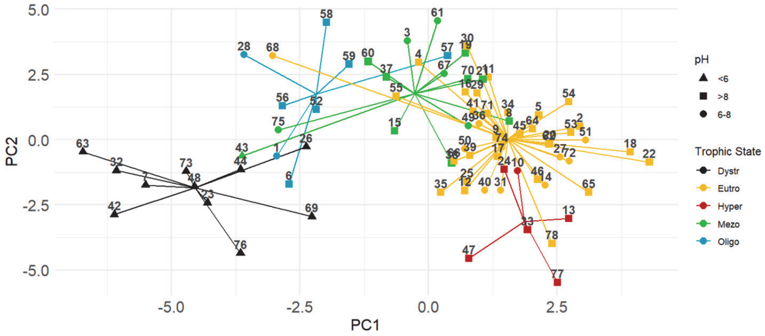


Fig. 4. Cladocera species-based Principal Component analysis (PCA). Lakes are marked based on their pH group and trophic state group. Proportion of variance PC1 = 0,14, PC2 = 0,1.

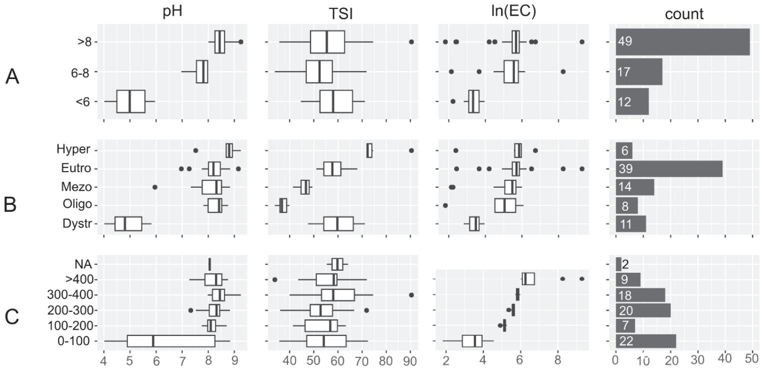


Fig. 5. Distribution of the pH, TSG, and EC groups in relation to pH, TSI, and EC. The last column shows the number of lakes in each group. A –pH groups. B – trophic state group, C – EC groups.

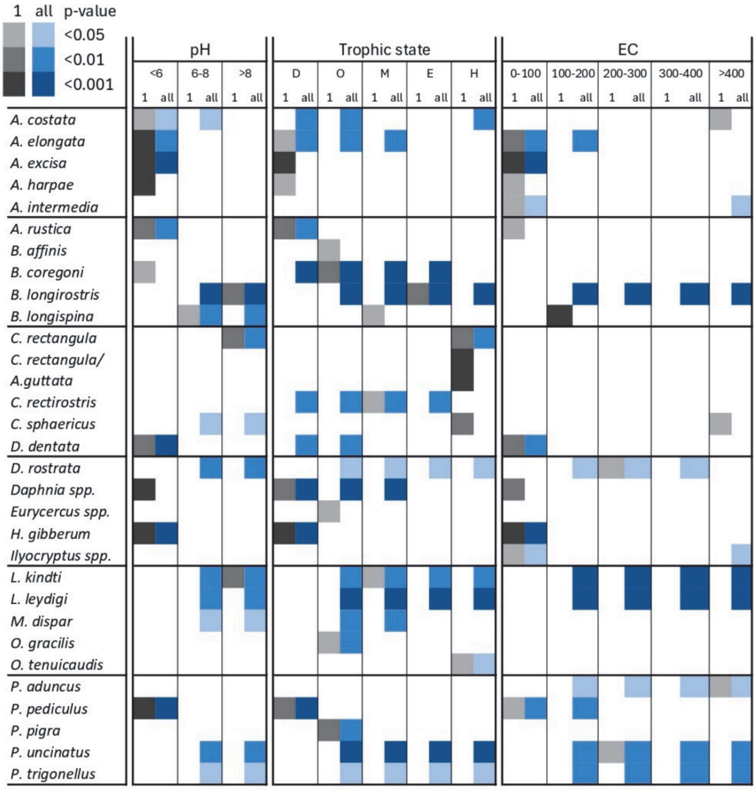


Fig. 6. Results of indicator species analysis. Columns 'pH $_{all}$', 'Trophic state $_{all}$', and 'EC $_{all}$' display the parameter combinations that species are indicative of by IndVal.g^{all} analysis (blue). Columns 'pH $_1$'', 'Trophic state $_1$'', and 'EC $_1$'' shows the specific conditions species are indicative of by IndVal.g^1 analysis (gray). The statistical significance of the IndVal.g result is indicated by color intensity. See complete information on indicator species statistics in Appendix D for pH, Appendix E for the trophic state group, and Appendix F for EC groups. Abbreviations: D- Dystrophic, O- Oligotrophic, M–Mesotrophic, E-Eutrophic, H-Hypereutrophic. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mesotrophic conditions. However, most of the studied dystrophic lakes had TSI values > 50 placing their productivity closer to the eutrophic lakes, even though we excluded Secchi depth from the calculations of TSI for this lake type (Fig. 5). Therefore, water chemistry results for dystrophic lakes of this study rather support the theory that dystrophic lakes can exhibit a range of nutrient enrichment levels and productivity, similar to non-dystrophic lakes (Järnefelt, 1958; Nürnberg and Shaw, 1999). Dystrophic lakes were first described as an extreme case of oligotrophic condition by Naumann in 1921 (cited in Jones, 1992**).** This statement still holds true in many sites of the Northern hemisphere even

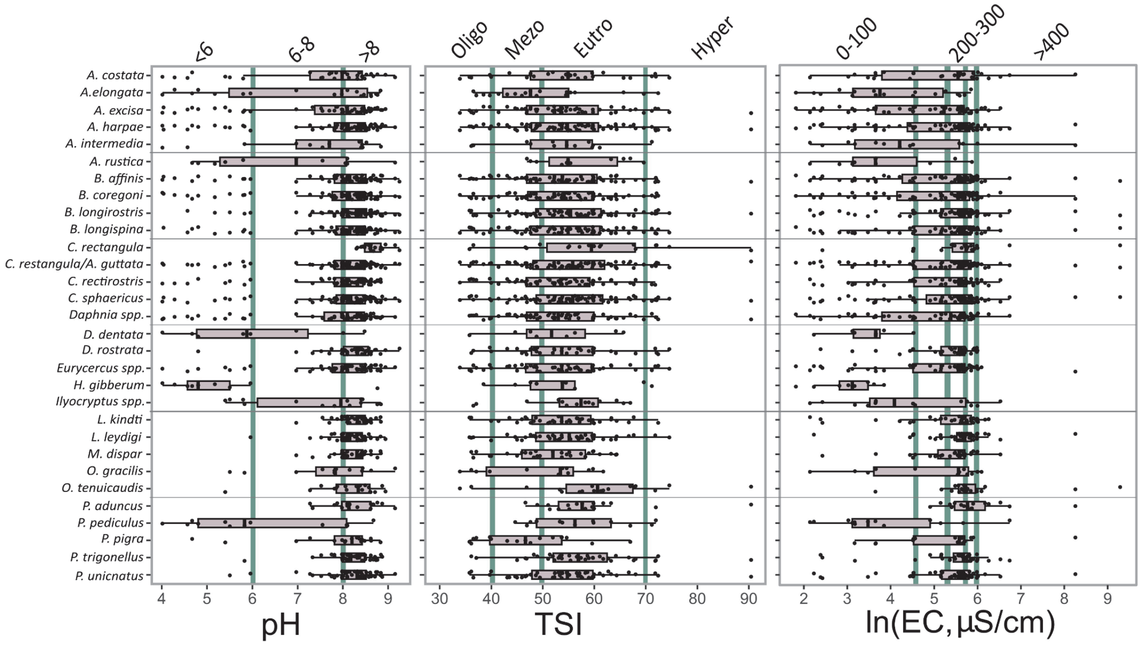


Fig. 7. Cladocera indicator species presence/absence based distribution regarding pH, TSI, and EC. Borders of the selected groups are indicated in the graphs with vertical lines.

though the definition and understanding of this lake type has evolved since then (Gray et al., 2022). Nonetheless cases where dystrophic lakes exhibit nutrient levels and productivity comparable to eutrophic non-dystrophic lakes are not rare (Grabowska et al., 2014; Gray et al., 2022; Karpowicz et al., 2023). It is possible, that the large amount of nutrient poor dystrophic lakes is not a result of fundamental properties of this lake type, but rather results from a fact that many dystrophic lakes are located in landscapes with weaker anthropogenic pressure. However, the variability of dystrophic lakes found in this study and literature could mean that studied dystrophic lakes do not fully cover the variability of this lake type and more extensive investigation of dystrophic lakes could be beneficial. In many European countries, oligotrophic lakes are also characterized by low pH (Macek et al., 2006; Huser et al., 2018; Cappelli et al., 2023), which has resulted in difficulties in distinguishing between the impact of acidic conditions and oligotrophy on Cladocera species assemblages (Lanka et al., 2024). This is not the case for the lakes of this dataset (Fig. 5) since most non-dystrophic lakes had a pH>7. Thus, the lake selection of this training set allows better distinguishing between the trophic state or pH as the driving factors for subfossil Cladocera assemblages.

All dystrophic and/or acidic lakes of the data set had low EC values (<50 μS/cm), which aligns with the literature on dystrophic lakes (Górniak, 2017; Cappelli et al., 2023). To our knowledge lakes with low pH and high EC can not be found in the Baltic countries, even though such combination has been found in other parts of the world (for example in mining, volcanic and brine lakes) (Lessmann et al., 2000; Armienta et al., 2008; Benison and Bowen, 2013). The lack of this environmental combination also means that EC cannot be considered entirely separately from pH in our dataset, which is also displayed by the correlation analysis (Fig. 2).

The correlation analysis showed no significant relationship between EC and any of the trophic state descriptive parameters (Fig. 2), even though a positive correlation between EC and nitrogen/phosphorous concentrations has been reported before (Wu et al., 2020). However, we still found a tendency for lakes with higher EC to generally have a higher trophic state (Fig. 5) and LOI_{carb} and LOI_{min} content of sediments (Fig. 2). Changes in LOI_{org}, LOI_{min}, and LOI_{carb} content are used as a proxy related to particle and nutrient input from the catchment in paleolimnology (Zawiska et al., 2020; Makohonienko et al., 2023) and in Baltic countries, carbonate bedrock is widespread (Nicodemus et al., 2018). Therefore, the cause of higher EC values and higher trophic state for lakes in fertile agricultural areas may be the same – the carbonate and nutrient input from the catchment through erosion.

The pH values were negatively correlated with C/N values and positively correlated with the LOI_{org}. The C/N ratio is indicative of the source of energy in the lake ecosystem food web–low C/N values are indicative of autochthonous production, but high C/N values of dominantly allochthonous production (Meyers et al., 1984; Meyers and Ishiwatari, 1993; Meyers and Teranes, 2001). Since most of our acidic lakes were also dystrophic, the elevated C/N values and low pH could have the same sources – dissolved humic matter imported from the catchment (Steinberg, 2004). Higher LOI_{org} content in naturally acidic lakes has been reported before (Steinberg, 1991). None of the sediment descriptive parameters were shown to be important as an explanatory variable for subfossil Cladocera assemblages. However, we can see that values of these parameters (C/N, LOI_{org}, LOI_{carb}, LOI_{min}) are connected to pH and EC and could be helpful for more successful separation between pH, TSG, and EC changes when assessing lake reference conditions.

4.2. *Cladocera as indicators of pH, TS and EC*

Indicator species are species that are sensitive to a particular environmental parameter/attribute and, as a result, can be used to assess the changes in this parameter (Siddig et al., 2016). An effective indicator species should respond to its environment in a predictable way and should be easy to interpret and detect (Dufrêne and Legendre, 1997; Butler et al., 2012).

To identify the most suitable indicator species applicable for analysis

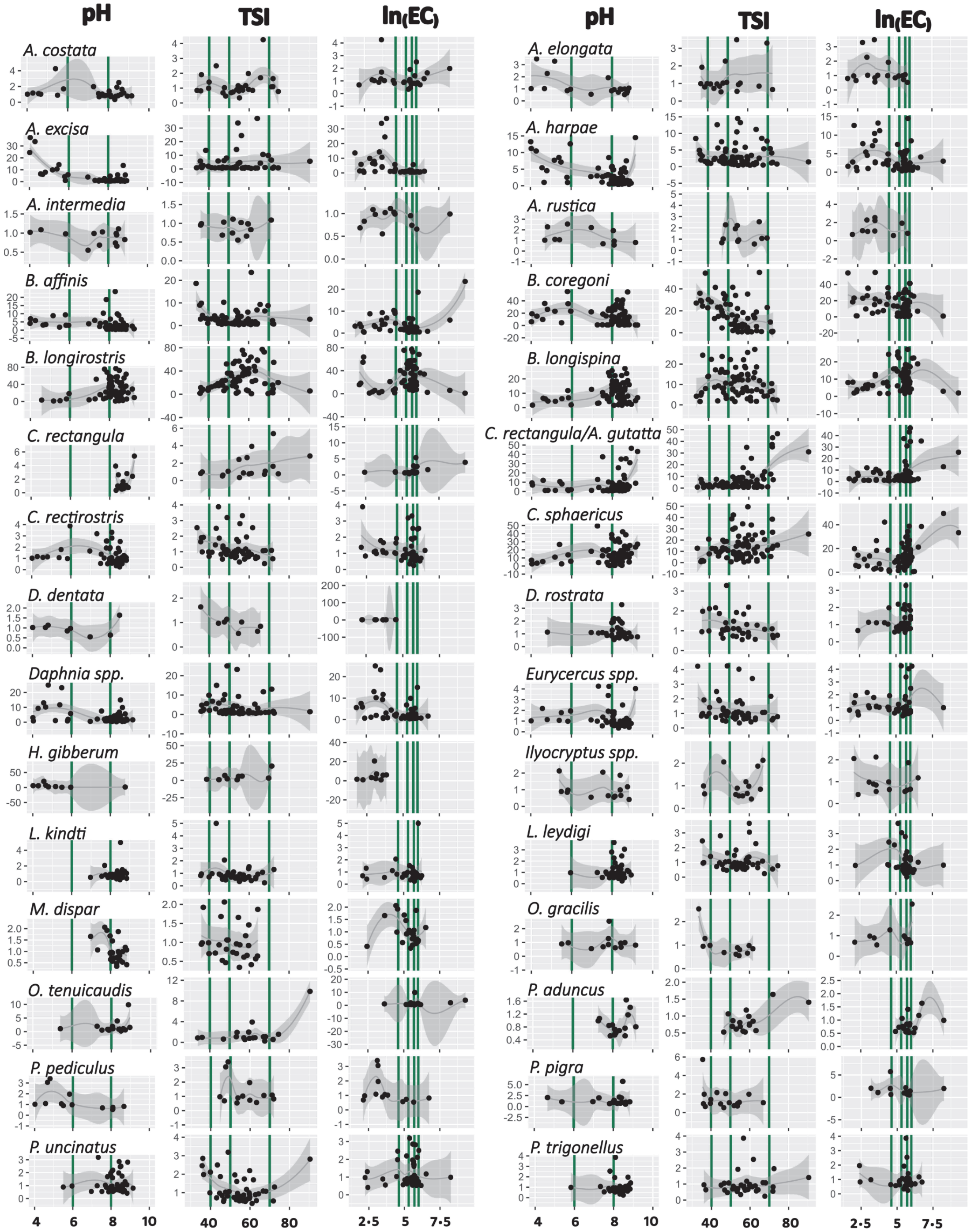


Fig. 8. Relative abundances of potential indicator species observations regarding pH, TSI, and EC. The LOESS and confidence interval shading are added to portray the general trend (gray). The green vertical lines highlight the boundary between the pH, TSG, and EC groups. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

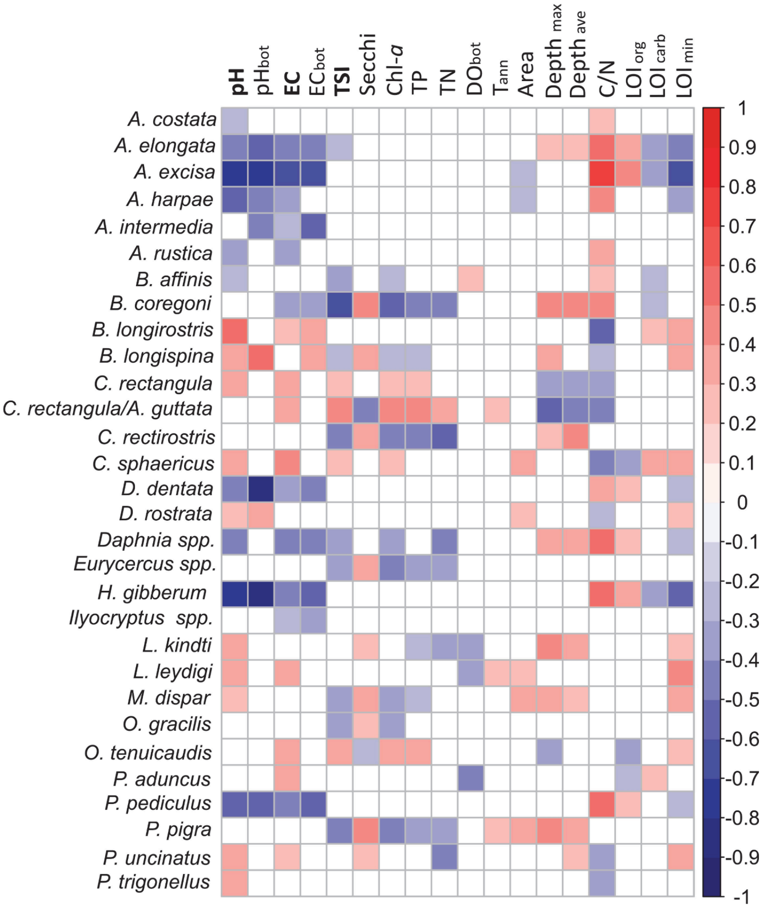


Fig. 9. Pearsons correlation between relative abundances of potential Cladocera indicator species and environmental parameters. Only statistically significant ($p < 0.05$) values are shown. Positive correlations between species and environmental parameters are depicted in red, and negative correlations in blue. The strength of the correlation is indicated by color intensity. To see the relative abundance of species in detail, see Appendix C. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of combined and separate effects of pH, TSG and EC, we employed the IndVal.g analysis, which considers both species response to the selected parameter and the likeliness of species detection (Dufrêne and Legendre, 1997; Podani and Csanyi 2010; Cáceres and Legendre, 2009). IndVal.g analysis results vary based on group combination criteria (IndVal.g^{all} or IndVal.g^{1}), emphasizing the importance of methodology in selecting indicator species.

Since different species have different likelihoods of observation, IndVal analyses each species independently (Dufrêne and Legendre. 1997; Cáceres and Legendre, 2009). However, this can complicate interpretation for species with low abundances, as minor increases (for example, from 1 % to 2 %) may appear more significant than it is. Most of the potential indicator species occur only in small relative abundances and could be affected by this issue (Fig. 8). Consequently, to use the indicator species identified by the IndVal.g analysis, we aimed to closely observe the behavior of each species within and outside their indicative lake group. Additionally, we sought to determine how each species could be interpreted when encountered in a paleolimnological sample.

Based on our dataset, the potential indicator species selected by IndVal.g analysis could be divided into six groups. The listing starts with pH as the most important explanatory variable:

1. Species that were indicative of pH<6, dystrophy, and low EC: *H. gibberum*, *A. excisa*, *P. pediculus*, *A. rustica*, *D. dentata;*
2. Species that overlap between pH<6/dystrophic, oligotrophic, and mesotrophic conditions: *Daphnia* spp., *A. elongata, B. coregoni*;
3. Species that overlap between lakes with EC>100 μS/C and alkaline/circum-neutral conditions (pH>6) (*D. rostrata*, *L. leydigi*, *P. uncinatus*, *P. trigonellus*);
4. Species indicative of other combinations of environmental groups: pH>6, oligotrophic, mesotrophic conditions (*M. dispar*);
5. Species that are indicative of only one parameter: (1) pH>6 (*L. kindtii)*, pH<6 (*A. harpae*); (2) TS – oligotrophic (*P. pigra*, *O. gracilis)*, mesotrophic (*B. longispina)*, eutrophic (*B. logirostris*), not hypertrophic (*C. rectirostris*) and hypereutrophic (*O. tenuicaudis*, *C. rectangula/ A. guttata, C. sphaericus*); (3) EC>100 (*P. aduncus*);
6. Species that can not be used as efficient indicators (*A. costata*, *A. intermedia*, *Ilyocryptus spp.*, *B. affinis*, *Eurycercus spp.*)

4.2.1. Species that were indicative of pH<6, dystrophy and low EC

Ind.Val.g analysis identified *Alona rustica*, *Alonella excisa*, *Drepanothrix dentata*, *Holopedium gibberum* and *Polyphemus pediculus* as indicator species for pH<6, dystrophic, and EC<100 μS/cm conditions. Species such as *A. rustica*, *D. dentata*, *H. gibberum,* and *P. pediculus* were generally found in small relative abundances and had their distribution median with lower pH and EC values compared to other potential indicator species (Figs. 7, 8). Therefore, these species' presence could indicate acidic/dystrophic and softwater lake conditions.

Previous literature has classified *A. rustica*, *H. gibberum,* and *P. pediculus* as acidophilic species (Krause-Dellin and Steinberg, 1986; Urtāne, 1998; De Eyto et al., 2003; Čeirāns, 2007). However, *D. dentata*, to our knowledge, has not been reported to have a relation to either TSG or pH. It has been mentioned that *D. dentata* is acidic conditions tolerant and has higher abundances in detritus-rich conditions (Fryer, 1972; Błędzki and Rybak, 2016), which could make peaty sediments of bog pools a favorable environment for this species. While IndVal.g classified *D. dentata* as a potential indicator for both oligotrophy and dystrophy, it was present in only one lake classified as oligotrophic. Therefore, we do not consider it a proper indicator species for oligotrophic conditions.

Based on our data, *H. gibberum* and *D. dentata* are highly specialized species for softwater (EC<100 μS/cm) conditions. While there were some outliers for these species in the pH groups, they were strictly restricted to the lake group with EC<100 μS/cm.

Lakes with pH<6 had a variety of dominant species, such as *A. excisa*, *B. coregoni*, *Daphnia spp*., and, on one occasion, *H. gibberum*. *H. gibberum* and *A. excisa* are mentioned in the literature as indicative of acidic conditions (Sandøy and Nilssen, 1986; Bērziņš and Bertilsson, 1990; Semenova and Napreenko, 2023). Although *A. excisa* was found in most lakes along the pH gradient, significant differences in its relative abundances between different pH groups were evident (Fig. 8). The average relative abundance of *A. excisa* was 13.5 % for sites with pH<6, compared to approximately 1.5 % for sites with pH>6. Even more, *A. excisa* reached its highest relative abundances (25–37 %) in the three most acidic sites (pH ≈4) of the training set. Literature agrees to *A. excisa* as an acidophilic species (Flössner, 200; Krause-Dellin and Steinberg, 1986), however we did not find in literature mentions of exact relative abundances that indicate acidic conditions. Based on the differences of average *A. excisa* percentages in sites with pH<6 and pH>6, we would consider that the site might be acidic if relative abundance exceeds 10 %.

4.2.2. Species that overlap between dystrophic/acidic, oligotrophic and mesotrophic conditions

Although dystrophic lakes were quite variable in their TSI values and did not fit with the assumption of dystrophic lakes being nutrient-poor, both PCA analysis (Fig. 4) and IndVal.g analysis (Fig. 6) showed that the species composition in oligotrophic and dystrophic lakes are somewhat similar. For example, IndVal.g^{all} analysis showed that such species as *A. elongata* and *Daphnia* spp. indicate dystrophic, oligotrophic, and mesotrophic conditions. In contrast, IndVal.g^{1} classified these species as indicators of dystrophic conditions.

Alonopsis elongata is often classified as an oligotrophic, acidophilic species with a preference for soft water conditions (Krauese-Dellin and Steinberg, 1986; De Eyto et al., 2003; Błędzki and Rybak, 2016; Fiłoc et al., 2018). The reason this species is observed more frequently in dystrophic lakes might be its preference for detritus as its food source (De Eyto and Irvine, 2001). It was present in approximately 50 % of dystrophic, oligotrophic and mesotrophic lakes, in comparison to 5 % of eutrophic and 15 % of hypereutrophic lakes (Appendix E), which means that it is indeed more likely to appear in dystrophic or nutrient-poor lakes. The exceptions to the rule were two eutrophic lakes (nr. 55 Sekšu, nr. 68 Ungurs) and one hypereutrophic lake (nr. 24 –Kooraste Linajärv). Lake Ungurs and Kooraste Linajärv are softwater (EC<100 μS/cm) lakes showcasing the EC preferences of this species. Based on IndVal.g analysis*,* *A. elongata* has a more statistically significant relationship to pH and EC than the TSG (Fig. 6). In cases where *A. elongata* was not found in pH<6 or EC<200 μS/cm the lakes were classified as oligotrophic or mesotrophic. This highlights how, in paleolimnology, alternative hypotheses for species presence should be considered, and different parameters can act as limiting for the same species.

Daphnia spp. generally displayed higher relative abundance values in dystrophic, oligotrophic, and mesotrophic conditions (Fig. 8, Appendix E), even though it was present across all trophic states. There are several challenges in making conclusions about past lake environments based on *Daphnia* spp. as their remains are not preserved in lake sediments as well as chydorids (Sarmaja-Korjonen, 2007; Leppänen and Weckström, 2016). Consequently, the distinction between *Daphnia* and *Ceriodaphnia* species in sediment records is often impossible. In our dataset, *Daphnia* spp. represents a group of species that could have different environmental preferences. For example, *Daphnia longispina* is typical for nutrient-poor lakes, while *Daphnia cucullata* occurs in more eutrophic lakes (Urtāne, 1998; Muñoz-Colmenares et al., 2021). Due to species-specific trophic state preferences of *Daphnia* spp. we can not unequivocally claim that *Daphnia* spp. prefers oligotrophic and mesotrophic conditions. The findings in the literature supporting *Daphnia* spp. as typical for oligotrophic lakes are somewhat contradictory, with some authors finding that nutrient-poor conditions can be favorable for large-sized Cladocera and some *Daphnia* species (Jensen et al., 2013; Nevalainen and Luoto, 2013; Beaver et al., 2020) and others finding just the opposite (Muñoz-Colmenares et al., 2021). Nevertheless, our results align with the literature to a degree- *Ceriodaphnia* spp. can be a dominant species in acidic/dystrophic lakes (Urtāne, 1998; Karpowicz et al., 2023). Other possible explanations for the increase in the relative abundance of *Daphnia* spp. could be a result of differences in the food web structure between dystrophic and non-dystrophic lakes. Dystrophic lakes are characterized by dark water color and low transparency, which reduce fish predation pressure on zooplankton due to poor visibility (Estlander et al., 2009; Zagars et al., 2024). This often results in an increase in the average size of the Cladocera (Estlander et al., 2009). *Daphnia* spp. contributes to these findings as a species group characterized by its large size (Błędzki and Rybak, 2016). It must be noted that the succession from Daphnia-dominated to Bosmina-dominated associations has also been linked to climate warming (Nevalainen et al., 2014), making it difficult to determine whether high *Daphnia spp*. abundance in historical samples is related to acidity/dystrophy, oligotrophic, mesotrophic, or cooler climatic conditions.

IndVal.g analysis classified *Bosmina coregoni* as either intolerant to hypereutrophic conditions (IndVal.g^{all}) or indicative of oligotrophic conditions (IndVal.g^{1}). The literature commonly supports the role of *B. coregoni* as an oligotrophy indicator (Gąsiorowski and Hercman, 2005; Bos and Cumming, 2003; Kamenik et al., 2007; Ochocka and Karpowicz, 2022). However, it has been mentioned that *B. coregoni* representation along trophic state gradient can differ when the taxonomical resolution is increased to the sub-species level (Hofmann, 1996; Urtāne, 1998). Although *B. coregoni* distribution covers TSI from oligotrophic to highly eutrophic conditions (Fig. 5), our results show a negative correlation between *B. coregoni* relative abundance and TSI (Fig. 4), suggesting that a higher relative abundance of *B. coregoni* in a sample indicates a lower trophic status of the lake. Two lakes, Ohepalu (lake nr 44, TSI=65, *B. coregoni* 65 %) and Kurtava (lake nr 26, TSI=59, *B. coregoni* 35 %), are outliers in the *B. coregoni*-TSI relationship. Both are dystrophic lakes and cluster near oligotrophic lakes in the PCA analysis (Fig. 4). The dominance of *B. coregoni* in these lakes highlights the similarity between some dystrophic and oligotrophic lakes.

An exception to the previously mentioned similarities of oligotrophic and dystrophic conditions is *Monospilus dispar*, which is an indicator of pH>6 and oligotrophic/mesotrophic conditions, based on IndVal.g analysis. Similar findings of *M. dispar* ecology have been reported by other authors (Krause-Dellin and Steinberg, 1986; Chen et al., 2010).

4.2.3. Species that overlap between lakes with alkaline/circumneutral (pH>6) and EC>100 μS/C conditions

Some Cladocera are intolerant to acidic conditions – reasons for this can be physiological, such as ion uptake inhibition in acidic conditions

(Smirnov, 2017), or indirect, such as availability of their preferred food source or habitats (Jones, 1992; Estlander et al., 2009). We identified four species that were indicative of non-acidic (pH>6), non-dystrophic, and non-softwater (EC>100 μS/cm) conditions. *Disparalona rostrata*, *Leydigia leydigi*, *Pleuroxus uncinatus* and *P. trigonellus* were common in circumneutral and alkaline conditions but appeared in acidic lakes only on one or two occasions. Similar results have been reported by some other authors (Krause-Dellin and Steinberg, 1986; Duigan and Kovach, 1991; Chen et al., 2010). For example, *D. rostrata* is known to have high Ca demand, which could explain its disappearance in acidic and softwater conditions (Shapiera et al., 2011). Since the observation frequency in EC<100 μS/cm compared to lakes with pH<6 was higher for *D. rostrata* (in 8 % of pH<6; 27 % of EC<100), *P. uncinatus* (in 16 % of pH<6; 36 % of EC<100), and *P. trigonellus* (in 8 % of pH<6; 18 % EC<100), it is possible that these species are more sensitive to pH than to EC. The preference for non-acidic conditions of *P. trigonellus* has been mentioned in literature (Błędzki and Rybak, 2016) and it has been marked as an indicator of high EC by Bjerring et al. (2009). However, *P. trigonellus* and *P. uncinatus* are usually either treated as generalist species with no environmental preference or in connection to eutrophication and human impacted sites (Hofmann, 1996; Tóth et al., 2019). *P. uncinatus* and *P. trigonellus* are both macrophyte associated species (Błędzki and Rybak, 2016), therefore it is possible that their absence in acidic softwater lakes is connected to absence of their preferred macrophyte habitats. In contrast, *L. leydigi* seems more strictly limited to non-acidic, non-softwater lakes (Fig. 7,8). *L. leydigi* is associated with upper layer of sediments in littoral and profundal zone, feeding on detritus (Sloka, 1981). In other studies, this species has sometimes been attributed to eutrophic waters with oxygen depletion (Hofmann, 1996; Błędzki &Rybak, 2016), however no such preference was found in this study (Fig. 7, Fig. 9).

4.2.4. *Species that are indicative of only one parameter*

Acroperus harpae is classified as indicative of pH<6 (Fig. 6). The association between *A. harpae* and pH is statistically highly significant (Fig. 6), and this species is considered tolerant to acidification (Zawisza et al., 2019). However, an increase in *A. harpae* is often interpreted as associated with macrophyte abundance (Kuczyńska-Kippen, 2008; Davidson et al., 2010; Mazei et al., 2020). While submerged macrophytes are typically absent from dystrophic lakes, other types, such as sphagnum mosses and floating leaf plants, can be present (Mäemets, 1968; Gray et al., 2022). Although *A. harpae* is not classically associated with sphagnum and detritus, this relation has been reported before (Henrikson, 1993; Zawisza et al., 2019). For example, Henrikson (1993) described *A. harpae* as abundant in both sphagnum and detritus substrates in acidic lakes.

Leptodora kindtii is a species that was classified as indicative of non-acidic, non-dystrophic conditions but showed no connection to EC. *L. kindtii* is a predatory species, and it has been estimated that it can eliminate up to 50 % of Cladocera production during the summer months (Karabin, 1974; Wojtal et al., 2004; Lesutienė et al., 2012). Given this significant predation pressure, the absence of *L. kindtii* in dystrophic lakes likely contributes to the observed increase in *Daphnia* spp. populations in these environments, as *L. kindtii* frequently preys on *Daphnia* spp. (Lunte and Luecke, 1990; Wojtal et al., 2004).

IndVal.g classified *Coronatella rectangula* as the only species indicative of alkaline conditions (pH>8). Nevertheless, the context of our methodology must be considered in these results. We only counted *C. rectangula* as a separate species if it was confirmed by the skeletal elements with the most distinguishable features – postabdomen. This skeletal element is usually not as common in samples as headshield and shell (Zharov et al., 2021), and the possibility of finding it increases if *C. rectangula/A. guttata* is the dominant species in the sample. *C. rectangula/A. guttata* becomes the dominant species (relative abundance > 20 %) in most of the hypereutrophic and some of the eutrophic lakes (Fig. 8). This result is similar to that of other authors, who have classified *C. rectangula* as an indicator of eutrophic conditions (Brodersen et al., 1998; Zawisza et al., 2016 a).

Bosmina longirostris and *Bosmina longispina* are common species that can be present in different environmental conditions. IndVal.g analysis classified both species as indicators of non-acidic (pH>6) conditions. *B. longirostris* and *B. longispina* were not present in acidic and dystrophic conditions in large relative abundances and were observed less frequently in acidic lakes (for example, *B. longirostris* is present in 40 % of pH<6 lakes, but > 90 % of pH>6 lakes). However, these species have large variability in their relative abundances also within lakes with pH>6 (Fig. 8), and it has been reported that *B. longirostris* sometimes can be the dominant species in dystrophic and acidic lakes as well (Malley and Chang, 1987; Karpowicz et al., 2023). Therefore, in our opinion, it could not be used as an indicator for lake pH based on the presence or relative abundance of this species in paleolimnological samples.

B. longirostris is commonly known as an indicator of eutrophic conditions (Boucherle and Züllig, 1983; Čeirāns, 2007; Adamczuk, 2016). The reason why we did not find a correlation between this species and TSI values is the fact that it has a bell-shaped distribution along the TSI value gradient, with the maximum relative abundances in the TSI values between 50 and 70, which is the TSI value range for eutrophic lakes. This species preference is captured by the IndVal.g^1 analysis (Fig. 6).

Our data shows that *Bosmina longispina* has maximum abundance in slightly eutrophic and mesotrophic conditions (Appendix D), but they can be present in oligotrophic to hypereutrophic conditions. Still, from other studies, *B. longispina* is known as a typical low phosphorus (Jensen et al., 2013) and low conductivity (Jensen et al., 2019) species. Our results suggest that in the Baltic States, this species is more tolerant to eutrophic conditions than *B. coregoni* but reaches maximum relative abundance in lakes with lower TSI values than *B. longirostris*. We can see in figure of RDA analysis (Fig. 3) that *B. longispina* is located somewhere between *B. coregoni* and *B. longirostris*, which could mean that in Baltic states in the succession oligotrophy->mesotrophy->eutrophy is accompanied by the species succession *B. coregoni*-> *B. longispina*-> *B. longirostris*.

We found two species that are clear oligotrophy indicators: *Paralona pigra* and *Ophryoxus gracilis* (Fig. 6). The same species have been reported as oligotrophy indicators in other studies (Brodersen et al., 1998; Walseng and Halvorsen, 2005). Neither *P. pigra* nor *O. gracilis* can be found in large abundance. Therefore, their indicative value depends on the species' presence in the sample rather than relative abundance.

A species that was classified as indicative of non-hypereutrophic conditions is *Camptocercus rectirostris*. In our dataset, this species is distributed along the whole TSI gradient but was observed with lesser frequency in hypertrophic lakes. The interpretation of this species presence in samples varies – it is sometimes attributed as species with a preference for moderate nutrient levels (Brodersen et al., 1998; Bishop et al., 2009) or classified as macrophyte-associated (Dong et al., 2020; Davidson et al., 2010). Our results extend to those of literature since eutrophication can result in the loss of macrophytes (Hough et al., 1989; Sand-Jensen et al., 2008).

Chidorus sphaericus is shown as a hypereutrophy indicator by IndVal.g^1 analysis. Several other studies have recognized this species as characteristic of a high trophic state (Haberman and Haldna, 2014; Shumate et al., 2002), but others have stated that it can be present in samples in large numbers in oligotrophic and mesotrophic lakes as well (De Eyto, 2001; Kamenik et al., 2007). Our results align with both findings – generally, *C. sphaericus* relative abundance can vary between < 1 % and 20 % independent of the lake's trophic status; however, the cases where this species' relative abundance is higher than this were only in eutrophic and hypereutrophic lakes. Therefore, we agree with other authors that high numbers of this species (>20 %) indicate eutrophic or hypereutrophic conditions, but any fluctuations below that seem subjectively uninterpretable. Still, it is worth mentioning that genetic analyses revealed differentiation within the *C. sphaericus*, suggesting that a cryptic species complex exists (Belyaeva and Taylor, 2009). This, in turn, can increase the variety of each sub-taxa's ecological preferences.

In literature*, Oxyurella tenuicaudis* has been reported from oligotrophic to eutrophic lakes (Błędzki and Rybak, 2016), undisturbed oxbow lakes (Berta et al., 2018), and hypereutrophic, EC>400 µS/cm oxbow lakes with rich patches of *Stratiotes aloides* (Strzałek and Koperski, 2019). The difficulties in pinpointing the ecological preference for this species have been connected to the fact that although *O. tenuicaudis* is widely distributed, it is rarely observed (Berta et al., 2018). In our dataset, *O. tenuicaudis* in small abundances was observed in 23 % of the lakes. The exception is lake nr 77 (Võnnu), which has the highest TSI value in the training set (TSI=90.4). In this lake, *O. tenuicaudis* reaches a relative abundance of 8 %. *O. tenuicaudis* has been associated with hypereutrophic conditions by Chen et al. (2010) as an indicator of high EC (Bjerring et al., 2009) and as a saltwater tolerant species (Błędzki and Rybak, 2016). Although the outlier might have highly influenced the IndVal.g index A (Appendix E), this species is more frequently observed in hypereutrophic lakes (observation frequency in dystrophic – 0.091, oligotrophic – 0.250, mesotrophic – 0.071, eutrophic – 0.282, hypereutrophic – 0.500). Therefore, we agree that this species could be indicative of hypereutrophic conditions.

Pleuroxus aduncus was recognized as an indicator of high EC (>400 µS/cm) by IndVal.g^1 analysis, which aligns with the findings of Bjerring et al. (2009). This species distribution was limited to lakes with pH>7 and EC>100 µS/cm. This species is most likely not recognized as an indicator of non-acidic conditions because of its low observation frequency compared to the overall number of sites with pH>6. *P. aduncus* reaches slightly higher relative abundance in sites with EC>400 µS/cm. However, these abundances are still low (an increase from 0.5 % to 2 %). Therefore, the results of IndVal.g^{all} analysis, which recognizes that this species is limited to lakes with EC above 100 µS/cm, should be considered more appropriate for interpreting *P. aduncus* in the paleolimnological samples.

4.2.5. *Species that do not make effective and simply interpretable indicators*

Although 30 species were recognized as potential indicators by IndVal.g analysis, five of them would be difficult to reliably interpret in paleolimnological samples in relation to pH, TSG, or EC. These species were *Alona costata*, *A. intermedia*, *Binapertura affinis*, *Eurycercus* sp., and *Ilyocyptus* spp..

Species with unusual combinations of environmental factors were *A. costata* (dystrophic, oligotrophic, hypereutrophic conditions and EC of > 400µS/cm), *Ilyocryptus* spp., and *A. intermedia* (EC 0–100 + >400 µS/cm, in IndVal.g^{all} analysis). This suggests that these species may be more influenced by parameters not measured in this study, and their relative abundances might not be driven by pH, TSG, or EC. Consequently, the statistically significant relationships observed with these factors may be coincidental.

Binapertura affinis and *Eurycercus* spp. are classified as indicators of oligotrophic conditions only by IndVal.g^1 analysis. Sometimes *Eurycercus* spp. and *B. affinis* are mentioned as indicators of low trophic state (Hofmann, 1996; Bos and Cumming, 2003). We found both species in lakes of all trophic states, and due to the significant influence of a few outliers on the increase of their average relative abundance values, we do not consider these species reliable indicators.

4.3. *Implications for lake management and restoration*

The established surface sediment training set based on Cladocera in Baltic countries is closing the knowledge gap between existing training sets from northern and central Europe (Nevalainen et.al., 2011**;** Zawisza et al., 2016b), contributing information necessary for improvement of lake management and restoration strategies that so far have been based on relatively short-term, sporadic data. This is especially relevant to lentic urban water ecosystems as surveys there are focused more towards public health, and regular national water framework directive monitoring is seldom performed. This situation presents certain limitations; despite the growing number of restoration techniques and nature-based solutions, the most effective management and restoration strategies require a thorough understanding of natural variability over time, baseline conditions, and ecosystem vulnerability (Smol, 1992; Watson and Medeiros, 2021). The findings of the present study will allow to consider specific biological and physicochemical parameters of Baltic countries in order to identify the cause of ecological changes in lakes and ponds and site-specific vulnerability. A historical perspective is crucial for setting evidence-based restoration targets, and determining the most appropriate management strategies. Understanding baseline conditions also helps to assess the state of lakes after restoration, including estimating the timescales for observing improvements. Therefore, this study offers a valuable toolbox for current and future decision-makers and ecosystem managers.

5. Conclusions

This research shows complex Cladocera species specific responses to a variety of environmental conditions and highlights the necessity to consider multiple possible drivers behind the changes in their relative abundance or presence for reference condition reconstruction.

Our hypothesis was partially confirmed since the species showed sensitivity to pH, trophic state and EC, with the pH being the most significant influencing factor. However, subfossil Cladocera sensitivity was not shown in all of our defined groups. Based on the results of this study, it should be possible to distinguish between lakes with pH<6 and pH>6, as well as EC<100 and EC>100 µS/cm, and all the TSG.

We found species that are indicative of

1. A combination of parameters: for pH<6, dystrophy and EC<100: *A. excisa, A. rustica*, *P. pediculus, H. gibberum,* and *D. dentata*; for pH>6 and EC>100: *D. rostrata*, *L. leydigi, P. uncinatus* and *P. trigonellus;* for pH>6 or oligotrophic/mesotrophic conditions *M. dispar*;
2. Species that can be indicative of several parameters that do not necessarily combine: *A. elongata* for oligotrophic/mesotrophic conditions or pH<6 or EC<200, *Daphnia spp*. for ologotrophic/mesotrophic conditions or pH<6;
3. Species indicative of one parameter: *B. coregoni*, *P. pigra*, *O. gracilis* – oligotrophy, *B. longispina*- mesotrophy, *B. longirostris* – eutrophy, *C. sphaericus*, *O. tenuicaudis*, *C. rectangula*/*A. gutatta* hypereutrophy, *L. kindti* pH>6, *P. aduncus* EC>100.

The results of indicator species (IndVal.g) analysis heavily depend on the environmental parameter selection and grouping criteria (IndVal.g^1 or IndVal.g^{all}). A more thorough look into the differences in the selected groups allowed us to identify species that, although shown to have a statistically significant relationship to some environmental factors, did not make convincing indicators for paleolimnological reconstructions.

We did not find a single indicator species that could be used as a perfect indicator for environmental reconstruction by itself. Therefore, we suggest that the whole Cladocera species assemblage should always be considered. Our findings underline the importance of a nuanced approach in ecological assessments and the need for careful consideration of multiple environmental parameters when using indicator species for reconstructing past ecological conditions.

While the current study focused on the influence of pH, trophic state, and EC on subfossil Cladocera assemblages, it would be beneficial to further investigate other promising parameters such as lake morphology, sediment composition, fish predation influence, and macrophyte abundance. Exploring these factors could subsequently improve the quality of lake ecosystem reconstructions.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used GPT4 in order to improve text readability. After using this tool authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

CRediT authorship contribution statement

Anna Lanka: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Anneli Poska:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization. **Varvara Bakumenko:** Writing – original draft, Investigation. **Inta Dimante-Deimantovica:** Writing – review & editing, Investigation, Conceptualization. **Merlin Liiv:** Writing – review & editing, Writing – original draft, Investigation. **Normunds Stivrins:** Writing – review & editing, Investigation. **Matiss Zagars:** Writing – review & editing, Investigation. **Siim Veski:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

This work was funded by the Doctoral School of Earth Sciences and Ecology, the European Union, European Regional Development Fund (ASTRA "TTÜ arenguprogramm aastateks 2016-2022″), ESF projects PRG 1993, TK 215, the post-doctoral project 1.1.1.2/VIAA/4/20/736: "Pristine peat lake ecosystems–aiming for ecological metrics that reflect undisturbed ecosystem functioning." and by Swedish strategic research area BECC (Biodiversity and Ecosystem Services in a Changing Climate); MERGE (ModElling the Regional and Global Earth system at Lund University). We would like to thank Erik Jeppesen and everyone else who helped to improve the quality of this work with helpful advice, but especially Kati Lind, Tiiu Alliksaar, Helen Tammert, Teet Jäetma, Anu Kisand for technical assistance, Ivan Krivokorin, Laura Grīnberga for help in the field works, Ingmar Ott, Jolanta Jēkabsone, Vahanas Grigorianas for help with acquiring information on the studied lakes, Liisa Nevalainen, Izabela Zawiska and Kay Van Damme for help with species determination, Suprosanna Shit, Zane Rekšņa and Jüri Vassiljev for assistance with data visualization.

Appendix A–F. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.112592.

References

Abell, J.M., Özkundakci, D., Hamilton, D.P., Reeves, P., 2020. Restoring shallow lakes impaired by eutrophication: approaches, outcomes, and challenges. Crit. Rev. Environ. Sci. Technol. 52 (7), 1199–1246. https://doi.org/10.1080/10643389.2020.1854564.

Adamczuk, M., 2016. Past, present, and future roles of small cladoceran Bosmina longirostris (OF Müller, 1785) in aquatic ecosystems. Hydrobiologia 767, 1–11. https://doi.org/10.1007/s10750-015-2495-7.

Adrian, R., O'Reilly, C.M., Zagarese, H., Baines, S.B., Hessen, D.O., Keller, W., Livingstone, D.M., Sommaruga, R., Straile, D., Van Donk, E., Weyhenmeyer, G.A., 2009. Lakes as sentinels of climate change. Limnol. Oceanogr. 54 (6part2), 2283–2297. https://doi.org/10.4319/lo.2009.54.6_part_2.2283.

Alliksaar, T. Heinsalu, A., Saarse, L., Salujõe, J., Veski, S. 2005. A 700-year decadal scale record of lake response to catchment land use from annually laminated lake sediments in southern Estonia. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie, 29 (1), 457−460.

Amoatey, P., Baawain, M.S., 2019. Effects of pollution on freshwater aquatic organisms. Water Environ. Res 91 (10), 1272–1287. https://doi.org/10.1002/wer.1221.

Aplinkos Apsaugos Agentūra, 2024. Ežerų ir tvenkinių monitoringo rezultatai. URL: https://aaa.lrv.lt/lt/veiklos-sritys/vanduo/upes-ezerai-ir-tvenkiniai/valstybinis-upiu-ezeru-ir-tvenkiniu-monitoringas/ezeru-ir-tvenkiniu-monitoringo-rezultatai/?fbclid=IwAR1Ab_0aJCnEdACdxKXQEouFIckTmfZrbmoYHuLejCsLZSvpOH2FboTuoJ4 (accessed 24.05.2024).

Armienta, M.A., Vilaclara, G., De la Cruz-Reyna, S., Ramos, S., Ceniceros, N., Cruz, O., Aguayo, A., Arcega-Cabrera, F., 2008. Water chemistry of lakes related to active and inactive Mexican volcanoes. J. Volcanol. Geoth. Res. 178 (2), 249–258. https://doi.org/10.1016/j.jvolgeores.2008.06.019.

Arsenault, J., Talbot, J., Moore, T.R., 2018. Environmental controls of C, N and P biogeochemistry in peatland pools. Sci. Total Environ. 631, 714–722. https://doi.org/10.1016/j.scitotenv.2018.03.064.

Baastrup-Spohr, L., Sand-Jensen, K., Olesen, S.C., Bruun, H.H., 2017. Recovery of lake vegetation following reduced eutrophication and acidification. Freshw. Biol. 62 (11), 1847–1857. https://doi.org/10.1111/fwb.13000.

Battarbee, R.W., 1990. The causes of lake acidification, with special reference to the role of acid deposition. *Philosophical Transactions of the Royal Society of London. B, Biological.* Sciences 327 (1240), 339–347. https://doi.org/10.1098/rstb.1990.0071.

Beaver, J.R., Tausz, C.E., Black, K.M., Bolam, B.A., 2020. Cladoceran body size distributions along temperature and trophic gradients in the conterminous USA, pp. 613–629 J. Plankton Res. 42 (6). https://doi.org/10.1093/plankt/fbaa053.

Belyaeva, M., Taylor, D.J., 2009. Cryptic species within the Chydorus sphaericus species complex (Crustacea: Cladocera) revealed by molecular markers and sexual stage morphology. Mol. Phylogenet. Evol. 50 (3), 534–546. https://doi.org/10.1016/j.ympev.2008.11.007.

Benison, K.C., Bowen, B.B., 2013. Extreme sulfur-cycling in acid brine lake environments of Western Australia. Chem. Geol. 351, 154–167. https://doi.org/10.1016/j.chemgeo.2013.05.018.

Bennion, H., Battarbee, R.W., Sayer, C.D., Simpson, G.L., Davidson, T.A., 2011. Defining reference conditions and restoration targets for lake ecosystems using palaeolimnology: a synthesis. J. Paleolimnol. 45, 533–544. https://doi.org/10.1007/s10933-010-9419-3.

Berman, J.J., 2016. Chapter 4—Understanding your data. *Data simplification*, pp.135-187.

Berta, C., Gyulai, I., Szabó, J.L., Simon, E., Nagy, A.S., Somlyai, I., Grigorszky, I., 2018. Cladocerans as indicators in the importance of passive nature conservation. Biologia 73, 875–884. https://doi.org/10.2478/s11756-018-0097-3.

Bērziņš, B., Bertilsson, J., 1990. Occurrence of limnic micro-crustaceans in relation to pH and humic content in Swedish water bodies. Hydrobiologia 199 (1), 65–71. https://doi.org/10.1007/BF00007834.

Birks, H.J.B., Birks, H.J.B., 1998. DG Frey and ES Deevey Review 1: numerical tools in palaeolimnology–Progress, potentialities, and problems. J. Paleolimnol. 20, 307–332. https://doi.org/10.1023/A:1008038808690.

Bishop, I.J., Bennion, H., Sayer, C.D., Patmore, I.R. and Yang, H., 2019. Filling the "data gap": Using paleoecology to investigate the decline of Najas flexilis (a rare aquatic plant). *Geo: Geography and Environment*, *6*(2), p.e00081.https://doi.org/10.1002/geo2.81.

Bjerring, R., Becares, E., Declerck, S., Gross, E.M., Hansson, L.A., Kairesalo, T., Nykänen, M., Halkiewicz, A., Kornijów, R., Conde-Porcuna, J.M., Seferlis, M., 2009. Subfossil Cladocera in relation to contemporary environmental variables in 54 Pan-European lakes. Freshw. Biol. 54 (11), 2401–2417. https://doi.org/10.1111/j.1365-2427.2009.02252.x.

Blanchet, C.C., Arzel, C., Davranche, A., Kahilainen, K.K., Secondi, J., Taipale, S., Lindberg, H., Loehr, J., Manninen-Johansen, S., Sundell, J., Maanan, M., 2022. Ecology and extent of freshwater browning-What we know and what should be studied next in the context of global change. Sci. Total Environ. 812, 152420 https://doi.org/10.1016/j.scitotenv.2021.152420.

Błędzki, L.A., Rybak, J.I., 2016. Freshwater Crustacean Zooplankton of Europe: Cladocera & Copepoda (Calanoida, Cyclopoida) Key to species identification, with notes on ecology, distribution, methods and introduction to data analysis. Springer.

Błędzki, L.A., Szeroczyńska, K., Puusepp, E., 2013. The late holocene appearance of European Bosmina (Eubosmina) thersites (Crustacea, Cladocera) in lakes surrounding the Baltic Sea. Hydrobiologia 715, 77–86. https://doi.org/10.1007/s10750-012-1376-6.

Bos, D.G., Cumming, B.F., 2003a. Sedimentary Cladoceran remains and their relationship to nutrients and other limnological variables in 53 lakes from Britich Columbia, Canada. Can. J. Fish Aquat.sci 60, 1177–1189. https://doi.org/10.1139/f03-097.

Bos, D.G., Cumming, B.F., 2003b. Sedimentary cladoceran remains and their relationship to nutrients and other limnological variables in 53 lakes from British Columbia, Canada. Can. J. Fish. Aquat. Sci. 60 (10), 1177–1189. https://doi.org/10.1139/f03-097.

Boucherle, M.M., Züllig, H., 1983. Cladoceran remains as evidence of change in trophic state in three Swiss lakes. Hydrobiologia 103, 141–146. https://doi.org/10.1007/BF00028442.

Brezonik, P.L., Bouchard Jr, R.W., Finlay, J.C., Griffin, C.G., Olmanson, L.G., Anderson, J.P., Arnold, W.A., Hozalski, R., 2019. Color, chlorophyll a, and suspended solids effects on Secchi depth in lakes: implications for trophic state assessment. Ecol. Appl. 29 (3), e01871 https://doi.org/10.1002/eap.1871.

Brodersen, K.P., Whiteside, M.C., Lindegaard, C., 1998. Reconstruction of trophic state in Danish lakes using subfossil chydorid (Cladocera) assemblages. Can. J. Fish. Aquat. Sci. 55 (5), 1093–1103. https://doi.org/10.1139/f98-008.

Butler, S.J., Freckleton, R.P., Renwick, A.R., Norris, K., 2012. An objective, niche-based approach to indicator species selection. Methods Ecol. Evol. 3 (2), 317–326. https://doi.org/10.1111/j.2041-210X.2011.00173.x.

Çakıroğlu, A.İ., Tavşanoğlu, Ü.N., Levi, E.E., Davidson, T.A., Bucak, T., Özen, A., Akyıldız, G.K., Jeppesen, E., Beklioğlu, M., 2014. Relatedness between contemporary and subfossil cladoceran assemblages in Turkish lakes. J. Paleolimnol. 52, 367–383. https://doi.org/10.1007/s10933-014-9799-x.

Cappelli, G., Gray, E., Gammell, M., Roden, C., Lally, H., 2023. Physico-chemical characterisation of protected lake habitats: A matter of dystrophy. Limnologica 103, 126123. https://doi.org/10.1016/j.limno.2023.126123.

Carlson, R.E., 1977. A trophic state index for lakes 1. Limnol. Oceanogr. 22 (2), 361–369. https://doi.org/10.4319/lo.1977.22.2.0361.

Carlson, R.E., 2007. Estimating Trophic State. *Lakeline* 27 (1), 25–28.

Čeirāns, A., 2007. Zooplankton indicators of trophy in Latvian lakes. Acta Univ. Latv. 723. Biology 61–69.

Chen, G., Dalton, C., Taylor, D., 2010. Cladocera as indicators of trophic state in Irish lakes. J. Paleolimnol. 44, 465–481. https://doi.org/10.1007/s10933-010-9428-2.

Cimdiņš, P., 2001. Limnoekoloģija. Latvijas Universitāte, Mācību apgāds, Riga, p. 159.

European Commission, 2014. Directive 2000/60/EC of the European Parliament and of the Council of 23 October 2000 establishing a framework for Community action in the field of water policy. URL: https://eur-lex.europa.eu/eli/dir/2000/60/oj (accessed: 23.05.2024).

Dauvalter, V., 1997. Heavy metal concentrations in lake sediments as an index of freshwater ecosystem pollution. In: Crawford, R.M.M. (Ed.), Disturbance and Recovery in Arctic Lands: an Ecological Perspective. Kluwer Academic Publishers, Dordrecht, pp. 333–351.

Davidson, T.A., Sayer, C.D., Langdon, P.G., Burgess, A.M.Y., Jackson, M., 2010. Inferring past zooplanktivorous fish and macrophyte density in a shallow lake: application of a new regression tree model. Freshw. Biol. 55 (3), 584–599. https://doi.org/10.1111/j.1365-2427.2009.02391.x.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90 (12), 3566–3574. https://doi.org/10.1890/08-1823.1.

De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. Oikos 119 (10), 1674–1684. https://doi.org/10.1111/j.1600-0706.2010.18334.x.

De Eyto, E., Irvine, K., 2001. The response of three chydorid species to temperature, pH and food. Hydrobiologia 459, 165–172. https://doi.org/10.1023/A:1012585217667.

De Eyto, E., Irvine, K., García-Criado, F., Gyllström, M., Jeppensen, E., Kornijow, R., Miracle, M.R., Nykanen, M., Bareiss, C., Cerbin, S., Salujõe, J., 2003. The distribution of chydorids (Branchiopoda, Anomopoda) in European shallow lakes and its application to ecological quality monitoring. Arch. Hydrobiol. 156 (2), 181–202. https://doi.org/10.1127/0003-9136/2003/0156-0181.

De Eyto, E., 2001. Chydorus sphaericus as a biological indicator of water quality in lakes. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, *27*(6), pp.3358-3362. doi.org/10.1080/03680770.1998.11902448.

Dong, X., Kattel, G., Jeppesen, E., 2020. Subfossil cladocerans as quantitative indicators of past ecological conditions in Yangtze River Basin lakes China. *Sci. Total Environ.* 728, 138794 https://doi.org/10.1016/j.scitotenv.2020.138794.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol. Monogr. 67 (3), 345–366. https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2.

Duigan, C.A., Kovach, W.L., 1991. A study of the distribution and ecology of littoral freshwater chydorid (Crustacea, Cladocera) communities in Ireland using multivariate analyses. J. Biogeogr. 267–280. https://doi.org/10.2307/2845397.

Eilers, J.M., Glass, G.E., Pollack, A.K., Sorensen, J.A., 1989. Changes in conductivity, alkalinity, calcium, and pH during a 50-year period in selected northern Wisconsin lakes. Can. J. Fish. Aquat. Sci. 46 (11), 1929–1944. https://doi.org/10.1139/f89-243.

Estlander, S., Nurminen, L., Olin, M., Vinni, M., Horppila, J., 2009. Seasonal fluctuations in macrophyte cover and water transparency of four brown-water lakes: implications for crustacean zooplankton in littoral and pelagic habitats. Hydrobiologia 620, 109–120. https://doi.org/10.1007/s10750-008-9621-8.

Farmer, A.M., 1990. The effects of lake acidification on aquatic macrophytes—a review. Environ. Pollut. 65 (3), 219–240. https://doi.org/10.1016/0269-7491(90)90085-Q.

Fiłoc, M., Kupryjanowicz, M., Rzodkiewicz, M., Suchora, M., 2018. Response of terrestrial and lake environments in NE Poland to Preboreal cold oscillations (PBO). Quat. Int. 475, 101–117. https://doi.org/10.1016/j.quaint.2016.02.052.

Flössner, D., 2000. Die Haplopoda unde Cladocera Mitteleuropas. Backhuys Publishers, Leiden, Netherlands.

Forró, L., Korovchinsky, N.M., Kotov, A.A., Petrusek, A., 2007. Global diversity of cladocerans (Cladocera; Crustacea) in freshwater. In: Balian, E.V., Lévêque, C., Segers, H., Martens, K. (Eds.), Freshwater Animal Diversity Assessment. Developments in Hydrobiology, vol 198. Springer, Dordrecht. https://doi.org/10.1007/978-1-4020-8259-7_19.

Frey, D.G., 1986. Cladocera analysis. In: Berglund, B.E. (Ed.), Handbook of Palaeoecology and Palaeohydrology. John Wiley & Sons Ltd., Chichester, pp. 667–692.

Fryer, G., 1974. Evolution and adaptive radiation in the macrothricidae (Crustacea: Cladocera): a study in comparative functional morphology and ecology. Philos. Trans. R. Soc., B 269 (898), 137–274. https://doi.org/10.1098/rstb.1974.0044.

García-Girón, J., Fernández-Aláez, C., Fernández-Aláez, M., Luis, B., 2018. Subfossil Cladocera from surface sediment reflect contemporary assemblages and their environmental controls in Iberian flatland ponds. Ecol. Ind. 87, 33–42.

Gąsiorowski, M., Hercman, H., 2005. Recent sedimentation and eutrophication of Kruklin Lake after artificial drop in water-level in the middle of 19th century. Stud. Quat. 22, 17–25.

Gąsiorowski, M., Sienkiewicz, E., Ciołko, U., Kaucha, K., Kupryjanowicz, M., Szal, M., 2021. Cultural eutrophication of a Central European lowland lake from the Bronze Age to the present recorded in diatom and Cladocera remains. Catena 204, 105404.

Górniak, A., 2017. A new version of the Hydrochemical Dystrophy Index to evaluate dystrophy in lakes. Ecol. Ind. 78, 566–573. https://doi.org/10.1016/j.ecolind.2017.03.030.

Górniak, A., Jekatierynczuk-Rudczyk, E., Dobrzyń, P., 1999. Hydrochemistry of three dystrophic lakes in Northeastern Poland. Acta Hydroch. Hydrob. 27 (1), 12–18, 10.1002/(SICI)1521-401X(199901)27:1<12::AID-AHEH12>3.0.CO;2-X.

Grabowska, M., Hindák, F., Hindáková, A., 2014. Phototrophic microflora of dystrophic Lake Sęczek, Masuria, Poland. Oceanol. Hydrobiol. Stud. 43, 337–345. https://doi.org/10.2478/s13545-014-0149-4.

Gray, E., Cappelli, G., Gammell, M.P., Roden, C.M., Lally, H.T., 2022. A review of dystrophic lake and pool habitat in Europe: an Irish perspective. J. Nat. Conserv. 68, 126–189. https://doi.org/10.1016/j.jnc.2022.126189.

Grizzetti, B., Pistocchi, A., Liquete, C., Udias, A., Bouraoui, F., Van De Bund, W., 2017. Human pressures and ecological status of European rivers. Sci. Rep. 7 (1), 205. https://doi.org/10.1038/s41598-017-00324-3.

Gutiérrez-Cánovas, C., Arias-Real, R., Bruno, D., Cabrerizo, M.J., González-Olalla, J.M., Picazo, F., Romero, F., Sanchez-Fernandez, D., Pallares, S., 2022. Multiple-stressors effects on Iberian freshwaters: a review of current knowledge and future research priorities. Limnetica 41 (2), 245–268.

Haberman, J., Haldna, M., 2014. Indices of zooplankton community as valuable tools in assessing the trophic state and water quality of eutrophic lakes: long term study of Lake Võrtsjärv. J. Limnol. 73 (2) https://doi.org/10.4081/jlimnol.2014.828.

Heinsalu, A., Alliksaar, T., 2009. Palaeolimnological assessment of environmental change over the last two centuries in oligotrophic Lake Nohipalu Valgjärv, southern Estonia. Estonian J. Earth Sci. 58 (2) https://doi.org/10.3176/earth.2009.2.03.

Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. J. Paleolimnol. 25, 101–110. https://doi.org/10.1023/A:1008119611481.

Henrikson, B.I., 1993. Sphagnum mosses as a microhabitat for invertebrates in acidified lakes and the colour adaptation and substrate preference in Leucorrhinia dubia (Odonata, Anisoptera). Ecography 16 (2), 143–153. https://www.jstor.org/stable/3683010.

Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers, D., Simmons, A., 2020. The ERA5 global reanalysis. Q. J. R. Meteorolog. Soc. 146 (730), 1999–2049. https://doi.org/10.1002/qj.3803.

Hill, M.O., Gauch Jr, H.G., 1980. Detrended correspondence analysis: an improved ordination technique. Vegetatio 42 (1), 47–58. https://doi.org/10.1007/BF00048870.

Hofmann, W., 1996. Empirical relationships between cladoceran fauna and trophic state in thirteen northern German lakes: analysis of surficial sediments. Hydrobiologia 318, 195–201. https://doi.org/10.1007/BF00016680.

Hofmann, W., 1998. Cladocerans and chironomids as indicators of lake level changes in north temperate lakes. J. Paleolimnol. 19, 55–62. https://doi.org/10.1023/A:1007999419765.

Hough, R.A., Fornwall, M.D., Negele, B.J., Thompson, R.L., Putt, D.A., 1989. Plant community dynamics in a chain of lakes: principal factors in the decline of rooted macrophytes with eutrophication. Hydrobiologia 173, 199–217. https://doi.org/10.1007/BF00008968.

Huser, B.J., Futter, M.N., Wang, R., Fölster, J., 2018. Persistent and widespread long-term phosphorus declines in Boreal lakes in Sweden. Sci. Total Environ. 613, 240–249. https://doi.org/10.1016/j.scitotenv.2017.09.067.

Järnefelt, H., 1958. On the typology of the northern lakes. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, *13*(1), pp.228-235. https://doi.org/10.1080/03680770.1956.11895403.

Jensen, T.C., Dimante-Deimantovica, I., Schartau, A.K., Walseng, B., 2013. Cladocerans respond to differences in trophic state in deeper nutrient poor lakes from Southern Norway. Hydrobiologia 715, 101–112. https://doi.org/10.1007/s10750-012-1413-5.

Jensen, T.C., Walseng, B., Hessen, D.O., Dimante-Deimantovica, I., Novichkova, A.A., Chertoprud, E.S., Chertoprud, M.V., Sakharova, E.G., Krylov, A.V., Frisch, D., Christoffersen, K.S., 2019. Changes in trophic state and aquatic communities in high Arctic ponds in response to increasing goose populations. Freshw. Biol. 64 (7), 1241–1254. https://doi.org/10.1111/fwb.13299.

Jolliffe, I.T., Cadima, J., 2016. Principal component analysis: a review and recent developments. Philos. Trans. R. Soc. A Math. Phys. Eng. Sci. 374 (2065), 20150202 https://doi.org/10.1098/rsta.2015.0202.

Jones, R.I., 1992. The influence of humic substances on lacustrine planktonic food chains. Hydrobiologia 229, 73–91. https://doi.org/10.1007/BF00006992.

Kamenik, C., Szeroczyńska, K., Schmidt, R., 2007. Relationships among recent Alpine Cladocera remains and their environment: implications for climate-change studies. Hydrobiologia 594, 33–46. https://doi.org/10.1007/s10750-007-9083-4.

Karabin, A., 1974. Studies on the predatory role of the cladoceran, Leptodora kindtii (Focke), in secondary production of two lakes with different trophy. Ekol. Pol 22, 295–310.

Karpowicz, M., Grabowska, M., Ejsmont-Karabin, J., Ochocka, A., 2023. Humic lakes with inefficient and efficient transfer of matter in planktonic food webs. Sci. Rep. 13 (1), 7913. https://doi.org/10.1038/s41598-023-35039-1.

Kaushal, S.S., Likens, G.E., Pace, M.L., Reimer, J.E., Maas, C.M., Galella, J.G., Utz, R.M., Duan, S., Kryger, J.R., Yaculak, A.M., Boger, W.L., 2021. Freshwater salinization syndrome: from emerging global problem to managing risks. Biogeochemistry 154, 255–292.

Keskkonnaseire infosüsteem, 2024. Programm: Väikejärvede seire. https://kese.envir.ee/kese/listParameterValueNew.action (accessed: 24.05.2024).

Klante, C., Larson, M., Persson, K.M., 2021. Brownification in Lake Bolmen, Sweden, and its relationship to natural and human-induced changes. J. Hydrol.: Reg. Stud. 36, 100863 https://doi.org/10.1016/j.ejrh.2021.100863.

Koff, T., Vandel, E., Marzecová, A., Avi, E., Mikomägi, A., 2016. Assessment of the effect of anthropogenic pollution on the ecology of small shallow lakes using the palaeolimnological approach. Estonian Journal of Earth Sciences 65 (4). https://doi.org/10.3176/earth.2016.19.

Korhola, A., Rautio, M. ,2001. Cladocera and Other Branchiopod Crustaceans. In: Smol, J.P., Birks, H.J.B., Last, W.M. (eds) Tracking Environmental Change Using Lake Sediments. Developments in Paleoenvironmental Research, vol 4. Springer, Dordrecht. https://doi.org/10.1007/0-306-47671-1_2.

Korhola, A., Olander, H., Blom, T., 2000. Cladoceran and chironomid assemblages as qualitative indicators of water depth in subarctic Fennoscandian lakes. J. Paleolimnol. 24, 43–54. https://doi.org/10.1023/A:1008165732542.

Korosi, J.B., Smol, J.P., 2012. Contrasts between dystrophic and clearwater lakes in the long-term effects of acidification on cladoceran assemblages. Freshw. Biol. 57 (12), 2449–2464. https://doi.org/10.1111/fwb.12012.

Korponai, J.L., Kövér, C., López-Blanco, C., Gyulai, I., Forró, L., Katalinic, A., Ketola, M., Nevalainen, L., Luoto, T.P., Sarmaja-Korjonen, K., Magyari, E.K., 2020. Effect of temperature on the size of sedimentary remains of littoral chydorids. Water 12 (5), 1309.

Krause-Dellin, D., Steinberg, C., 1986. Cladoceran remains as indicators of lake acidification. Hydrobiologia 143 (1), 129–134. https://doi.org/10.1007/BF00026655.

Kuczyńska-Kippen, N., 2009. The Impact of the Macrophyte Substratum and Season on Crustacean Zooplankton Communities of Three Shallow and Macrophyte-Dominated Lakes. J. Freshwater Ecol. 24 (3), 375–382. https://doi.org/10.1080/02705060.2009.9664309.

Kurek, J., Korosi, J.B., Jeziorski, A., Smol, J.P., 2010. Establishing reliable minimum count sizes for cladoceran subfossils sampled from lake sediments. J. Paleolimnol. 44, 603–612. https://doi.org/10.1007/s10933-010-9440-6.

Lanka, A., Dimante-Deimantovica, I., Saarni, S., Stivrins, N., Tylmann, W., Zawiska, I., Veski, S., 2024. Urbanization-driven Cladocera community shifts in the lake-a case study from Baltic region, Europe. Anthropocene, 100439. https://doi.org/10.1016/j.ancene.2024.100439.

Le Moal, M., Gascuel-Odoux, C., Ménesguen, A., Souchon, Y., Étrillard, C., Levain, A., Moatar, F., Pannard, A., Souchu, P., Lefebvre, A., Pinay, G., 2019. Eutrophication: a new wine in an old bottle? Sci. Total Environ. 651, 1–11. https://doi.org/10.1016/j.scitotenv.2018.09.139.

Leppänen, J.J., Weckström, J., 2016. Varying degradation of subfossil Daphnia longispina during the past 250 years and the discovery of fossil helmet-type head shields: preliminary results. Adv. Oceanogr. Limnol. 7 (2) https://doi.org/10.4081/aiol.2016.6293.

Lepš, J., Šmilauer, P., 2003. Multivariate Analysis of Ecological DataUsing CANOCO. Cambridge University Press, Cambridge, p. 280.

Lessmann, D., Fyson, A., Nixdorf, B., 2000. Phytoplankton of the extremely acidic mining lakes of Lusatia (Germany) with pH≤ 3. Hydrobiologia 433 (1), 123–128. https://doi.org/10.1023/A:1004018722898.

Lesutienė, J., Semenova, A., Grinienė, E., Gasiūnaitė, Z.R., Savickytė, V., Dmitrieva, O., 2012. Abundance dynamics and functional role of predaceous Leptodora kindtii in the Curonian Lagoon. Cent. Eur. J. Biol. 7, 91–100. https://doi.org/10.2478/s11535-011-0098-5.

Liiv, M., Alliksaar, T., Freiberg, R., Heinsalu, A., Ott, I., Reitalu, T., Tõnno, I., Vassiljev, J., Veski, S., 2018. Drastic changes in lake ecosystem development as a consequence of flax retting: a multiproxy palaeolimnological study of Lake Kooraste Linajärv, Estonia. Veg. Hist. Archaeobotany 27, 437–451. https://doi.org/10.1007/s00334-017-0650-y.

Lindenmayer, D.B., Likens, G.E., 2011. Direct measurement versus surrogate indicator species for evaluating environmental change and biodiversity loss. Ecosystems 14, 47–59. https://doi.org/10.1007/s10021-010-9394-6.

Lunte, C.C., Luecke, C., 1990. Trophic interactions of Leptodora in lake Mendota. Limnol. Oceanogr. 35 (5), 1091–1100. https://doi.org/10.4319/lo.1990.35.5.1091.

LVĢMC, 2022. Virszemes ūdeņu tipi, references apstākļi, ūdensobjektu grupēšana [WWW document]. URL:https://videscentrs.lvgmc.lv/files/Udens/UBA_2022_2027/Daugavas%20UBAP%202022-2027%20pielikumi/II%20nodalas%20pielikumi/2.4.1.a%20piel.%20Udenu%20tipologija.pdf (accessed 23.05.2024).

Macek, M., Callieri, C., Simek, K., Vázquez, A.L., 2006. Seasonal dynamics, composition and feeding patterns of ciliate assemblages in oligotrophic lakes covering a wide pH range. Arch. Hydrobiol. 166 (2), 261.

Mäemets, A., 1968. Eesti järved. Valgus, Tallinn.

Mäemets, A., 1983. Rotifers as indicators of lake types in Estonia. Hydrobiologia 104, 357–361. https://doi.org/10.1007/BF00045991.

Makohonienko, M., Płóciennik, M., Papiernik, P., Kittel, P., Gałka, M., Mroczkowska, A., Apolinarska, K., Okupny, D., Panfil, M., Kotrys, B., Luoto, T.P., 2023. Environmental changes during mesolithic-neolithic transition in kuyavia lakeland, central poland. Quat. Int. 644, 196–221. https://doi.org/10.1016/j.quaint.2021.11.020.

Malley, D.F. and Chang, P.S.S., 1987. Increase in the abundance of Cladocera at pH 5.1 in experimentally-acidified Lake 223, Experimental Lakes Area, Ontario. In *Acidic Precipitation: Proceedings of the International Symposium on Acidic Precipitation Muskoka, Ontario, September 15–20, 1985* (pp. 629-637). Springer Netherlands.

Mazei, Y.A., Tsyganov, A.N., Bobrovsky, M.V., Mazei, N.G., Kupriyanov, D.A., Gałka, M., Rostanets, D.V., Khazanova, K.P., Stoiko, T.G., Pastukhova, Y.A., Fatynina, Y.A., 2020. Peatland development, vegetation history, climate change and human activity in the Valdai uplands (Central European Russia) during the Holocene: a multi-proxy palaeoecological study. Diversity 12 (12), 462. https://doi.org/10.3390/d12120462.

Meerhoff, M., Teixeira-de Mello, F., Kruk, C., Alonso, C., Gonzalez-Bergonzoni, I., Pacheco, J.P., Lacerot, G., Arim, M., Beklioğlu, M., Brucet, S., Goyenola, G., 2012. Environmental warming in shallow lakes: a review of potential changes in community structure as evidenced from space-for-time substitution approaches. Adv. Ecol. Res. 46, 259–349. https://doi.org/10.1016/B978-0-12-396992-7.00004-6.

Meyers, P. A., Teranes, J. L. (2001). Sediment organic matter. In: Last, W. M., Smol, J. P. (eds.), Tracking Environmental Change Using Lake Sediments. Volume 2: Physical and Geochemical Methods. Kluwer Academic Publishers, Dordrecht, pp. 239–269.

Meyers, P.A., Ishiwatari, R., 1993. Lacustrine organic geochemistry—an overview of indicators of organic matter sources and diagenesis in lake sediments. Org Geochem. 20, 867–900. https://doi.org/10.1016/0146-6380(93)90100-P.

Meyers, P.A., Leenheer, M.J., Eadie, B.J., Maule, S.J., 1984. Organic geochemistry of suspended and settling particulate matter in Lake Michigan. Geochim. Cosmochim. Acta 48, 443–452. https://doi.org/10.1016/0016-7037(84)90273-4.

Milan, M., Bigler, C., Tolotti, M., Szeroczyńska, K., 2017. Effects of long term nutrient and climate variability on subfossil Cladocera in a deep, subalpine lake (Lake Garda, northern Italy). J. Paleolimnol. 58, 335–351. https://doi.org/10.1007/s10933-017-9981-z.

Moss, B., Kosten, S., Meerhoff, M., Battarbee, R.W., Jeppesen, E., Mazzeo, N., Havens, K., Lacerot, G., Liu, Z., De Meester, L., Paerl, H., 2011. Allied attack: climate change and eutrophication. Inland Waters 1 (2), 101–105. https://doi.org/10.5268/IW-1.2.359.

Muñoz-Colmenares, M.E., Sendra, M.D., Sòria-Perpinyà, X., Soria, J.M., Vicente, E., 2021. The use of zooplankton metrics to determine the trophic status and ecological potential: an approach in a large Mediterranean watershed. Water 13 (17), 2382. https://doi.org/10.3390/w13172382.

Nature conservation agency Republic of Latvia, 2020. Nature data management system Ozols. URL: https://www.daba.gov.lv/en/nature-data-management-system-ozols [accessed: 26.06.2024].

Nevalainen, L., 2011. Intra-lake heterogeneity of sedimentary cladoceran (Crustacea) assemblages forced by local hydrology. Hydrobiologia 676 (1), 9–22. https://doi.org/10.1007/s10750-011-0707-3.

Nevalainen, L., Luoto, T.P., 2013. Limnological deterioration forces community and phenotypic changes in Cladocera: tracking eutrophication of Mallusjärvi, a lake in southern Finland. Boreal Environ. Res. 18 (3–4), 209.

Nevalainen, L., Sarmaja-Korjonen, K., Luoto, T.P., 2011. Sedimentary Cladocera as indicators of past water-level changes in shallow northern lakes. Quat. Res. 75 (3), 430–437. https://doi.org/10.1016/j.yqres.2011.02.007.

Nevalainen, L., Ketola, M., Korosi, J.B., Manca, M., Kurmayer, R., Koinig, K.A., Psenner, R., Luoto, T.P., 2014. Zooplankton (Cladocera) species turnover and long-term decline of Daphnia in two high mountain lakes in the Austrian Alps. Hydrobiologia 722, 75–91. https://doi.org/10.1007/s10750-013-1676-5.

Nevalainen, L., Rantala, M.V., Luoto, T.P., 2015. Sedimentary cladoceran assemblages and their functional attributes record late Holocene climate variability in southern Finland. J. Paleolimnol. 54, 239–252. https://doi.org/10.1007/s10933-015-9849-z.

Nikodemus, O., Kļaviņš, M., Krišjāne, Z., Zelčs, V. (red), 2018. Latvija, zeme, daba, tauta. Latvijas Universitātes akadēmiskais apgāds. Rīga, pp 298-321.

Nürnberg, G.K., 1996. Trophic state of clear and colored, soft-and hardwater lakes with special consideration of nutrients, anoxia, phytoplankton and fish. Lake Reservoir Manage. 12 (4), 432–447. https://doi.org/10.1080/07438149609354283.

Nürnberg, G.K., Shaw, M., 1998. Productivity of clear and humic lakes: nutrients, phytoplankton, bacteria. Hydrobiologia 382, 97–112. https://doi.org/10.1023/A:1003445406964.

ÓSullivan, P.E., Reynolds, C.S., 2004. The lakes handbook, limnology and limnetic ecology (Vol 1). Blackwell Science ltd. United Kingdom, 699 pp.

Ochocka, A., Karpowicz, M., 2022. Assessment potential of zooplankton to establish reference conditions in lowland temperate lakes. Diversity 14 (6), 501. https://doi.org/10.3390/d14060501.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneau, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2022._vegan: Community Ecology Package_. R package version 2.6-4, <https://CRAN.R-project.org/package=vegan>.

Ott, I., 2005. Some principles of ecological quality classification in Estonian lakes. In *Proceedings of the 21th Meeting of the ICP waters programme Task Force in Tallinn, Estonia, October 17–19* (Vol. 84, No. 2006, pp. 8-14). Norwegian University of Science and Technology.

Podani, J., Csányi, B., 2010. Detecting indicator species: some extensions of the IndVal measure. Ecol. Ind. 10 (6), 1119–1124. https://doi.org/10.1016/j.ecolind.2010.03.010.

Radosavljevic, J., Slowinski, S., Shafii, M., Akbarzadeh, Z., Rezanezhad, F., Parsons, C.T., Withers, W., Van Cappellen, P., 2022. Salinization as a driver of eutrophication symptoms in an urban lake (Lake Wilcox, Ontario, Canada). Sci. Total Environ. 846, 157336 https://doi.org/10.1016/j.scitotenv.2022.157336.

Sand-Jensen, K., Pedersen, N.L., Thorsgaard, I., Moeslund, B., Borum, J. and Brodersen, K.P., 2008. 100 years of vegetation decline and recovery in Lake Fure, Denmark. *Journal of Ecology*, *96*(2), pp.260-271.https://doi.org/10.1111/j.1365-2745.2007.01339.x.

Sandøy, S., Nilssen, J.P., 1986. A geographical survey of littoral crustacea in Norway and their use in paleolimnology. Hydrobiologia 143, 277–286. https://doi.org/10.1007/BF00026671.

Sarmaja-Korjonen, K., 2007. Subfossil shell margins and tail spines of Daphnia in Finnish lake sediments-is Daphnia underrepresented in cladocera analysis? Stud. Quat. 61–64.

Semenova, A.S., Napreenko, M.G., 2023. First data on the species composition and development of cladocera (crustacea: branchiopoda) in mire ecosystems (Kaliningrad Oblast, Russia). Inland Water Biology 16 (5), 805–820. https://doi.org/10.1134/S1995082923050115.

Shapiera, M., Jeziorski, A., Yan, N.D., Smol, J.P., 2011. Calcium content of littoral Cladocera in three softwater lakes of the Canadian Shield. Hydrobiologia 678, 77–83. https://doi.org/10.1007/s10750-011-0824-z.

Shumate, B.C., Schelske, C.L., Crisman, T.L., Kenney, W.F., 2002. Response of the cladoceran community to trophic state change in Lake Apopka, Florida. J. Paleolimnol. 27, 71–77. https://doi.org/10.1023/A:1013599502262.

Siddig, A.A., Ellison, A.M., Ochs, A., Villar-Leeman, C., Lau, M.K., 2016. How do ecologists select and use indicator species to monitor ecological change? Insights from 14 years of publication in Ecological Indicators. Ecol. Ind. 60, 223–230. https://doi.org/10.1016/j.ecolind.2015.06.036.

Sloka N. 1981. Latvijas PSR dzīvnieku noteicējs. Latvijas kladoceru (Cladocera) fauna un noteicējs. Rīga, P.Stučkas Valsts universitāte, 146 lpp.

Smirnov, N.N., 2017. Physiology of the Cladocera. Academic press.

Smol, J.P., 1992. Paleolimnology: an important tool for effective ecosystem management. J. Aquat. Ecosyst. Health 1, 49–58.

Smol, J.P., 2008. Pollution of lakes and rivers, a paleoenvironmental perspective, second edition. Blackwell Publishing, 400 p.

Søndergaard, M., Jensen, J.P., Jeppesen, E., Møller, P.H., 2002. Seasonal dynamics in the concentrations and retention of phosphorus in shallow Danish lakes after reduced loading. Aquat. Ecosyst. Health Manag. 5 (1), 19–29. https://doi.org/10.1080/14634980260199936.

Steinberg, C., 1991. Fate of organic matter during natural and anthropogenic lake acidification. Water Res. 25 (12), 1453–1458. https://doi.org/10.1016/0043-1354(91)90174-O.

Steinberg, C.E.V., 2004. Regulatory impacts of humic substances in lakes. In ÓSullivan, P.E., Reynolds, C.S (ed) *The Lakes Handbook: Limnology and Limnetic Ecology*, pp.153-196.

Stekhoven, D.J. and Buehlmann, P., 2012. `MissForest - nonparametric missing value imputation for mixed-type data. Bioinformatics, 28(1) 2012, 112-118. doi: 10.1093/bioinformatics/btr597.

Stivrins, N., Grudzinska, I., Elmi, K., Heinsalu, A., Veski, S., 2018. Determining reference conditions of hemiboreal lakes in Latvia, NE Europe: a palaeolimnological approach. In: Annales De Limnologie-International Journal of Limnology, Vol. 54. EDP sciences, p. p. 22)..

Stivrins, N., Trasune, L., Jasiunas, N., Kalnina, L., Briede, A., Maksims, A., Steinberga, D., Jeskins, J., Rendenieks, Z., Bikse, J., Kalvans, A., 2022. Indicative value and training set of freshwater organic-walled algal palynomorphs (non-pollen palynomorphs). Quat. Sci. Rev. 282, 107450 https://doi.org/10.1016/j.quascirev.2022.107450.

Strzałek, M., Koperski, P., 2019. The effect of dense patches of Stratiotes aloides L. on the spatial structure of microcrustacean assemblages in an oxbow lake. Ecohydrol. Hydrobiol. 19 (1), 75–82. https://doi.org/10.1016/j.ecohyd.2018.08.003.

Szeroczyńska, K., Sarmaja-Korjonen, K., 2007. Atlas of subfossil Cladocera from central and northern Europe. Friends of the Lower Vistula Society, Swiecie.

Terasmaa, J., 2018. Estonia, the land of lakes. *Dynamiques environnementales. Journal international de géosciences et de l'environnement*, (42), pp.358-366. https://doi.org/10.4000/dynenviron.2504.

Tichá, A., Vondrák, D., Moravcová, A., Chiverrell, R., Kuneš, P., 2023. Climate-related soil saturation and peatland development may have conditioned surface water brownification at a central European lake for millennia. Sci. Total Environ. 858, 159982 https://doi.org/10.1016/j.scitotenv.2022.159982.

Tóth, M., Van Hardenbroek, M., Bleicher, N., Heiri, O., 2019. Pronounced early human impact on lakeshore environments documented by aquatic invertebrate remains in waterlogged Neolithic settlement deposits. Quat. Sci. Rev. 205, 126–142. https://doi.org/10.1016/j.quascirev.2018.12.015.

Tumurtogoo, U., Figler, A., Korponai, J., Sajtos, Z., Grigorszky, I., Berta, C., Gyulai, I., 2022. Density and diversity differences of contemporary and subfossil cladocera assemblages: a case study in an oxbow lake. Water 14 (14), 2149. https://doi.org/10.3390/w14142149.

Urtāne, L., 1998. Cladocera kā Latvijas ezeru tipu un trofiskā stāvokļa indikatori [Cladocera as indicators of lake type and trophic status in Latvia]. University of Latvia. Doctoral thesis.

Van Den Wollenberg, A.L., 1977. Redundancy analysis an alternative for canonical correlation analysis. Psychometrika 42 (2), 207–219. https://doi.org/10.1007/BF02294050.

Velle, G., Brodersen, K.P., Birks, H.J.B. and Willassen, E., 2012. Inconsistent results should not be overlooked: A reply to Brooks et al.(2012). *The Holocene*, *22*(12), pp.1501-1508. https://doi.org/10.1177/0959683612449765.

Walseng, B. and Halvorsen, G., 2005. Littoral microcrustaceans as indices of trophy. *Internationale Vereinigung für theoretische und angewandte Limnologie: Verhandlungen*, *29*(2), pp.827-829. doi.org/10.1080/03680770.2005.11902795.

Walther, A., Linderholm, H.W., 2006. A comparison of growing season indices for the Greater Baltic Area. Int. J. Biometeorol. 51, 107–118. https://doi.org/10.1007/s00484-006-0048-5.

Watson, V.T., Medeiros, A.S., 2021. The value of paleolimnology in reconstructing and managing ecosystem vulnerability: a systematic map. Facets 6 (1), 517–536. https://doi.org/10.1139/facets-2020-0067.

Wojtal, A., Frankiewicz, P., Wagner-Łotkowska, I., Zalewski, M., 2004. The evaluation of the role of pelagic invertebrate versus vertebrate predators on the seasonal dynamics of filtering Cladocera in a shallow, eutrophic reservoir. Hydrobiologia 515, 123–135. https://doi.org/10.1023/B:HYDR.0000027324.44452.9e.

Woolway, R.I., Kraemer, B.M., Lenters, J.D., Merchant, C.J., O'Reilly, C.M., Sharma, S., 2020. Global lake responses to climate change. Nature Rev. Earth Environ. 1 (8), 388–403. https://doi.org/10.1038/s43017-020-0067-5.

Wu, T., Zhu, G., Zhu, M., Xu, H., Zhang, Y., Qin, B., 2020. Use of conductivity to indicate long-term changes in pollution processes in Lake Taihu, a large shallow lake. Environ. Sci. Pollut. Res. 27, 21376–21385. https://doi.org/10.1007/s11356-020-08590-x.

Zagars, M., Christoffersen, K.S., Cremona, F., 2024. Lake food web structure in Teici Nature reserve, Latvia: fish presence shapes functioning of pristine bog lake food webs. Hydrobiologia 1–17. https://doi.org/10.1007/s10750-024-05525-2.

Zawiska, I., Dimante-Deimantovica, I., Luoto, T.P., Rzodkiewicz, M., Saarni, S., Stivrins, N., Tylmann, W., Lanka, A., Robeznieks, M., Jilbert, T., 2020. Long-term consequences of water pumping on the ecosystem functioning of lake sekšu. Latvia. *Water* 12, 1459. https://doi.org/10.3390/w12051459.

Zawisza, E., Filbrandt-Czaja, A., Correa-Metrio, A., 2016 a.. Subfossil Cladocera and pollen as indicators of natural and anthropogenic trophic changes of Lake Jelonek (Tuchola Forest, N Poland) during the Holocene. Adv. Oceanogr. Limnol. 7 (2) https://doi.org/10.4081/aiol.2016.6234.

Zawisza, E., Zawiska, I., Correa-Metrio, A., 2016. b. Cladocera community composition as a function of physicochemical and morphological parameters of dystrophic lakes in NE Poland. Wetlands 36, 1131–1142. https://doi.org/10.1007/s13157-016-0832-x.

Zawisza, E., Zawiska, I., Szeroczyńska, K., Correa-Metrio, A., Mirosław-Grabowska, J., Obremska, M., Rzodkiewicz, M., Słowiński, M., Woszczyk, M., 2019. Dystrophication of lake Suchar IV (NE Poland): an alternative way of lake development. Limnetica 38 (1), 391–416.

Zettler, M.L., Proffitt, C.E., Darr, A., Degraer, S., Devriese, L., Greathead, C., Kotta, J., Magni, P., Martin, G., Reiss, H., Speybroeck, J., 2013. On the myths of indicator species: issues and further consideration in the use of static concepts for ecological applications. PLoS One 8 (10), e78219. https://doi.org/10.1371/journal.pone.0078219.

Zharov, A.A., Tchabovsky, A.V., Kotov, A.A., 2021. Disproportion among Cladocera (Crustacea) skeletal components in lake sediment taphocoenoses and significance with respect to two methods of sub-fossil enumeration. J. Paleolimnol. 1–13. https://doi.org/10.1007/s10933-021-00224-7.

Appendix 2

Article II

Lanka, A., Dimante-Deimantovica, I., Saarni, S., Stivrins, N., Tylmann, W., Zawiska, I. and Veski, S., (2024). Urbanization-driven Cladocera community shifts in the lake-a case study from Baltic region, Europe. *Anthropocene*, p.100439. https://doi.org/10.1016/j.ancene.2024.100439

Anthropocene 46 (2024) 100439

Contents lists available at ScienceDirect

Anthropocene

journal homepage: www.elsevier.com/locate/ancene

Urbanization-driven Cladocera community shifts in the lake - a case study from Baltic region, Europe

Anna Lanka[a,*], Inta Dimante-Deimantovica[b,c], Saija Saarni[d,e], Normunds Stivrins[a,b,f,g], Wojciech Tylmann[h], Izabela Zawiska[i], Siim Veski[a]

[a] *Department of Geology, Tallinn University of Technology, Ehitajate tee 5, Tallinn19086, Estonia*
[b] *Lake and Peatland Research Centre, Puikule, Aloja, Latvia*
[c] *Latvian Institute of Aquatic Ecology, Voleru 4, Riga LV-1007, Latvia*
[d] *Faculty of Biological and Environmental Sciences, Aquatic Biogeochemistry Research Unit, Ecosystems and Environment Research Program, University of Helsinki, P.O. Box 65, Helsinki FI-00014, Finland*
[e] *Department of Geography and Geology, University of Turku, Turku 20014, Finland*
[f] *Department of Geography, University of Latvia, Jelgavas 1, Riga LV-1004, Latvia*
[g] *Institute of History of Latvia, University of Latvia, Latvia*
[h] *Faculty of Oceanography and Geography, University of Gdańsk, Bażyńskiego 4, Gdańsk PL-80309, Poland*
[i] *Institute of Geography and Spatial Organisation, Polish Academy of Sciences, Twarda 51/55, Warsaw PL- 00818, Poland*

ARTICLE INFO

Keywords:
Urbanization
Eutrophication
Cladocera
Lake
Subfossils

ABSTRACT

Our research aimed to evaluate, how urbanization affects lake ecosystems and Cladocera in particular. For this purpose, we chose a small urban lake with a well-documented history. Lake Velnezers (located in Riga, Latvia) is currently surrounded by apartment building complexes. Construction works around this lake started in the 1950s and continued up until the 1970s. To investigate how the transition from forested to agricultural and further urbanized land affected the lake ecosystem we took a sediment core that covers the time period from before 1875–2018. We evaluated ecological changes in the lake based on chemical and Cladocera species composition in sediment records and linked these changes to the historical information about alterations in the landscape around Velnezers. Our results show lake transitioned from oligotrophic to eutrophic conditions already before urbanization. The Lake ecosystem reacted to urbanization gradually, showing small changes in the beginning. However, in the 1980s lake experienced rapid deterioration in water quality – sediment records show an increase in heavy metal pollution, anoxia, and nutrient input. These stressors resulted in Cladocera functional group structure changes and loss of Cladocera species richness and diversity. Improvements in nature protection – such as wastewater management have reduced heavy metal and nutrient input into Lake Velnezers towards the present. However, previous deterioration, i.e. loss of species diversity and phosphorous legacy effect do not allow natural lake recovery under current conditions.

1. Introduction

Anthropogenic activities in the second half of the 20th century have led to cumulative pressure on freshwater ecosystems (Matthews, 2016; Grizzetti et al., 2017). Multiple stressors include, among others, climate change, pollution by toxic substances, an increase in nutrient loading due to agriculture and urban development, hydrological alterations (Zawiska et al., 2020), and invasive species introduction (Janse et al., 2015). Consequently, freshwater ecosystems experience deterioration demonstrating the decline of ecosystem services provided such as reduced local biodiversity, loss of freshwater areas, and poor water quality (Ahmed et al., 2022).

Urbanization is not among the stressors foreseen to withhold and most likely it will increase in the future. Already in 2008, the global urban population exceeded the rural population. It is expected that two-thirds of the world population will live in urban areas by 2050 (United Nations, n.d.) and the world's ice-free urbanized land will increase from 2.06 % in 2000–4.71 % by 2040 (Van Vliet et al., 2017). Therefore, urban development has been included in the United Nations Development Goals, i.e. to make cities and human settlements inclusive, safe,

---

* Corresponding author.
E-mail address: anna.lanka@taltech.ee (A. Lanka).

https://doi.org/10.1016/j.ancene.2024.100439
Received 18 March 2024; Received in revised form 24 May 2024; Accepted 30 May 2024

resilient, and sustainable ("Goal 11," n.d.).

The direct impact of urban expansion is not only related to the transformation of natural areas. A significant part of new urban territories are former agricultural lands. Hence, bearing in mind freshwater ecosystems, one anthropogenic stressor is replacing the other, transforming the landscape and changing the impacting variables (Beckers et al., 2020; Güneralp et al., 2020). Understanding interactions between historical landscape, land use, and lake ecology development is crucial for targeted lake management. For this reason, the utilization of lake sediment records is of great help since the chemical, physical, and biological signals accumulated in lake sediments turn to be reliable archives for past changes. Moreover, the human-environment interactions after the great acceleration (also referred to as Anthropocene), i.e. human settlement strategies and land use effect, are identified among 50 priority research questions in paleoecology (Seddon et al., 2014).

In this study, we investigate cumulative and often cascading effects of human-induced changes within and around the lake. The study lake (Velnezers) is located in the capital of Latvia, Riga, Northeastern Europe (Fig. 1).

The first substantial human impact near Lake Velnezers was recorded around CE 1600 when minor adjacent territory of the lake was cleared from the surrounding pine forest for agricultural purposes (Pujate, 2015; Kalnina et al., 2019). The area was completely transformed into agricultural lands by the beginning of the 20th century. The replacement of agricultural land with urban area started in the 1950s with the development of private houses (Pumpurs, 1959; General base, 1963) and reached its current state by the beginning of the '70 s with the construction of multi-story residential houses surrounding the lake (Fig. 2). Nowadays the lake is located in one of the largest suburban areas of Riga city - Jugla. From a population of approx. 3000 inhabitants in 1936 this area has reached a population of more than 26000 people at present (apkaimes, n.d.).

In this study, we wanted to explore how the lake responds to different transformations – from the agricultural pressure on a relatively untouched lake to a fully urbanized environment. To reveal the changes in past water quality we used the chemical composition of sediments and subfossil Cladocera remains as our proxy. Cladocera are widely used to track and interpret human-environment interactions through time, e.g. climate, lake water level change, acidity, eutrophication, and alien species impact (Burge et al., 2018). Intensive agriculture is known to be the cause of eutrophication and excess sediment loads (Donohue and Garcia Molinos, 2009; Nevalainen and Luoto, 2017; Tumurtogoo et al., 2022), while urbanization can increase the invasive potential of alien species and is related to variety of physical (temperature increase and geomorphological changes) and chemical (nutrients and pollutants increase) impacts (Gao et al., 2022; Santana Marques et al., 2020). Hence both agriculture (i.e. increase in nutrient levels) and urbanization can change the distribution pattern of lakes inhabiting zooplankton including Cladocera species diversity and functional group's structure (Otake et al., 2021; Richard Albert et al., 2010; Shen et al., 2021). In fact, Schacht et al. (2022) found that agriculture and urbanization explain the greatest proportion of variation in water quality, while increased human activity can even predominate the impact of climate change (Jensen et al., 2020). Still, studies on the cascading effects impact on Cladcocera are scarce. Therefore, this study contributes to the limited knowledge on the specific impacts of human-induced changes on lake ecosystems. This knowledge is crucial for understanding the interactions between human activities, land use, and freshwater ecosystems and provides valuable insights for sustainable lake use practices, i. e. enables targeted lake management strategies.

Considering the previous research and the fact that urbanization around Velnezers occurred quite rapidly, we hypothesize that urbanization will have a more prominent impact on the lake's ecosystem compared to earlier disturbances. Our established primary research question is how do lake conditions vary between different stages of its surrounding landscape development – urbanization, agriculture, and relatively undisturbed landscape? The more specific questions were: how do Cladocera species and functional group structure respond to urban stressors?

2. Material and methods

2.1. Study site description

Lake Velnezers (56.976385 °N, 24.247066 °E 4.6 m a.s.l.) is located in the eastern part of the capital city of Latvia – Riga (Fig. 1). It is a small (3.5 ha) lake with a mean depth of 3.5 m and a maximum depth of 7.4 m (Dručka, 2014). Geologically lake Velnezers has glaciokarst origin and lies within the Baltic Ice Lake glaciolimnic sediments (clay, silt, sand). The total Quaternary sediment thickness in the area reaches 35 m. Sand

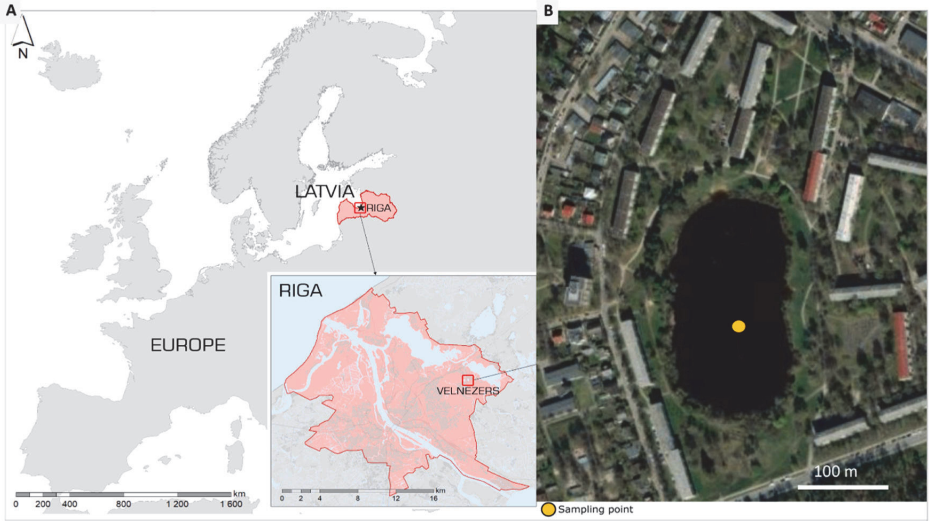


Fig. 1. (A) Sampling area – Lake Velnezers (Latvia, Northern Europe) location in Riga city and (B) sampling point indicated with a yellow dot.

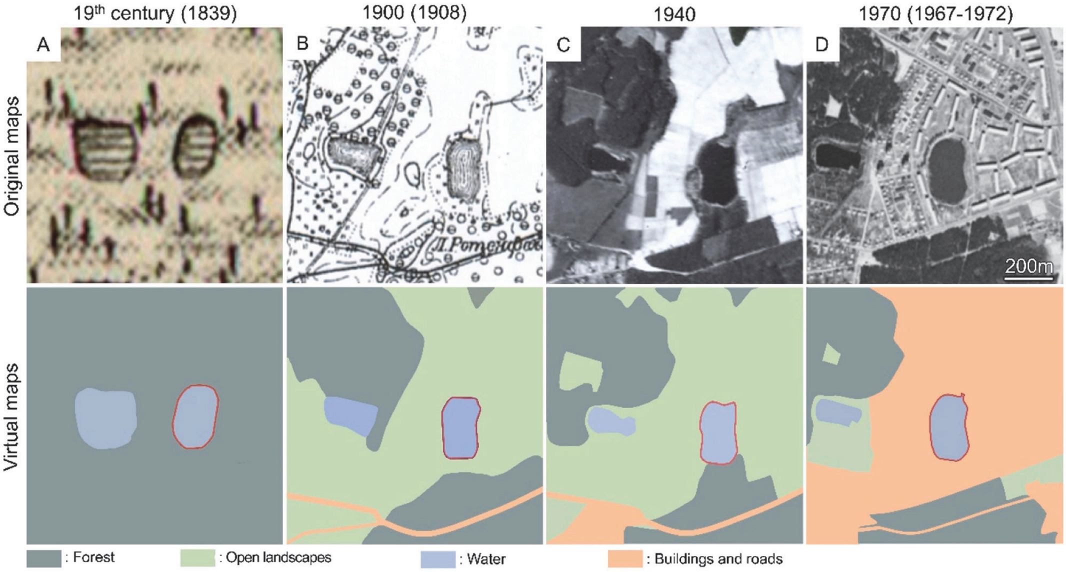


Fig. 2. Lake Velnezers landscape development based on maps and aerial photos throughout the time (from 19th to 20th century). Forest (dark green), open landscapes consisting of meadows, agricultural lands, possibly also grazed wetlands (light green), and old agricultural lands starting to be gradually urbanized (orange). Map references: A (Specialcharde von Livland, 1839), B (Military topographic map, 1908), C (NARA, 1940), D (USGS, 1967–1972).

dune formations around the lake took place 11 700–5000 years ago (Grudzinska et al., 2017). Lake's topography is characterized by a gentle shoreline but steep underwater slopes. There is no inflow to nor outflow from the lake Velnezers. Therefore, it is fed by precipitation and groundwater discharge.

Lake Velnezers is a brown water eutrophic to hypertrophic lake (Druvietis, 2012) reaching total phosphorous concentration up to 100 µg/l (SIA 2022; Dimante-Deimantovica 2019 unpubl.) with higher values during spring and autumn season. Water transparency changes seasonally from 1 m (winter and spring) to <0.5 m during June-October (Robežnieks, 2022). Lakes average pH is 7 (SIA 2022). Lake Velnezers littoral zone is characterized by approximately 2–3 m wide marshy shoreline in the western part of the lake. Submerged macrophyte zone is absent and algal bloom has been observed in Lake Velnezers (Balode et al. 2006; Druvietis et al., 2017; Līcīte, 2017).

2.2. Sediment core collection

A 33 cm long surface sediment core was collected from lakes Velnezers depression, close to the deepest part (Fig. 1) on 14th February 2019 using a Kayak/HTH gravity-type corer with an inner diameter of 8 cm. Sediment core was divided into 1 cm cross sections and stored in a cold room.

2.3. Core chronology

The sediment core was dated with ^{210}Pb in the Gdańsk University Geochronology Laboratory according to the standard procedure (Tylmann et al., 2016). The activity of total ^{210}Pb was determined indirectly by measuring ^{210}Po using alpha spectrometry. Dry and homogenized sediment samples of 0.2 g were transferred into Teflon containers, spiked with ^{209}Po yield tracer, and digested with concentrated HNO_3, $HClO_4$, and HF at a temperature of 100°C using a CEM Mars 6 microwave digestion system. After 24 hours the solution was transferred into a Teflon beaker, evaporated with 6 M HCl to dryness, and then dissolved in 0.5 M HCl. Polonium isotopes were spontaneously deposited within four hours on silver discs. After deposition, discs were analyzed for ^{210}Po and ^{209}Po using a 7200–04 APEX Alpha Analyst integrated alpha-spectroscopy system (Canberra) equipped with PIPS A450–18AM detectors. Samples were counted for 24 hours.

The Bayesian age-depth modeling *Plum* for the core was built in an R environment using package '*rplum*' (Aquino-López et al., 2018). *Plum* is a Bayesian forward model that simultaneously integrates two different processes, such as the behavior of the ^{210}Pb flux and the variation of ^{210}Pb with depth, and an age-depth function (Blaauw and Christen, 2011). In comparison to the traditional implementation of the Constant Flux model (also known as the Constant Rate of Supply model), which is a reverse and deterministic model, the recently developed Bayesian *Plum* model is more flexible forward model that allows coping with non-ideal ^{210}Pb depth profiles (e.g., can easily handle gaps and can include other types of dating information) providing an estimate of most appropriate/likely age distributions. *Plum* Bayesian age-depth models become more precise with increasing dating densities (they 'learn' to produce more accurate and precise chronology during the modeling process), whereas classical linear interpolation does not (Aquino-López et al., 2020).

2.4. Chemical analysis of sediments

Loss on Ignition analysis was done according to a standardized methodology (Walter E. Dean 1974; Heiri et al., 2001). For C/N analysis homogenized sub-samples were freeze-dried and grinded in agate mortar. The total carbon (TC) and total nitrogen (TN) contents were analyzed using thermal combustion elemental analyses (Element Analyzer Vario EL III) with an uncertainty of ±5 %. Approximately 7–8 mg of material was weighed into tin cups for analyses that were performed at an accredited laboratory (ISO/IEC/17025). To estimate sediment chemical composition a small sub-sample was collected from homogenized sediment slices, from each sediment depth, and freeze-dried for the major element concentration. Approximately 0.1 g sample was collected in pre-weighed Teflon vials for HNO3 digestion. 25 ml of 65 % HNO_3 was added, and the temperature was set to 160 ∘C for 30 minutes. The vials were covered with loose caps to allow the escape of gases and volatiles during the digestion. The remaining acid was diluted with 10 ml of distilled water and weighed. 1 ml of the resulting solution was diluted to 9 ml of 0.5 mol/l HNO3 in 15 ml centrifuge tubes to achieve the final acid concentration of approximately 1 mol/L HNO3 and suitable element concentration for the ICP-OES analysis. Calcium (Ca), Copper (Cu), Iron (Fe), Potassium (K), Magnesium (Mg), Manganese (Mn), Phosphorous (P), Lead (Pb), Sulfur (S), and Zinc (Zn) concentrations were determined using Thermo Scientific iCAP6000 ICP-OES accompanied with a concentric nebulizer. In addition, certified control samples and blank samples were used to assess the analytical process. Finally, the dilution factors were calculated based on weighed samples and used to correct the results.

2.5. Cladocera analysis

From each sediment layer 1 cm^3 subsample was taken for Cladocera analysis and prepared in laboratory according to standard procedure (Frey, 1986), heated in 10 % KOH, and sieved using 38 μm mesh size. After the treatment, samples were diluted with 10 ml of water and colored with Safranin O. Right before Cladocera analysis diluted sample was homogenized and 0.1 ml was measured to prepare a microscopy slide. For each subsample, 1–2 slides were examined under a light microscope at 100x, 200x, and 400x magnification. We calculated the Total Cladocera flux, expressed as the sum of specimens per square centimeter per year (specimens/cm2/year), following the methodology employed by Zawiska et al. (2017).

All recognizable skeletal elements were counted (head shield, shell, postabdomen, etc.) until at least 70 individuals were found (Kurek et al., 2010). All slides were scanned fully to avoid counting bias. Identification of Cladocera species was based on the identification key by Krystina Szeroczyńska and Sarmaja-Korjonen (2007). Cladocera functional groups were distinguished based on the species description from the literature (Flössner, 2000; Bledzki and Rybak, 2016). The selected functional groups were body size and habitat preference. For the analysis of body size, we classified each species into one of three groups: large (>1 mm), medium (0,5–1 mm) or small (<0,5 mm). The classification was based on the average size of a female. We divided Cladocera into 4 groups based on their habitat preference – pelagic, sediment-associated, vegetation-associated, and unspecified. Species were included in the group unspecified if they were mentioned as common both in sediment and vegetation habitats. See more detailed information on functional groups in the supplementary file (Appendix 1).

2.6. Statistical analysis and data visualization

Data visualization for stratigraphic diagrams was done using Tilia 3.0.1 (Grimm, 2011). We performed Bray-Courtis dissimilarity (Faith et al., 1987) based temporally constrained hierarchical clustering (CONISS) analysis (Grimm, 1987) to distinguish changes in the Cladocera community structure. The number of significant clusters was determined using the broken stick method (Jackson, 1993). Cluster analysis was done using R 4.3.0 software (R Core Team 2023) vegan package (Oksanen et al. 2017). We calculated Simpsons diversity index (Simpson, 1949) using program Past 4.0.1 (Hammer et al., 2001).

3. Results

3.1. Core chronology

The depth profile of excess ^{210}Pb shows an overall consistent decline in activities with mass depth (Fig. 3). However, a zone of irregularly fluctuating activities is clearly visible at the depth range of 0–7 cm indicating surface sediment mixing. The exponential decrease below this section proves no major disturbance of the sediment column and relatively stable mass accumulation rates. The lowest sediment depth associated with the age, according to the *Plum* age-depth model, is 29 cm and the average age is 1882 (min 1850, max 1905). In our study, we further use the average age from the model, but the possible age-range distribution of each particular depth can be learned from Fig. 3. Beyond that age, the model did not produce chronology as excess ^{210}Pb was not traceable. The age-depth model shows continuous sedimentation with an average sediment accumulation rate of 0.45 cm per year. Quality of the modeling was appropriate and acceptable (Fig. 3) as it shows the assessed processing parameters.

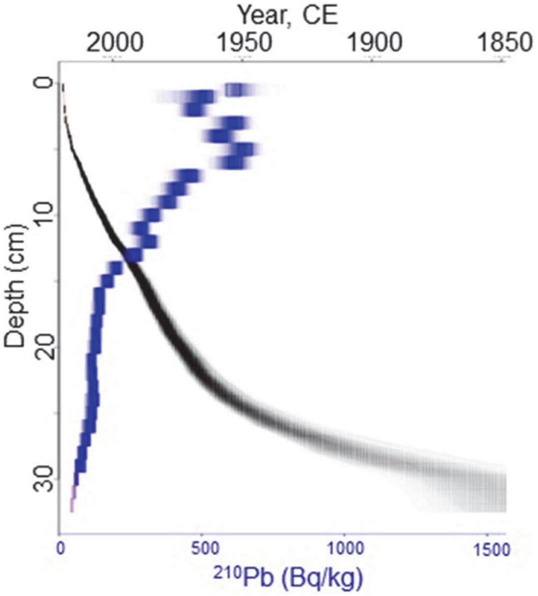


Fig. 3. Lake Velnezers chronology where: (1) blue-scale indicates the modeled ^{210}Pb values (based on the posterior values for the age model and the ^{210}Pb parameters), (2) blue boxes indicate the measured values, (3) grey-scale is the age-depth model at 95 % probability range.

3.2. Sediment chemical composition

In data analysis we distinguished 4 zones of the sediment core (Fig. 4). **Zone 1** is the lower zone based on Cladocera species assemblage cluster analysis results (see more detailed description of Cladocera further in the text). The rest of the core is split into three zones (**Zone 2, Zone 3, Zone 4**) based on historical events that might have influenced the lake. All time periods given describing zones according to the chronology model are approximate:

Zone 1 (33rd to 27th cm, date unknown - 1920);

Zone 2 (27th to 20th cm, years 1920–1970) refers to time period before the completion of the apartment building complex around Lake Velnezers;

Zone 3 (20th cm to 14th cm, years 1970–1990) represents the fully urbanized stage during the Soviet Union;

Zone 4 (14th to 1st cm, years 1990–2018) represents the most recent history of the lake after the collapse of the Soviet Union. Since samples in the depth of 1–3 cm all corresponded to the year 2018, in further result analysis we combined these samples into one.

Lake Velnezers sediment contains relatively low carbonate matter throughout the studied period ranging from 1.83 % (before 1875, Zone 1) to 4.21 % (year 1998, Zone 4) decreasing again towards most recent years. Greater variability is observed for content shifts in organic matter

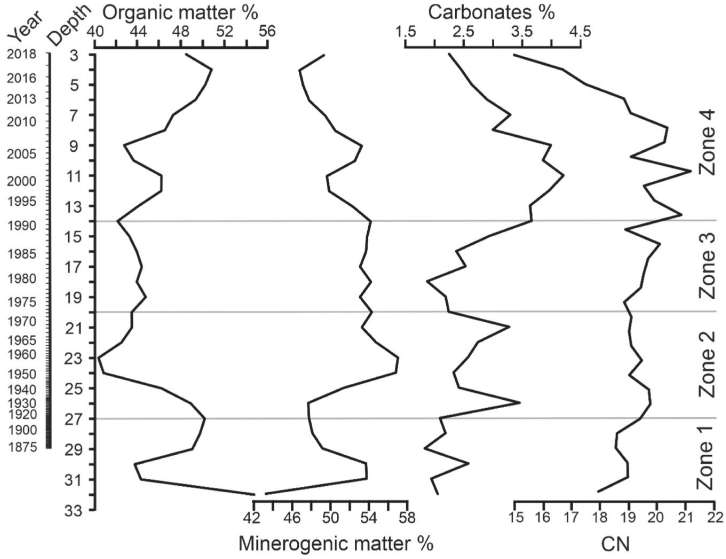


Fig. 4. Loss on Ignition (LOI) results expressed in percentages and carbon/nitrogen (CN) expressed as an atomic ratio in the sediment profile of Lake Velnezers.

(40.40–55.15 %) and mineral matter (43.10–57.03 %). Mineral matter reaches its highest value at the beginning of Zone 2 (57.03 %), and consequently, organic matter has its lowest value at the same time (40.40) %. The C/N values vary between 17.9 and 20.8 across Zone 1, Zone 2, and Zone 3. In Zone 4 C/N values decrease from 21,2 to 14,9 towards the topmost sediment layer (Fig. 4).

The major elements investigated can be categorized as those that:

1) reflect input of terrigenous minerogenic material (K) and calcite minerals (Ca);

2) are redox-sensitive elements (Fe, S, Mn, P);

3) are trace metals (Pb, Zn, Cu).

All the elements show a similar trend as to their concentrations - lowest values are observed at Zone 1 and increase towards Zone 4 followed by a decline in the very upper sediments of Zone 4.

The exception is P which shows the maximum values within Zone 2 and Zone 3, but its lowest concentrations within Zone 4. K shows fluctuations with increasing frequency from Zone 2 to the end of Zone 4. Pb, S, and Fe have their distinguished maximum peaks in Zone 4 from early 90ties to 2010, while Zn, Mn, Mg, and Cu display high concentrations throughout Zone 4 (Fig. 5).

3.3. *Cladocera assemblages*

In the sediment core of Lake Velnezers, we found 42 taxa of

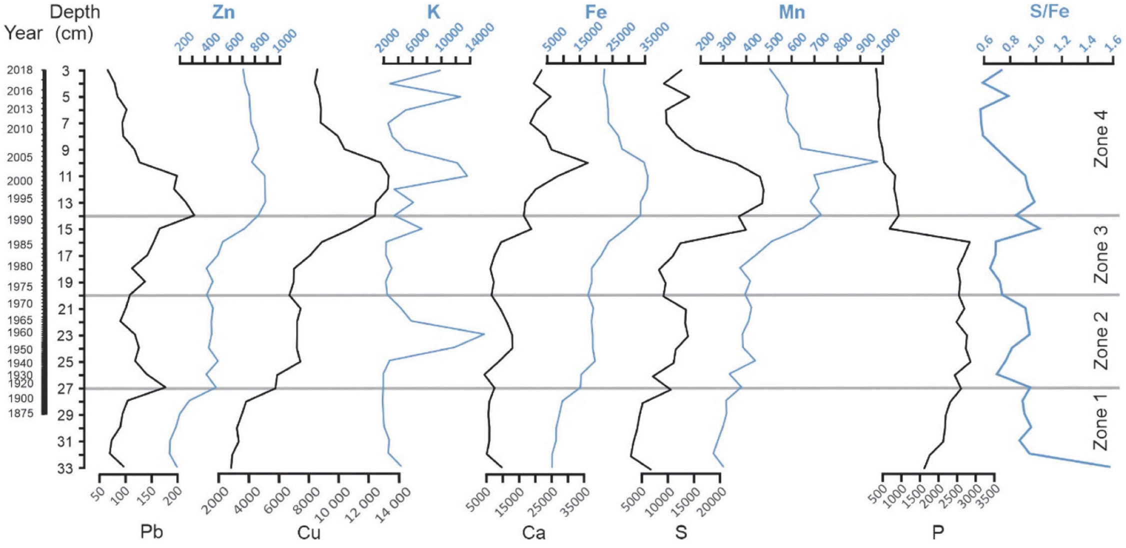


Fig. 5. Vertical distribution of major elements (mg/kg) in Lake Velnezers sediment core.

Cladocera (Fig. 6). *Bosmina* (*Eubosmina*) *longispina* and *Bosmina* (*E.*) *coregoni* were merged into Eubosmina spp. subgenus group. For several other taxa identification until genus level was possible, i.e. *Daphnia*, *Eurycercus*, *Simocephalus*, *Ilyocryptus*. Pelagic species dominate throughout the core, of those particularly abundant are bosminids. The rest of the taxa are divided into vegetation-associated, sediment-associated, or unspecified habitat groups, of those chydorids, i.e. *Alonella nana*, *Chydrous sphaericus*, and *Alonella excisa* are dominant. Only four species occurred in every sample of the core (n=33) - *Bosmina (Bosmina) longirostris*, *Bosmina* (*Eubosmina*) sp., *A. nana* and *A. excisa*.

Zone 1 is characterized by the dominance of pelagic species belonging to daphnias and bosminids. The proportion of *Bosmina (B.) longirostris* is increasing towards the upper sediments of Zone 1. While *B. longirostris* is rising from 1 % at the lowest sediment layer to 75 % of all Cladocera by the end of Zone 1, other dominant species *Eubosmina* spp. and *Daphnia* spp. abundance is decreasing. For both species, the highest values within the core are reached within Zone 1. *Holopedium gibberum* is present in almost all samples of Zone 1, gradually decreasing and disappearing completely above Zone 1.

As to littoral species in this period they contribute less to the total species richness compared to Zones 2–4. In Zone 1 78 % of all the species found are littoral, while in Zone 2–4 on average 82 % of all Cladocera species found are typical for the littoral zone. At the same time, while the littoral species' richness increases, their abundance decreases. For example, *A. nana* and *Acroperus harpae* are experiencing a decline, decreasing from 17 % and 6 % at the beginning of Zone 1–2 % and less than 1 % at the end of it accordingly. Only a few sediments associated species are found within Zone 1 and some species or genus are not occurring at all, e.g. *Pleuroxus* spp., *Leydigia* spp., *Monospilus dispar*, *Leptodora kindti* (Fig. 6). Total Cladocera flux cannot be properly evaluated, since our dating does not reach the bottom part of the core, but as far as data are available total Cladocera flux here is lowest among all distinguished time zones (Fig. 7).

Other zones differ from Zone 1 noticeably, i.e. Zone 2–4 is characterized by *Bosmina (B.) longirostris* dominance (on average 70 % thorough Zone 2–4), increase in the number of sediment-associated Cladocera species (five species in Zone 1 versus 9 species in Zone 2–4), a considerable decrease of *Daphnia* sp. and rapidly increasing total Cladocera flux. In Zone 2 several species appear for the first time and continuously or periodically are also present in Zones 3 and 4, i.e. *Leptodora kindti*, *Pleuroxus* spp., *Leydigia acanthocercoides, L. leydigi*, *Phreatalona protzi*, *Monospilus dispar*, *Disparalona rostrata* (Fig. 6). Species that continuously appear in Zone 1–2, but afterwards appear rarely are *Alonopsis elongata*, *Alona intermedia*, *and Acantholeberis curvirostris*. During Zone 3 there is an increase of littoral species individuals' proportion (22 % compared to 18 % in Zone 2) even though pelagic *Bosmina (B.) longirostris* still is the dominant species in Zone 3 (64 %) (Figs. 6, 7).

Zone 4 is characterized by a further increase of *Bosmina (B.) longirostris* proportion (72 %) and an increase of total Cladocera flux, which reaches its peak at the 4th cm. On the contrary, *Eubosmina* sp. proportion decreases from 17 % on average throughout Zone 1–3–4 % in Zone 4. In this zone several species have disappeared (or disappear towards upper sediment layers) from the sediment records completely – such as *Alona intermedia*, *A. rustica*, *A. costata*, *P. truncatus*, *Acantholeberis curvirostris*, *Latona setifera*, and *Ilycryptus* spp. (Figs. 6, 7).

The very last few cm (3 cm and above) of Zone 4 somehow differs from the rest of Zone 4 – species diversity slightly increases, pelagic small species ratio stays the same as total Cladocera flux decreases, *B. (B.) longirostris* decreases and on contrary *Eubosmina* spp. increases (Figs. 6, 7).

As we move towards the upper layers of the core, there is a tendency of declining species diversity among Cladocera, accompanied by a decrease in the ratio of littoral, large pelagic, and medium-sized pelagic species compared to the increasing abundance of small pelagic species (Fig. 7).

4. Discussion

The historical maps of Lake Velnezers reveal transformations in its surrounding landscape, transitioning from a forested environment to an agricultural one and eventually becoming urbanized. Over time, the lake has witnessed alterations in subfossil Cladocera and sediment chemical composition. These changes include a shift in dominant pelagic species, a reduction in species diversity, local extinction of certain species, and the emergence of new ones. Significant fluctuations in sediment

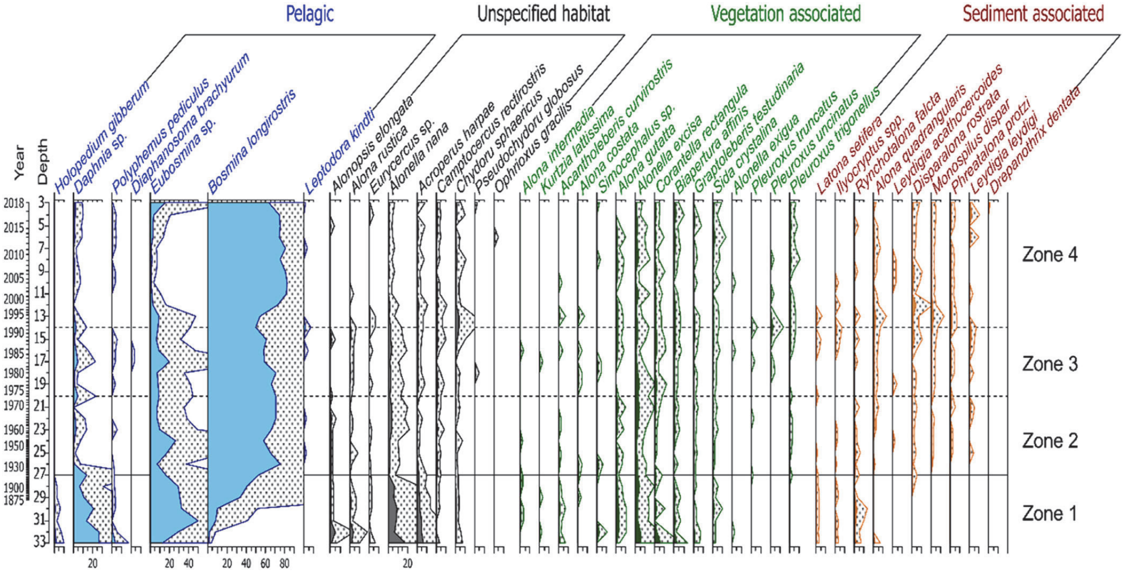


Fig. 6. Cladoceran assemblages based on habitat preference throughout the sediment core of Lake Velnezers. The diagram shows the relative abundance of the taxa.

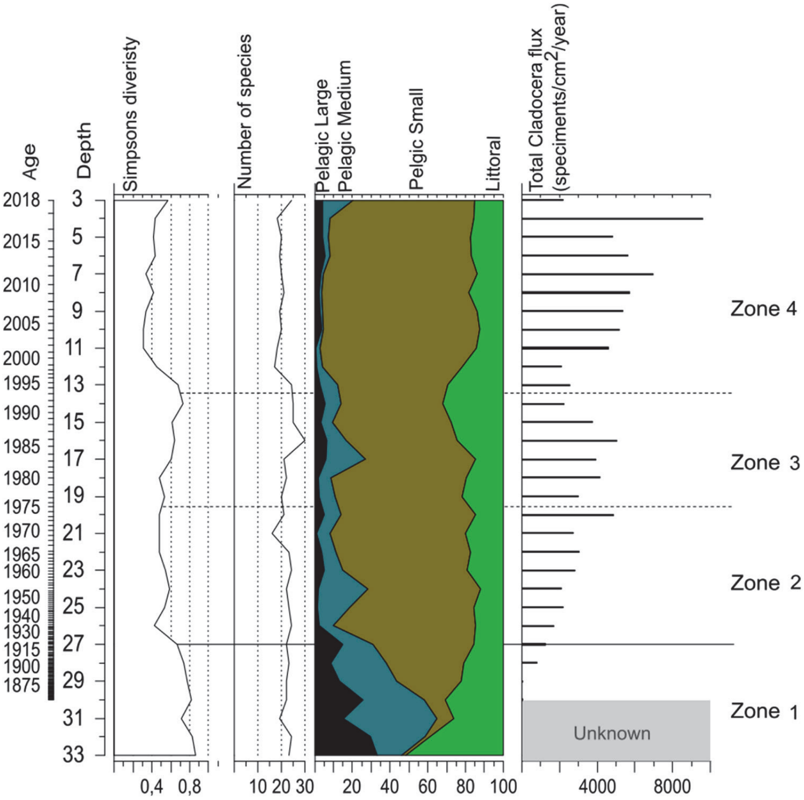


Fig. 7. Summary of parameters describing subfossil Cladocera communities throughout the sediment core of Lake Velnezers. The colorful diagram depicted the relative abundance of Large pelagic (Black), Medium pelagic (Blue), Small pelagic (Brown), and Littoral (Green) species. Total Cladocera flux shows the calculated number of Cladocera individuals deposited in the sediments per year.

chemistry are evident, including a rapid decrease in phosphorus (P) concentration starting from the late 1980s toward most recent sediments, as well as variations in other major elements.

Despite our initial hypothesis focusing on the impact of rapid urbanization on Lake Velnezers' ecosystem, our research indicates that substantial changes were already underway before urbanization occurred. To test our hypothesis, we selected zones based on historical events such as the construction of an apartment complex and the collapse of the Soviet Union. Our findings extend those of Heinsalu and Aliksaar (2009), and Noges et al. (2020) revealing that shifts in Lake Velnezers ecosystem are aligning with the end of the Soviet era.

The sediment core of Lake Velnezers extends back to a period before 1875. Sediments from the year 1850 are generally considered representative of reference conditions for many lakes in Europe (Battarbee, 1999; Battarbee et al. 2011). The term "reference conditions" describes the natural state of a lake, untouched by human influence, serving as a baseline for understanding ecological changes over time (Bennion et al., 2011). **Zone 1 (starting date unknown to 1920)** exhibits a noticeable change in Cladocera composition towards the year 1920 (Fig. 6), revealing that our core does not extend deep enough into sediments to fully capture the state of the lake before considerable human impact. Pujate (2015) in her research on Lake Velnezers identified a sediment layer of reference conditions below 65 cm core depth. This depth was marked by a rapid increase in minerogenic matter proportion in the lake sediments and the presence of macrofossils indicating landscape opening. These changes are likely a result of partial forest clearing for agricultural purposes (Stankevica et al. 2015; Kalnina et al., 2019).

Despite the fact that our study is missing a clear reference conditions zone, it is obvious that at the beginning of Zone 1 lake Velnezers is in an oligotrophic state, and the ecosystem conditions gradually deteriorate by the end of Zone 1. The lowest part of Zone 1 (before 1875) is characterized by relatively high species diversity, dominance of large and medium-sized pelagic Cladocera (Fig. 7), as well as presence of several species that indicate oligotrophic conditions, such as *Holopedium gibberum*, *Alonopsis elongata*, *Latona setifera* (Fig. 6) (Bledzki and Rybak, 2016). The same species are sometimes attributed to acidic, softwater lakes (Krause-Dellin and Steinberg, 1986; Brodersen et al., 1998).

Throughout Zone 1 several changes occur that indicate an increase in trophic degree. Such changes include large and medium-sized planktonic Cladocera (such as *Daphnia* spp., *Eubosmina* spp.) replacement by small-sized planktonic *Bosmina (Bosmina) longirostris*, which is a common eutrophication-induced species succession (Boucherle and Züllig 1983; Chen et al., 2010; Adamczuk, 2016; Nevalainen and Luoto, 2017).

These changes are accompanied by disappearance or reduction in relative abundance for species indicative of good water quality. For instance, one of the most significant indications for lakes increase in trophic stratus through Zone 1 is the disappearance of *H. gibberum*, which only lives in nutrient-poor soft water lakes (Urtāne, 1998; Flössner, 2000; Bos and Cumming, 2003; Čeirāns, 2007; Jensen et al., 2013). According to Bērziņš and Bertilsson (1989), this species maximum abundance is under 20 μg/l of total phosphorous. Another example is *Alona intermedia* with optimum at 30 μg/l total phosphorous

(Brodersen et al., 1998), which is common in Zone 1 but disappears afterward.

Sediment chemistry data shows a gradual increase in concentrations of Fe, P, and S towards the end of Zone 1 (Fig. 5), which also may suggest a gradual eutrophication. Human-induced external input of P can lead to enrichment of P in surface sediments (Carey and Rydin, 2011; Hupfer and Lewandowski, 2008). The increasing concentrations of P since the latter half of the 19th century are likely related to excess nutrient loading from the cultivated areas and geochemical focusing of P, Mn, and Fe in the deepest part of the basin (Jilbert et al., 2020; Jilbert and Slomp, 2013; Scholtysik et al., 2022).

The sediments within **Zone 2 (1920–1970)** record the shift from agricultural land to an urban environment near Lake Velnezers (Fig. 2). Lake Velnezers reaches a new stable state as a turbid eutrophic lake. Throughout this period Cladocera species composition remains relatively stable, especially when compared to Zone 1.

In Zone 1, we observed the simultaneous reduction in littoral species relative abundance (Fig. 7) and species indicative of oligotophy (Fig. 6). Despite this, eight new littoral species (six sediment-associated and two vegetation-associated ones) emerged at the beginning of Zone 2. Therefore, we cannot attribute the reduction of littoral species' relative abundance to unfavorable conditions for littoral species, but rather to the proliferation of *B. longirostris*, which is indicative of eutrophication (Chen et al., 2010; Adamczuk, 2016).

Increase of eutrophication is usually negatively correlated with littoral species diversity and richness. This phenomenon is commonly associated with the loss of submerged macrophytes and therefore – available microhabitats (Declerck et al., 2011; Velghe et al., 2012; Celewicz-Gołdyn and Kuczyńska-Kippen, 2017). In Velnezers, we observed an increase in littoral species richness after initial eutrophication in Zone 1 (Fig. 6). The species succession between zones 1 and 2 suggests that the changes in trophy were accompanied by an increase in pH and conductivity. While *H. gibberum,* a species that has an oligotrophic, softwater and acidophilic preference (Bērziņš and Bertillson 1989; Bērziņš and Bertilsson, 1990), disappears by the end of Zone 1, *Disparalona rostrata*, a species known to have an alkaline preference (Krause-Dellin and Steinberg, 1986), emerges at the beginning of Zone 2. However, we do not think that lake pH reached alkaline conditions during this time, since such acidophilic species as *A. elongata*, *A. rustica*, and *P. pediculus* **(**Bledzki and Rybak, 2016**)** persist in the lake, suggesting the transition from slightly acidic to neutral conditions at the beginning of Zone 2.

It is important to note that in Latvia the cause of low pH in lakes is the enrichment with humic substances (Druvietis et al., 1998; Ozoliņš et al. 2021). Therefore, it is reasonable to assume that Lake Velnezers displayed the properties of a humic, low pH lake during Zone 1. Dystrophic lakes often exhibit low species diversity (Zawisza et al., 2016). The appearance of several new species might be the result of an increase in pH due to eutrophication at the beginning of zone 2. Zone 2 exhibits higher concentrations of Fe, P, and S. However, there is no significant variation in the concentrations of these elements (Fig. 5). This supports the idea of a new balance in the lake ecosystem, as suggested by Cladocera species.

At the beginning of the period described by Zone 2 agriculture is the most significant, but not the only human activity influencing Lake Velnezers. This lake also served such purposes as horse swimming and laundry, leading to dissatisfaction with the water quality among local residents and those who used it for recreation (Leja, 1941; Pumpurs, 1959). Agricultural activity in the vicinity of Lake Velnezers continued until at least the year 1940 (Fig. 2).

K is a common component of feldspar and clay minerals and its occurrence in the sediments points to catchment erosion and accumulation of detrital material (Dean, 2002; Shanahan et al., 2008). Ca, on the other hand, can be derived either from biogenic or inorganic sources (Dean, 2002; Shanahan et al., 2008; Zolitschka et al., 2015). The simultaneous short-lived increase in K and Ca between 1940 and 1960 suggests that elevated Ca concentrations in the sediment are indicative of carbonate mineral-bearing bedrock as the source. Although natural events (such as flooding) could contribute to catchment erosion, the overall extent of these changes, combined with consistently low background conditions, suggests that human activities are probably responsible for these single events.

The precise date for the first buildings appearing around Lake Velnezers remains unknown but a news article from 1959 (Pumpurs, 1959) suggests the year 1950 as the approximate start of urbanization in this area. While enhanced erosion is previously closely related to land use changes at the catchments (Saarni et al., 2017; Johansson et al., 2019), the increase of minerogenic matter (Fig. 4) and concomitant short-lived increase of Ca and K hint at a punctuated erosion event in the period between the years 1940 and 1960 (Fig. 5), further supporting this claim. Therefore, urbanization in the Lake Velnezers area occurs with the general global trend known as a "great acceleration" (Steffen et al., 2015; McCarthy et al., 2023; Walker et al., 2024).

Zone 3 (1970–1990) describes changes in lake Velnezers after urbanization during the Soviet Union period. While initially landscape transition into a fully urbanized area does not seem to bring any significant changes in the ecosystem, several parameters point towards a further increase of eutrophication.

Chemical analysis reveals a rise in the concentration of several elements from the middle of Zone 3 to Zone 4. The increased concentration of carbonates and calcium at the Zone 3–4 boundary suggests a shift towards seasonal carbonate supersaturation in the water column, driven by enhanced photosynthetic CO2 uptake during phytoplankton blooms. The Ca precipitation is well described from naturally eutrophic alkaline lakes in the Baltic region, but also following anthropogenic eutrophication (Roeser et al., 2021; Scholtysik et al., 2022; Zolitschka et al., 2015).

The significant decrease in P concentration at a depth of 15 cm indicates a substantial shift in sedimentary conditions. Under oxic conditions and neutral pH, phosphate can coprecipitate with sedimentary Fe and Mn oxides (Slomp et al., 1996; Gunnars et al., 2002), or be incorporated into biomass as a result of microbial processes (Glächter et al., 1988). These conditions likely characterized Zone 1, 2, and the early part of Zone 3.

However, phosphate bound to oxides and polyphosphates in sediments can dissolve back into the water column under reducing conditions (Hupfer and Lewandowski, 2008; Jilbert and Slomp, 2013). These conditions may arise at the lake bottom due to increased oxygen demand from organic matter accumulation, decomposition, and limited water exchange. Additionally, reducing conditions extend deeper into the sediment column, where microbial activity consumes oxygen, leading to phosphate dissolution into porewater and subsequent diffusion back to the water column (Hupfer and Lewandowski, 2008; Jilbert et al., 2020).

Signs of eutrophication are accompanied by an increase in S concentration, possibly due to organic matter and sewage inputs. Fe forms sulfides more readily than P (Scholtysik et al., 2022). The observed rise in Fe concentration and a sulfur-to-iron (S/Fe) ratio towards the end of Zone 3 suggest enhanced pyrite formation. This implies that P is no longer concealed in the sediments – Fe is bound by S leading to enhanced P release and promoting internal loading (Couture et al., 2016; Jilbert et al., 2020). This possible shift to pyrite formation as well as the steep decrease of P concentrations in the sediments suggest at least seasonally anoxic conditions in the basin of Lake Velnezers during this period.

Throughout Zone 3 there is an increase of such elements as Pb, Cu, and Zn. Pb reflects the anthropogenic activities at the catchment, but atmospheric fallout can contribute significantly to Pb concentrations. The increasing trend of Pb concentration in Lake Velnezers record since the early 20th century (sediment depth of 27 cm) is similar to the trends observed in Fennoscandian lakes (Brännvall et al., 1999; Meriläinen et al., 2010).

However, the decrease in Pb concentration in sediments around the 70's following the energy crisis is not detected in Lake Velnezers' record.

The major source of Cu and Zn possibly originates from untreated wastewater (Meriläinen et al., 2010; Jilbert et al., 2020), with part of the total concentrations likely derived through atmospheric fallout. Both elements display similar trends with Pb until the mid-90 s. Lake Velnezers likely received untreated wastewater from intentional and unintentional sources through the urbanization stage. There are reports of direct wastewater discharges in Velnezers, which resulted in insufficient water quality (Gurina, 1980). This type of pollution could also originate from untreated wastewater from nearby factories through groundwater sources (Pumpa, 1980; Niedre, 1986; Juhna and Kļaviņs 2001). This could explain the excess input of S, nutrients, and trace metals at the end of Zone 3.

The peaks of Cu, Pb, and various other chemical elements align with a decline in the total flux of Cladocera (Fig. 7). Between 1985 and 1990 total Cladocera flux reduced by more than a half. These findings suggest that urbanization caused oxygen depletion, elevated nutrient levels, and contamination by heavy metals have induced stress on the Cladocera population. Both heavy metal contamination and toxins from cyanobacteria blooms can lead to morphological abnormalities in Cladocera (de Melo et al., 2017; Alvarado-Flores et al., 2022; Panarelli et al., 2023). *B.* (*B.) longirostris* relative abundance slightly reduced in Zone 3. During the whole urbanization phase (Zone 3 and Zone 4) relative abundance of *B. (B.) longirostris* exceeds 50 % (Fig. 6), which suggests that the abundance of *B. (B.) longirostris* has a strong influence on the total Cladocera flux values (Fig. 7). This could mean that the reduction in total Cladocera flux also portrays the decrease in the abundance *B.(B.) longirostris*. The reduction of total Cladocera flux and *B. (B.) longirostris* relative abundance between 1985 and 1990 aligns with the rapid increase in heavy metal pollution and elements indicative of anoxic conditions (Fe, S) (Fig. 5). It has been reported in literature, that Cu toxicity significantly affects the mortality and fecundity rates of *B. (B.) longirostris* (Koivisto and Ketola, 1995) and oxygen depletion can influence the behavior and abundance of zooplankton (Ekau et al., 2010; Doubek et al., 2018). Therefore, we conclude that urbanization caused pollution and eutrophication can have negative effects even on species that are considered tolerant of a wide range of ecological conditions (Bledzki and Rybak, 2016).

Finally, Zone 4 (1990–2018) describes changes in the lake ecosystem after the collapse of the Soviet Union. In research from post-Soviet countries, it is sometimes found, that after the collapse of the Soviet Union lakes experience re-oligotrophication (Heinsalu and Alliksaar, 2009). Similarly, lakes in other European countries have been reported to improve in water quality due to a reduction in fertilizer use after 1990 (Jeppesen et al., 2005). For lake Velnezers that is not really the case. After the collapse of the Soviet Union, the lake conditions continued to deteriorate. Cladocera species diversity decreased to its lowest point (Fig. 4) and several Cladocera species, such as *A. rustica*, *A. costata*, *A. intermedia*, *L. setifera* and *A. curvirostris*, disappeared completely.

In the initial ten years represented by Zone 4, concentrations of Pb, Cu, S, and Fe remained high (Fig. 5). Pb enrichment in lake sediments in recent history is linked to gasoline additives (Brännvall et al., 1999; Meriläinen et al., 2010). The steady increase of Pb from 18 cm to peak concentrations in the 1990s (at sediment depth of 10–13 cm) denotes the expansion of private car use after the collapse of the Soviet Union when the number of private cars doubled within a decade. In the period between the year 1980 and 2000 private car ownership increased from 66 to 237 cars per 1000 population (Official statistics, 2023) which is more than a threefold increase. In the capital city of Latvia – Riga (where the lake Velnezers is located) this increase could be even higher due to higher income. Similar trends in increased car ownership have been observed in other post-Soviet countries after regaining independence (Pucher, 1999). The decline in Pb concentration since about 2002 is related to the ban of Pb additives in the early 21st century, which has previously been shown to result in a rapid decrease of Pb concentrations in sediment archives (Brännvall et al., 1999; Meriläinen et al., 2010).

The Jugla area, to which Velnezers belongs, was connected to Riga's central wastewater system during the 1990s (Rīgas Ūdens, 2022), likely explaining the rapid decrease in S and Cu and the steady reduction in Zn trends towards the present. However, these positive changes are accompanied by an increase in organic matter accumulation and a decrease in the C/N ratio (Fig. 4). Autochthonous algae typically have a lower C/N ratio compared to terrestrial plants. Therefore, a decrease in the C/N ratio suggests increased autochthonous production (Meyers and Ishiwatari, 1993; Meyers, 1997). The decay of the larger mass of organic matter in the bottom sediments following human activities increases oxygen consumption and can lead to anoxia in the deepest parts of the lake basins (Salminen et al., 2021).

The previously described peak in heavy metal pollution, oxygen depletion, and eutrophication between 1985 and 2000, caused by urbanization, significantly affected the species composition of Cladocera. Around the year 2000, we observe a reduction in heavy metal pollution and elements associated with anoxia. Concurrently, total Cladocera flux and the relative abundance of B. (B.) longirostris increased (Fig. 6, Fig. 7).

Cladocera species diversity reached its lowest point around the year 2000 and showed little improvement for most of Zone 4 (Fig. 7). By this time, several species preferring low nutrient concentrations had either completely or temporarily disappeared, including *A. elongata*, *A. rustica*, *Eurycercus* sp., *A. intermedia*, *A. costata*, and *L. setifera* (Hofmann, 1996; Bledzki and Rybak, 2016). Additionally, some littoral species not reported to be nutrient-sensitive, such as Ilyocryptus spp. and *A. curvirostris*, disappeared shortly after (around 2004). Unlike *B. (B.) longirostris*, these species did not recover after the reduction in pollution and nutrient input.

Whether urbanization-induced eutrophication, pollution, anoxia, or a combination of several stressors led to the disappearance of these species remains unknown. More studies on the effects of multiple stressors, heavy metal toxicity, and anoxia tolerance on littoral species are necessary to determine the exact causes of their disappearance. Nonetheless, these observations highlight the negative effects of urbanization on the Cladocera.

With the decrease of pollutants, the flux of Cladocera steadily rises across Zone 4, peaking in 2016. The increase in subfossil Cladocera flux is regarded as indicative of increase in live Cladocera abundance (Nykänen et al., 2009), and is frequently linked to either eutrophication or warming (Manca et al., 2007; Zawiska et al., 2017; Cremona et al., 2021).

It is reported that eutrophication and its effects are increased by climate warming. Such effects can include decreased dissolved oxygen, cyanobacteria blooms (Moss et al., 2011; Meerhoff et al., 2022), and even changes in the zooplankton community (Visconti et al., 2008). Considering the high level of human pressure on Lake Velnezers nutrient enrichment should be regarded as the primary influence on the lake ecosystem. However, there has been an approximately two-degree C° increase of annual mean temperature in Riga city between 1981 and 2018 (World Bank Group, 2022) that could further contribute to the negative effects of nutrient input.

We only see improvements regarding Cladocera species composition at the very upper sediment layers (the years 2016–2018). Such improvements include a slight increase in species diversity, reduction of Cladocera flux, and simultaneous increase of *Eubosmina* genus group (from 4 % to 16 %) and decrease of *Bosmina (B.) longirostris* (from 74 % to 64 %) (Fig. 6). Usually, the replacement of *Eubosmina* species by *B. (B.) longirostris* is known as eutrophication-induced common species succession (Adamczuk, 2016). In the Lake Velnezers case, we can see a reversion of this trend in recent year sediments. While the small temporal coverage of these improvements suggests exercising caution when making assumptions about directions of further lake development, we argue that this shift indicates potential for lake ecological state improvement.

It is known from other studies that lake re-oligotrophication or at least eutrophication decrease is possible after reduction of nutrient loading. The effect size and time lag of this process can vary between lakes – lakes with shorter water residence time tend to recover more rapidly (Jeppesen et al., 2005). Previous research has shown that the legacy effect can release more P from sediments than the amount of external input from agricultural lands in modern days (Jilbert et al., 2020). Hence, it is likely, that under the eutrophic conditions with large phytoplankton production, the legacy P enrichments will continue to leach from sediments back to water, delaying the recovery of the lake (Jilbert et al., 2020; Niemistö et al., 2012).

In the Winter or 2024 mass fish deaths were reported in Lake Velnezers, as well as year-round anoxia in water layers deeper than two meters below water surface (Interreg-Baltic, 2024), highlighting the bad ecological condition that continue to persist even after reduction in pollution. According to the latest update from the lake governing municipality, the lake has been chosen as the first pilot lake in Baltic countries for PAC (polyaluminium chloride) treatment to bind P in sediments (Interreg-Baltic, 2023; Rīgas pašvaldība, 2024), possibly solving these issues in the future.

5. Conclusions

In conclusion, we can confirm the hypothesis that urbanization has a more explicit effect on the lake's ecosystem than earlier human-driven disturbances. While agriculture had a notable effect on the ecosystem, cumulative effects of agriculture and urbanization drove Velnezers into a state beyond the possibility of recovering naturally. Under urbanization, lake Velnezers turned into a hypereutrophic lake with anoxia and heavy metal pollution problems due to nutrient and metal input from untreated wastewater and car exhaust gases. This caused a loss of species diversity and under urbanization pressure, the dominance of small-sized *Bosmina* (*B.*) *longirostris* became even more extreme and several species disappeared. In comparison, the transition from a low disturbance regime to agriculture brought noticeable changes in the lake ecosystem in a way that it transitioned from an oligotrophic to a eutrophic lake. However, during this stage, there does not seem to be any anoxia or pollution issues. Even though small-sized pelagic *Bosmina* (*B.*) *longirostris* was dominant, littoral taxa richness (especially sediment-associated) was high.

Following the conservation policies such as redirection of waste waters and Pb additive ban in fuel, the lake water quality has slightly improved. Velnezers is a lake with no inflow or outflow and most likely historical internal rather than external load of P plays a crucial role here. The high legacy concentrations of P in the reactive layer continue to release P into the water through anoxic sediments, hindering the lake's recovery process. This highlights the necessity for stronger intervention to restore lake water quality.

CRediT authorship contribution statement

Izabela Zawiska: Writing – review & editing. **Wojciech Tylmann:** Writing – review & editing, Writing – original draft, Investigation. **Normunds Stivrins:** Writing – review & editing, Writing – original draft, Investigation, Formal analysis. **Saija Saarni:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Formal analysis. **Inta Dimante-Deimantovica:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Investigation, Funding acquisition, Conceptualization. **Anna Lanka:** Writing – review & editing, Writing – original draft, Visualization, Project administration, Investigation, Formal analysis, Data curation, Conceptualization. **Siim Veski:** Writing – review & editing, Supervision, Funding acquisition, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT in order to improve text readability. After using this tool authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgements

The authors would like to thank Anneli Poska, Triin Reitalu, Varvara Bakumenko, Eliise Kara, and Sophie Graul for their help in data analysis and visualization. We are also grateful to Samuel Hartikainen and Timo Saarinen for their help in sample collection. The research was funded by the European Regional Development Fund, 1.1.1.2 Post-doctoral project No.1.1.1.2/VIAA/2/18/359, and the Latvian Institute of Aquatic Ecology. ESF project PRG 1993, TK 215, and AL was funded by the Doctoral School of Earth Sciences and Ecology, supported by the European Union, European Regional Development Fund (ASTRA "TTÜ arenguprogramm aastateks 2016-2022"). Additional funding came from the University of Latvia Grant Nr. AAp2016/B041//Zd2016/AZ03 and Y5-AZ03_ZF-N-110.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.ancene.2024.100439.

References

Adamczuk, M., 2016. Past, present, and future roles of small cladoceran Bosmina longirostris (O. F. Müller, 1785) in aquatic ecosystems. Hydrobiologia 767, 1–11. https://doi.org/10.1007/s10750-015-2495-7.

Ahmed, S.F., Kumar, P.S., Kabir, M., Zuhara, F.T., Mehjabin, A., Tasannum, N., Hoang, A. T., Kabir, Z., Mofijur, M., 2022. Threats, challenges and sustainable conservation strategies for freshwater biodiversity. Environ. Res. 214, 113808 https://doi.org/10.1016/j.envres.2022.113808.

Alvarado-Flores, J., Arzate-Cárdenas, M.A., Pérez-Yañez, D., Cejudo, E., 2022. Environmental stressor induces morphological alterations in zooplankton. Lat. Am. J. Aquat. Res. 50 (1), 1–12. https://doi.org/10.3856/vol50-issue1-fulltext-2774.

apkaimes [WWW Document] n.d. Jugla.URL ⟨https://apkaimes.lv/jugla/⟩ (Accessed 14 March 2024).

Aquino-López, M.A., Blaauw, M., Christen, J.A., Sanderson, N.K., 2018. Bayesian analysis of 210Pb dating. J. Agric., Biol. Environ. Stat. 23, 317–333. https://doi.org/10.1007/s13253-018-0328-7.

Aquino-López, M.A., Ruiz-Fernández, A.C., Blaauw, M., Sanchez-Cabeza, J.-A., 2020. Comparing classical and Bayesian 210Pb dating models in human-impacted aquatic environments. Quat. Geochronol. 60, 101–106. https://doi.org/10.1016/j.quageo.2020.101106.

Balode, M., Purina, I., Strake, S., Purvina, S., Pfeifere, M., Barda, I., Povidisa, K., 2006. Toxic cyanobacteria in the lakes located in Rīga (the capital of Latvia) and its surroundings: present state of knowledge. Afr. J. Mar. Sci. 28, 225–230. https://doi.org/10.2989/18142320609504152.

Battarbee, R.W., 1999. The importance of palaeolimnology to lake restoration. In The Ecological Bases for Lake and Reservoir Management: Proceedings of the Ecological Bases for Management of Lakes and Reservoirs Symposium, held 19–22 March 1996, Leicester, United Kingdom. Springer Netherlands, pp. 149–159.

Battarbee, R.W., Morley, D., Bennion, H., Simpson, G.L., Hughes, M., Bauere, V., 2011. A palaeolimnological meta-database for assessing the ecological status of lakes. J. Paleolimnol. 45, 405–414. https://doi.org/10.1007/s10933-010-9417-5.

Beckers, V., Poelmans, L., Van Rompaey, A., Dendoncker, N., 2020. The impact of urbanization on agricultural dynamics: a case study in Belgium. J. Land Use Sci. *15* (5), 626–643. https://doi.org/10.1080/1747423X.2020.1769211.

Bennion, H., Battarbee, R.W., Sayer, C.D., Simpson, G.L., Davidson, T.A., 2011. Defining reference conditions and restoration targets for lake ecosystems using palaeolimnology: a synthesis. J. Paleolimnol. 45, 533–544. https://doi.org/10.1007/s10933-010-9419-3.

Bērziņš, B., Bertilsson, J., 1989. On limnic micro-crustaceans and trophic degree. Hydrobiologia 185, 95–100. https://doi.org/10.1007/BF00010808.

Bērziņš, B., Bertilsson, J., 1990. Occurrence of limnic micro-crustaceans in relation to pH and humic content in Swedish water bodies. Hydrobiolgia 199, 65–71. https://doi.org/10.1007/BF00007834.

Blaauw, M., Christen, J.A., 2011. Flexible paleoclimate age-depth models using an autoregressive gamma process. Bayesian Anal. 6 https://doi.org/10.1214/11-BA618.

Bledzki, L.A., Rybak, J.I., 2016. Freshwater Crustacean Zooplankton of Europe: Cladocera & Copepoda (Calanoida, Cyclopoida) Key to species identification, with notes on ecology, distribution, methods and introduction to data analysis. Springer.

Bos, D.G., Cumming, B.F., 2003. Sedimentary Cladoceran remains and their relationship to nutrients and other limnological variables in 53 lakes from British Columbia, Canada. Can. J. Fish. Aquat. Sci. 60, 1177–1189. https://doi.org/10.1139/f03-097.

Boucherle, M.M., Züllig, H., 1983. Cladoceran remains as evidence of change in trophic state in three Swiss lakes. Hydrobiologia 103, 141–146. https://doi.org/10.1007/BF00028442.

Brännvall, M.L., Bindler, R., Renberg, I., Emteryd, O., Bartnicki, J., Billström, K., 1999. The medieval metal industry was the cradle of modern large-scale atmospheric lead pollution in Northern Europe. Environ. Sci. 33, 4391–4395. https://doi.org/10.1021/es990279n.

Brodersen, K.P., Whiteside, M.C., Lindegaard, C., 1998. Reconstruction of trophic state in Danish lakes using subfossil chydorid (Cladocera) assemblages. Can. J. Fish. Aquat. Sci. 55, 1093–1103. https://doi.org/10.1139/f98-008.

Burge, D.R.L., Edlund, M.B., Frisch, D., 2018. Paleolimnology and resurrection ecology: The future of reconstructing the past. Evolut. Appl. 11, 42–59. https://doi.org/10.1111/eva.12556.

Carey, C.C., Rydin, E., 2011. Lake trophic status can be determined by the depth distribution of sediment phosphorus. Limnol. Oceanogr. 56, 2051–2063. https://doi.org/10.4319/lo.2011.56.6.2051.

Čeirāns, A., 2007. Zooplankton indicators of trophy in Latvian lakes. Acta Univ. Latv. 723, 61–69 (Biology).

Celewicz-Gołdyn, S., Kuczyńska-Kippen, N., 2017. Ecological value of macrophyte cover in creating habitat for microalgae (diatoms) and zooplankton (rotifers and crustaceans) in small field and forest water bodies. PLoS One 12 (5), e0177317. https://doi.org/10.1371/journal.pone.0177317.

Chen, G., Dalton, C., Taylor, D., 2010. Cladocera as indicators of trophic state in Irish lakes. J. Paleolimnol. 44, 465–481. https://doi.org/10.1007/s10933-010-9428-2.

Couture, R.M., Fischer, R., Van Cappellen, P., Gobeil, C., 2016. Non-steady state diagenesis of organic and inorganic sulfur in lake sediments. Geochim. Et. Cosmochim. Acta 194, 15–33. https://doi.org/10.1016/j.gca.2016.08.029.

Cremona, F., Blank, K., Haberman, J., 2021. Effects of environmental stressors and their interactions on zooplankton biomass and abundance in a large eutrophic lake. Hydrobiologia 848, 4401–4418. https://doi.org/10.1007/s10750-021-04653-3.

de Melo, R., Coelho, P.N., dos Santos-Wisniewski, M.J., Wisniewski, C., 2017. Morphological abnormalities in cladocerans related to eutrophication of a tropical reservoir. J. Limnol. 94–102. https://doi.org/10.4081/jlimnol.2016.1395.

Dean Jr., Walter E., 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other methods. SEPM JSR Vol. 44. https://doi.org/10.1306/74D729D2-2B21-11D7-8648000102C1865D.

Dean, W., 2002. A 1500-year record of climatic and environmental change in ElkLake, Clearwater County, Minnesota II: geochemistry, mineralogy, and stableisotopes. J. Paleolimnol. 27, 301–319. https://doi.org/10.1023/A:1016054522905.

Declerck, S.A.J., Bakker, E.S., Van Lith, B., Kersbergen, A., Van Donk, E., 2011. Effects of nutrient additions and macrophyte composition on invertebrate community assembly and diversity in experimental ponds. Basic Appl. Ecol. 12, 466–475. https://doi.org/10.1016/j.baae.2011.05.001.

Donohue, I., Garcia Molinos, J., 2009. Impacts of increased sediment loads on the ecology of lakes. Biol. Rev. 84, 517–531. https://doi.org/10.1111/j.1469-185X.2009.00081.x.

Doubek, J.P., Campbell, K.L., Doubek, K.M., Hamre, K.D., Lofton, M.E., McClure, R.P., Ward, N.K., Carey, C.C., 2018. The effects of hypolimnetic anoxia on the diel vertical migration of freshwater crustacean zooplankton. Ecosphere 9, e02332. https://doi.org/10.1002/ecs2.2332.

Dručka, A., 2014. Antropogēnās ietekmes liecības Rīgas Velnezera nogulumos [Evidence of anthropogenic influence in the sediments of The Riga Velnezers]. Batchelor theses. University of Latvia.

Druvietis I., 2012. Peculiarities of phytoplankton communities in clear water and brown water shallow lakes in Latvia. Conference paper BALWOIS, Ohrid, Republic of Macedonia.

Druvietis, I., Dobkeviča, L., Dunke, M., 2017. Peculiarities of phytoplankton communities in urban lakes of Riga city and it's vicinity. Environ. Exp. Biol. 15, 71–72 (Abstract of the 75th Scientific conference of the University of Latvia).

Druvietis, I., Springe, G., Urtane, L., Klavins, M., 1998. Evaluation of plankton communities in small highly humic bog lakes in Latvia. Environ. Int. 24, 595–602. https://doi.org/10.1016/S0160-4120(98)00038-5.

Ekau, W., Auel, H., Pörtner, H.-O., Gilbert, D., 2010. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). Biogeosciences 7, 1669–1699. https://doi.org/10.5194/bg-7-1669-2010.

Faith, D.P., Minchin, P.R., Belbin, L., 1987. Compositional dissimilarity as a robust measure of ecological distance. Vegetatio 69, 57–68. https://doi.org/10.1007/BF00038687.

Flössner, D., 2000. Die Haplopoda unde Cladocera Mitteleuropas. Backhuys Publishers, Leiden, Netherlands.

Frey, D.G., 1986. Cladocera analysis. In: Berglund, B.E. (Ed.), Handbook of Holocene Palaeoecology and Palaeohydrology. Wiley, Chichester, pp. 667–692.

Gao, J., Huang, Y., Zhi, Y., Yao, J., Wang, F., Yang, W., Han, L., Lin, D., He, Q., Wei, B., Grieger, K., 2022. Assessing the impacts of urbanization on stream ecosystem functioning through investigating litter decomposition and nutrient uptake in a forest and a hyper-eutrophic urban stream. Ecol. Indic. 138, 108859 https://doi.org/10.1016/j.ecolind.2022.108859.

General base, 1963. 1963 Генеральный штаб 25k [map] 1:25`000. URL ⟨https://vesture.dodies.lv/#m=14/56.97495/24.24871&l=O/GE1⟩ (Accessed 14 March 2024).

Goal 11: Sustainable cities and communities [WWW Document], n.d. The Global Goals. URL ⟨https://globalgoals.org/goals/11-sustainable-cities-and-communities/⟩ (Accessed 14 March 2024).

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. Comput. Geosci. 13 (1), 13–35. https://doi.org/10.1016/0098-3004(87)90022-7.

Grimm, E.C., 2011. TILIA 1.7.16 software. Illinois State Museum,Research and Collection Center, Springfield.

Grizzetti, B., Pistocchi, A., Liquete, C., Udias, A., Bouraoui, F., Van De Bund, W., 2017. Human pressures and ecological status of European rivers. Sci. Rep. 7, 205. https://doi.org/10.1038/s41598-017-00324-3.

Grudzinska, I., Vassiljev, J., Saarse, L., Reitalu, T., Veski, S., 2017. Past environmental change and seawater intrusion into coastal Lake Lilaste, Latvia. J. Paleolimnol. 57, 257–271. https://doi.org/10.1007/s10933-017-9945-3.

Güneralp, B., Reba, M., Hales, B.U., Wentz, E.A., Seto, K.C., 2020. Trends in urban land expansion, density, and land transitions from 1970 to 2010: A global synthesis. Environ. Res. Lett. *15* (4), 044015. DOI:10.1088/1748-9326/ab6669.

Gunnars, A., Blomqvist, S., Johansson, P., Andersson, C., 2002. Formation of Fe (III) oxyhydroxide colloids in freshwater and brackish seawater, with incorporation of phosphate and calcium. Geochim. Et. Cosmochim. Acta *66* (5), 745–758. https://doi.org/10.1016/S0016-7037(01)00818-3.

Gurina, I., 1980. Tautas veselības labā, Rīgas pilsētas tautas deputātu domes sesija, Gaiļezers un citi. Rīgas Balss 124, 30 May 1980. Availabe at: ⟨http://periodika.lv/periodika2-viewer/?lang=fr#panel:pa⟩|issue:512512|article:DIVL26|query:notek%C5%ABde%C5%86i%20Velnezer%C4%81%20.

Hammer, Ø., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4 (1), 9.

Heinsalu, A., Alliksaar, T., 2009. Paleolimnological asessment of the reference conditions and ecological status of lakes in Estonia – implications for the European Union Water Framework Directive. Est. J. Earth Sci. 58 (4), 334–341. https://doi.org/10.3176/earth.2009.4.11.

Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. J. Paleolimnol. 25, 101–110. https://doi.org/10.1023/A:1008119611481.

Hofmann, W., 1996. Empirical relationships between cladoceran fauna and trophic state in thirteen northern German lakes: analysis of surficial sediments. Hydrobiologia 318, 195–201. https://doi.org/10.1007/BF00016680.

Hupfer, M., Lewandowski, J., 2008. Oxygen Controls the Phosphorus Release from Lake Sediments – a Long-Lasting Paradigm in Limnology. Int. Rev. Hydrobiol. 93, 415–432. https://doi.org/10.1002/iroh.200711054.

Interreg-Baltic, 2023. Swedish-Latvian team visit the pilot lake in Riga. [WWW Document] URL ⟨https://interreg-baltic.eu/project-posts/trust-alum/swedish-and-latvian-teams-visit-the-pilot-lake-in-riga-2/⟩ (Accessed 14 March 2024).

Interreg-Baltic 2024, Mass fish death in the pilot lake call for urgent water treatment [WWW document]. URL: ⟨https://interreg-baltic.eu/project-posts/trust-alum/mass-ive-fish-death-in-the-pilot-lake-highlight-the-urgent-need-for-water-treatment/⟩ (Accessed 29 April 2024).

Jackson, D.A., 1993. Stopping Rules in Principal Components Analysis: A Comparison of Heuristical and Statistical Approaches. Ecology 74, 2204–2214. https://doi.org/10.2307/1939574.

Janse, J.H., Kuiper, J.J., Weijters, M.J., Westerbeek, E.P., Jeuken, M.H.J.L., Bakkenes, M., Alkemade, R., Mooij, W.M., Verhoeven, J.T.A., 2015. GLOBIO-Aquatic, a global model of human impact on the biodiversity of inland aquatic ecosystems. Environ. Sci. Policy 48, 99–114. https://doi.org/10.1016/j.envsci.2014.12.007.

Jensen, T.C., Dimante-Deimantovica, I., Schartau, A.K., Walseng, B., 2013. Cladocerans respond to differences in trophic state in deeper nutrient poor lakes from Southern Norway. Hydrobiologia 715, 101–112. https://doi.org/10.1007/s10750-012-1413-5.

Jensen, T.C., Zawiska, I., Oksman, M., Słowiński, M., Woszczyk, M., Luoto, T.P., Tylmann, W., Nevalainen, L., Obremska, M., Schartau, A.K., Walseng, B., 2020. Historical human impact on productivity and biodiversity in a subalpine oligotrophic lake in Scandinavia. J. Paleolimnol. 63, 1–20. https://doi.org/10.1007/s10933-019-00100-5.

Jeppesen, E., Søndergaard, M., Jensen, J.P., Havens, K.E., Anneville, O., Carvalho, L., Coveney, M.F., Deneke, R., Dokulil, M.T., Foy, B., Gerdeaux, D., Hampton, S.E., Hilt, S., Kangur, K., Köhler, J., Lammens, E.H.H.R., Lauridsen, T.L., Manca, M., Miracle, M.R., Moss, B., Nõges, P., Persson, G., Phillips, G., Portielje, R., Romo, S., Schelske, C.L., Straile, D., Tatrai, I., Willén, E., Winder, M., 2005. Lake responses to reduced nutrient loading – an analysis of contemporary long-term data from 35 case studies. Freshw. Biol. 50, 1747–1771. https://doi.org/10.1111/j.1365-2427.2005.01415.x.

Jilbert, T., Jokinen, S., Saarinen, T., Mattus-Kumpunen, U., Simojoki, A., Saarni, S., Salminen, S., Niemistö, J., Horppila, J., 2020. Impacts of a deep reactive layer on sedimentary phosphorus dynamics in a boreal lake recovering from eutrophication. Hydrobiologia 847, 4401–4423. https://doi.org/10.1007/s10750-020-04289-9.

Jilbert, T., Slomp, C.P., 2013. Iron and manganese shuttles control the formation of authigenic phosphorus minerals in the euxinic basins of the Baltic Sea. Geochim. Et. Cosmochim. Acta 107, 155–169. https://doi.org/10.1016/j.gca.2013.01.005.

Johansson, M., Saarni, S., Sorvari, J., 2019. Ultra-high-resolution monitoring of the catchment response to changing weather conditions using online sediment trapping. Quaternary 2, 18. https://doi.org/10.3390/quat2020018.

Juhna, T., Kļaviņs, M., 2001. Water-quality changes in Latvia and Riga 1980-2000: possibilities and problems. Ambio 30 (4-5), 306–314. PMID: 11697267.

Kalnina, L., Ceriņa, A., Kiziks, K., Stankeviča, K., Pujate, A., Dručka, A., 2019. Evidence of human impact and vegetation change during the Late Iron age and the Medieval Livonian period at some sites along the lower course of the river Daugava. In: Pluskowski, A. (Ed.), Ecol. Crusad., Colon., Relig. Convers. Mediev. Balt. 129–146 (Terra Sacra II. Brepols).

Koivisto, S., Ketola, M., 1995. Effects of copper on life-history traits of Daphnia pulex and Bosmina longirostris. Aquat. Toxicol. 32, 255–269. https://doi.org/10.1016/0166-445X(94)00094-7.

Krause-Dellin, D., Steinberg, C., 1986. Cladoceran remains as indicators of lake acidification. Hydrobiologia 143, 129–134. https://doi.org/10.1007/BF00026655.

Kurek, J., Korosi, J.B., Jeziorski, A., Smol, J.P., 2010. Establishing reliable minimum count sizes for cladoceran subfossils sampled from lake sediments. J. Paleolimnol. 44, 603–612. https://doi.org/10.1007/s10933-010-9440-6.

Leja, F., 1941. Darbs un atpūta. Pad. Latv. 126, 28. May 1941.

Līcīte, V., 2017. ES nozīmes ūdeņu biotopu inventarizācijas anketa, Velnezers. 4 September 2017. 17VL008_59_1, Dabas Aizsardzības Pārvalde, Sigulda.

Manca, M., Torretta, B., Comoli, P., Amsinck, S.L., Jeppesen, E., 2007. Major changes in trophic dynamics in large, deep sub-alpine Lake Maggiore from 1940s to 2002: a high resolution comparative palaeo-neolimnological study. Freshw. Biol. 52, 2256–2269. https://doi.org/10.1111/j.1365-2427.2007.01827.x.

Matthews, N., 2016. People and fresh water ecosystems: pressures, responses and resilience. Aquat. Procedia 6, 99–105. https://doi.org/10.1016/j.aqpro.2016.06.012.

McCarthy, F.M., Patterson, R.T., Head, M.J., Riddick, N.L., Cumming, B.F., Hamilton, P. B., Pisaric, M.F., Gushulak, A.C., Leavitt, P.R., Lafond, K.M., Llew-Williams, B., Marshall, M., Heyde, A., Pilkington, P.M., Moraal, J., Boyce, J.I., Nasser, N.A., Walsh, C., Garvie, M., Roberts, S., Rose, N.L., Cundy, A.B., Gaca, P., Milton, A., Hajdas, I., Crann, C.A., Boom, A., Finkelstein, S.A., McAndrews, J.H., 2023. The varved succession of Crawford Lake, Milton, Ontario, Canada as a candidate Global boundary Stratotype Section and Point for the Anthropocene series. Anthr. Rev. 10, 146–176. https://doi.org/10.1177/20530196221149281.

Meerhoff, M., Audet, J., Davidson, T.A., De Meester, L., Hilt, S., Kosten, S., Liu, Z., Mazzeo, N., Paerl, H., Scheffer, M., Jeppesen, E., 2022. Feedback between climate change and eutrophication: revisiting the allied attack concept and how to strike back. Inland Waters *12* (2), 187–204. https://doi.org/10.1080/20442041.2022.2029317.

Meriläinen, J.J., Kustula, V., Witick, A., Haltia-Hovi, E., Saarinen, T., 2010. Pollution history from 256 BC to AD 2005 inferred from the accumulation of elements in a varve record of Lake Korttajärvi in Finland. J. Paleolimnol. 44, 531–545. https://doi.org/10.1007/s10933-010-9435-3.

Meyers, P.A., 1997. Organic geochemical proxies of paleoceanographic, paleolimnologic, and paleoclimatic processes. Org. Geochem. 27, 213–250. https://doi.org/10.1016/S0146-6380(97)00049-1.

Meyers, P.A., Ishiwatari, R., 1993. Lacustrine organic geochemistry—an overview of indicators of organic matter sources and diagenesis in lake sediments. Org. Geochem. 20, 867–900. https://doi.org/10.1016/0146-6380(93)90100-P.

Military topographic map, 1908. Военно-топографическая карта 1908 (1 verst) [map] URL ⟨https://vesture.dodies.lv/#m=15/56.97800/24.25077&l=O/7⟩ (Accessed 14 March 2024).

Moss, B., Kosten, S., Meerhoff, M., Battarbee, R.W., Jeppesen, E., Mazzeo, N., Havens, K., Lacerot, G., Liu, Z., De Meester, L., Paerl, H., 2011. Allied attack: climate change and eutrophication. Inland Waters *1* (2), 101–105. https://doi.org/10.5268/IW-1.2.359.

NARA, 1940. map] URL. NARA Aerophoto 1940. ⟨https://vesture.dodies.lv/#m=15/56.97800/24.25077&l=O/N⟩ (Accessed 14 March 2024).

Nevalainen, L., Luoto, T.P., 2017. Relationship between cladoceran (Crustacea) functional diversity and lake trophic gradients. Funct. Ecol. 31, 488–498. https://doi.org/10.1111/1365-2435.12737.

Niedre, M., 1986. Mēs - pilsētai, Pilsēta - Mums. Pelēki zilie ūdeņi. Rīgas Balss 17, 21 January 1986. Available at: ⟨http://periodika.lv/periodika2-viewer/?lang=fr#panel:pa⟩|issue:501886|article:DIVL161|query:Velnezer%C4%81%20Juglas%20ezeros%20.

Niemistö, J., Tamminen, P., Ekholm, P., Horppila, J., 2012. Sediment resuspension: rescue or downfall of a thermally stratified eutrophic lake? Hydrobiologia 686, 267–276. https://doi.org/10.1007/s10750-012-1021-4.

Noges, T., Janatian, N., Laugaste, R., Noges, P., 2020. Post-soviet changes in nitrogen and phosphorus stoichiometry in two large non-stratified lakes and the impact on phytoplankton. Glob. Ecol. Conserv. 24, e01369.

Nykänen, M., Vakkilainen, K., Liukkonen, M., Kairesalo, T., 2009. Cladoceran remains in lake sediments: a comparison between plankton counts and sediment records. J. Paleolimnol. 42, 551–570. https://doi.org/10.1007/s10933-008-9304-5.

Official statistics, 2023. Passenger cars per 1,000 population at the end of year 1980 -2022. [WWW Document] URL ⟨https://data.stat.gov.lv/pxweb/en/OSP_PUB/START_NOZ_TR_TRC/TRC010/⟩ (Accessed 14 March 2024).

Oksanen J., Blanchet G.F., Friendly M. et al. (2017) Vegan: communityecology package. R package version 2.4-3. ⟨https://CRAN.R-project.org/package=vegan⟩.

Otake, Y., Ohtsuki, H., Urabe, J., Kimura, S., Yamada, K., Yoshida, T., 2021. Long-term dynamics of a cladoceran community from an early stage of lake formation in Lake Fukami-ike, Japan. Ecol. Evol. 11, 1240–1253. https://doi.org/10.1002/ece3.7112.

Ozoliņš, D., Skuja, A., Jēkabsone, J., Kokorite, I., Avotins, A., Poikane, S., 2021. How to assess the ecological status of highly humic lakes? Development of a new method based on benthic invertebrates. Water 13 (2), 223. https://doi.org/10.3390/w13020223.

Panarelli, E.A., Martins, H.L., Sousa, F.D.R., Millan, R.N., 2023. Morphological abnormalities in Bosmina freyi population (Cladocera: Bosminidae) from small urban reservoirs. Limnologica 102, 126108. https://doi.org/10.1016/j.limno.2023.126108.

Pucher, J., 1999. The transformation of urban transport in the Czech Republic, 1988–1998. Transp. Policy 6, 225–236. https://doi.org/10.1016/S0967-070X(99)00023-2.

Pujate, A., 2015. Vides apstākļu izmaiņu un cilvēka darbības pēdas Rīgas līča piekrastes ezeru nogulumos [Traces of environmental change and human impact in the sediments of lakes along the coast of the gulf of Riga]. Doctoral thesis. University of Latvia.

Pumpurs, R., 1959. Nevar atļaut Velna ezerā mazgāt veļu. Cīņa 155, 4 July 1959.

R Core Team, 2023. R: A Language and Environment for Statistical Computing_. R Foundation for Statistical Computing, Vienna, Austria. URL ⟨https://www.R-project.org/⟩ (Accessed 14 March 2024).

Richard Albert, M., Chen, G., MacDonald, G.K., Vermaire, J.C., Bennett, E.M., Gregory-Eaves, I., 2010. Phosphorus and land-use changes are significant drivers of cladoceran community composition and diversity: an analysis over spatial and temporal scales. Can. J. Fish. Aquat. Sci. 67, 1262–1273. https://doi.org/10.1139/F10-058.

Rīgas pašvaldība, 2024. Velnezerā plānota ūdens attīrīšana skābekļa daudzuma palielināšanai. [WWW Document] URL ⟨https://mvd.riga.lv/velnezera-planota-udens-attirisana-skabekla-daudzuma-palielinasanai/⟩ (Accessed 14 March 2024).

Rīgas Ūdens, 2022. Vēsture. [WWW Document] ⟨https://www.rigasudens.lv/lv/vesture⟩ (Accessed 14 March 2024).

Robežnieks, M. 2022. 20.-21. Gadsimta nogulumu uzkrāšanās procesu izvērtējums dažādas ģenēzes un trofijas ezeros Latvijas teritorijā [Assessment of 20th-21st century sediment accumulation processes in lakes of different genesis and throphicity in the territory of Latvia]. Batchelor thesis. University of Latvia.

Roeser, P., Dräger, N., Brykała, D., Ott, F., Pinkerneil, S., Gierszewski, P., Lindemann, C., Plessen, B., Brademann, B., Kaszubski, M., Fojutowski, M., Schwab, M.J., Słowiński, M., Błaszkiewicz, M., Brauer, A., 2021. Advances in understanding calcite varve formation: new insights from a dual lake monitoring approach in the southern Baltic lowlands. Boreas 50, 419–440. https://doi.org/10.1111/bor.12506.

Saarni, S., Lensu, A., Tammelin, M., Haltia, E., Saarinen, T., 2017. Winter climate signal in boreal clastic-biogenic varves: a comprehensive analysis of three varved records from 1890 to 1990 AD with meteorological and hydrological data from Eastern Finland. GFF 139, 314–326. https://doi.org/10.1080/11035897.2017.1389984.

Salminen, S., Tammelin, M., Jilbert, T., Fukumoto, Y., Saarni, S., 2021. Human actions were responsible for both initiation and termination of varve preservation in Lake Vesijärvi, southern Finland. J. Paleolimnol. 66, 207–227. https://doi.org/10.1007/s10933-021-00200-1.

Santana Marques, P., Resende Manna, L., Clara Frauendorf, T., Zandonà, E., Mazzoni, R., El-Sabaawi, R., 2020. Urbanization can increase the invasive potential of alien species. J. Anim. Ecol. 89, 2345–2355. https://doi.org/10.1111/1365-2656.13293.

Schacht, J.R.S., MacKeigan, P.W., Taranu, Z.E., Huot, Y. and Gregory-Eaves, I., 2022. Agricultural land use and lake morphology explain substantial variation in water quality across Canada. Preprint. ⟨https://europepmc.org/article/ppr/ppr538681⟩.

Scholtysik, G., Goldhammer, T., Arz, H.W., Moros, M., Littke, R., Hupfer, M., 2022. Geochemical focusing and burial of sedimentary iron, manganese, and phosphorus during lake eutrophication. Limnol. Oceanogr. 67, 768–783. https://doi.org/10.1002/lno.12019.

Seddon, A.W.R., Mackay, A.W., Baker, A.G., Birks, H.J.B., Breman, E., Buck, C.E., Ellis, E. C., Froyd, C.A., Gill, J.L., Gillson, L., Johnson, E.A., Jones, V.J., Juggins, S., Macias-Fauria, M., Mills, K., Morris, J.L., Nogués-Bravo, D., Punyasena, S.W., Roland, T.P., Tanentzap, A.J., Willis, K.J., Aberhan, M., Van Asperen, E.N., Austin, W.E.N., Battarbee, R.W., Bhagwat, S., Belanger, C.L., Bennett, K.D., Birks, H.H., Bronk Ramsey, C., Brooks, S.J., De Bruyn, M., Butler, P.G., Chambers, F.M., Clarke, S.J., Davies, A.L., Dearing, J.A., Ezard, T.H.G., Feurdean, A., Flower, R.J., Gell, P., Hausmann, S., Hogan, E.J., Hopkins, M.J., Jeffers, E.S., Korhola, A.A., Marchant, R., Kiefer, T., Lamentowicz, M., Larocque-Tobler, I., López-Merino, L., Liow, L.H., McGowan, S., Miller, J.H., Montoya, E., Morton, O., Nogué, S., Onoufriou, C., Boush, L.P., Rodriguez-Sanchez, F., Rose, N.L., Sayer, C.D., Shaw, H.E., Payne, R., Simpson, G., Sohar, K., Whitehouse, N.J., Williams, J.W., Witkowski, A., 2014. Looking forward through the past: identification of 50 priority research questions in palaeoecology. J. Ecol. 102, 256–267. https://doi.org/10.1111/1365-2745.12195.

Shanahan, T.M., Overpeck, J.T., Hubeny, J.B., King, J., Hu, F.S., Hughen, K., Miller, G., Black, J., 2008. Scanning micro-X-ray fluorescence element mapping: a new tool for the study of laminated sediment records. Geochem., Geophys., Geosyst. 9 https://doi.org/10.1029/2007GC001800.

Shen, J., Qin, G., Yu, R., Zhao, Y., Yang, J., An, S., Liu, R., Leng, X., Wan, Y., 2021. Urbanization has changed the distribution pattern of zooplankton species diversity and the structure of functional groups. Ecol. Indic. 120, 106944 https://doi.org/10.1016/j.ecolind.2020.106944.

SIA "Vides konsultāciju birojs", 2022. Velnezera raksturojums un ekspluatācijas (apsaimniekošanas) noteikumi.

Simpson, E.H., 1949. Measurement of Diversity, 688–688 Nature 163. https://doi.org/10.1038/163688a0.

Slomp, C.P., Van der Gaast, S.J., Van Raaphorst, W., 1996. Phosphorus binding by poorly crystalline iron oxides in North Sea sediments. Mar. Chem. *52* (1), 55–73. https://doi.org/10.1016/0304-4203(95)00078-X.

Specialcharde von Livland, 1839 [map] URL ⟨https://vesture.dodies.lv/#m=15/56.97800/24.25077&l=O/1⟩ (accessed 3.14.24).

Stankevica, K., Pujate, A., Kalnina, L., Klavins, M., Cerina, A., Drucka, A., 2015. Records of the anthropogenic influence on different origin small lake sediments of Latvia. Baltica 28 (2), 135–150 (Vilnius).

Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O., Ludwig, C., 2015. The trajectory of the Anthropocene: the great acceleration. Anthr. Rev. *2* (1), 81–98. https://doi.org/10.1177/2053019614564785.

Szeroczyńska, K., Sarmaja-Korjonen, K., 2007. Atlas of subfossil Cladocera from central and northern Europe. Friends of the Lower Vistula Society, Swiecie.

Tumurtogoo, U., Figler, A., Korponai, J., Sajtos, Z., Grigorszky, I., Berta, C., Gyulai, I., 2022. Density and diversity differences of contemporary and subfossil cladocera assemblages: a case study in an oxbow lake. Water 14, 2149. https://doi.org/10.3390/w14142149.

Tylmann, W., Bonk, A., Goslar, T., Wulf, S., Grosjean, M., 2016. Calibrating 210Pb dating results with varve chronology and independent chronostratigraphic markers: Problems and implications. Quat. Geochronol. 32, 1–10. https://doi.org/10.1016/j.quageo.2015.11.004.

United Nations, n.d. Sustainable cities and human settlements | Department of Economic and Social Affairs [WWW Document]. URL ⟨https://sdgs.un.org/topics/sustainable-cities-and-human-settlements⟩ (Accessed 14 March 2024).

Urtāne, L., 1998. Cladocera kā Latvijas ezeru tipu un trofiskā stāvokļa indikatori [Cladocera as indicators of lake type and trophic status in Latvia]. Doctoral thesis. University of Latvia.

USGS, 1967-1972. 1967-1972. gadi. USGS EROS Archive. Declassified CORONA Satellite Imagery. [map] URL ⟨https://vesture.dodies.lv/#m=15/56.97800/24.25077&l=O/B⟩ (Accessed 14 March 2024).

Van Vliet, J., Eitelberg, D.A., Verburg, P.H., 2017. A global analysis of land take in cropland areas and production displacement from urbanization. Glob. Environ. Change 43, 107–115. https://doi.org/10.1016/j.gloenvcha.2017.02.001.

Velghe, K., Vermaire, J.C., Gregory-Eaves, I., 2012. Declines in littoral species richness across both spatial and temporal nutrient gradients: a palaeolimnological study of two taxonomic groups. Freshw. Biol. 57, 2378–2389. https://doi.org/10.1111/fwb.12017.

Visconti, A., Manca, M., De Bernardi, R., 2008. Eutrophication-like response to climate warming: an analysis of Lago Maggiore (N. Italy) zooplankton in contrasting years. J. Limnol. *67* (2), 87. https://doi.org/10.4081/jlimnol.2008.87.

Walker, M.J.C., Bauer, A.M., Edgeworth, M., Ellis, E.C., Finney, S.C., Gibbard, P.L., Maslin, M., 2024. The Anthropocene is best understood as an ongoing, intensifying, diachronous event. Boreas 53, 1–3. https://doi.org/10.1111/bor.12636.

World Bank Group 2022. Climate Change Knowledge Portal for Development Practitioners and Policy makers [WWW document]. URL: ⟨https://climateknowledgeportal.worldbank.org/country/latvia/climate-data-historical⟩ (accessed 4.29.24).

Zawiska, I., Dimante-Deimantovica, I., Luoto, T.P., Rzodkiewicz, M., Saarni, S., Stivrins, N., Tylmann, W., Lanka, A., Robeznieks, M., Jilbert, T., 2020. Long-term consequences of water pumping on the ecosystem functioning of Lake Sekšu, Latvia. Water 12, 1459. https://doi.org/10.3390/w12051459.

Zawiska, I., Luoto, T.P., Nevalainen, L., Tylmann, W., Jensen, T.C., Obremska, M., Słowiński, M., Woszczyk, M., Schartau, A.K., Walseng, B., 2017. Climate variability and lake ecosystem responses in western Scandinavia (Norway) during the last Millennium. Palaeogeogr., Palaeoclimatol., Palaeoecol. 466, 231–239. https://doi.org/10.1016/j.palaeo.2016.11.034.

Zawisza, E., Zawiska, I., Correa-Metrio, A., 2016. Cladocera community composition as a function of physicochemical and morphological parameters of dystrophic lakes in NE Poland. Wetlands 36, 1131–1142. https://doi.org/10.1007/s13157-016-0832-x.

Zolitschka, B., Francus, P., Ojala, A.E.K., Schimmelmann, A., 2015. Varves in lake sediments – a review. Quat. Sci. Rev. 117, 1–41. https://doi.org/10.1016/j.quascirev.2015.03.019.

Appendix 3

Article III
Zawiska, I., Dimante-Deimantovica, I., Luoto, T.P., Rzodkiewicz, M., Saarni, S., Stivrins, N., Tylmann, W., **Lanka, A.**, Robeznieks, M. and Jilbert, T., (2020). Long-term consequences of water pumping on the ecosystem functioning of Lake Sekšu, Latvia. *Water*, *12*(5), p.1459. https://doi.org/10.3390/w12051459

water

MDPI

Article

Long-Term Consequences of Water Pumping on the Ecosystem Functioning of Lake Sekšu, Latvia

Izabela Zawiska [1,*], Inta Dimante-Deimantovica [2,3], Tomi P. Luoto [4], Monika Rzodkiewicz [5], Saija Saarni [6], Normunds Stivrins [7,8,9], Wojciech Tylmann [10], Anna Lanka [2,11], Martins Robeznieks [2,12] and Tom Jilbert [6]

[1] Institute of Geography and Spatial Organisation, Polish Academy of Sciences, Twarda 51/55, PL-00818 Warsaw, Poland
[2] Latvian Institute of Aquatic Ecology, Agency of Daugavpils University, Voleru 4, LV-1007 Riga, Latvia; inta.dimante-deimantovica@lhei.lv (I.D.-D.); anna.lanka0@gmail.com (A.L.); martinsrobez@gmail.com (M.R.)
[3] Norwegian Institute for Nature Research, Gaustadalléen 21, NO-0349 Oslo, Norway
[4] Faculty of Biological and Environmental Sciences, Ecosystems and Environment Research Programme, University of Helsinki, Niemenkatu 73, FI-15140 Lahti, Finland; tomi.luoto@helsinki.fi
[5] Institute of Geoecology and Geoinformation, Adam Mickiewicz University, Bogumiła Krygowskiego 10, PL-61680 Poznań, Poland; monika.rzodkiewicz@amu.edu.pl
[6] Faculty of Biological and Environmental Sciences, Aquatic Biogeochemistry Research Unit, Ecosystems and Environment Research Program, University of Helsinki, P.O. Box 65, FI-00014 Helsinki, Finland; saija.saarni@helsinki.fi (S.S.); tom.jilbert@helsinki.fi (T.J.)
[7] Department of Geography, University of Latvia, Jelgavas 1, LV-1004 Riga, Latvia; normunds.stivrins@lu.lv
[8] Department of Geology, Tallinn University of Technology, Ehitajate tee 5, EST-19086 Tallinn, Estonia
[9] Lake and Peatland Research Centre, LV-4063 Puikule, Aloja, Latvia
[10] Faculty of Oceanography and Geography, University of Gdańsk, Bażyńskiego 4, PL-80309 Gdańsk, Poland; wojciech.tylmann@ug.edu.pl
[11] Faculty of Biology, University of Latvia, Jelgavas 1, LV-1004 Riga, Latvia
[12] Department of Geology, University of Latvia, Jelgavas 1, LV-1004 Riga, Latvia
* Correspondence: izawiska@twarda.pan.pl

Received: 4 April 2020; Accepted: 16 May 2020; Published: 20 May 2020

Abstract: Cultural eutrophication, the process by which pollution due to human activity speeds up natural eutrophication, is a widespread and consequential issue. Here, we present the 85-year history of a small, initially *Lobelia–Isoëtes* dominated lake. The lake's ecological deterioration was intensified by water pumping station activities when it received replenishment water for more than 10 years from a eutrophic lake through a pipe. In this study, we performed a paleolimnological assessment to determine how the lake's ecosystem functioning changed over time. A multi-proxy (pollen, Cladocera, diatoms, and Chironomidae) approach was applied alongside a quantitative reconstruction of total phosphorus using diatom and hypolimnetic dissolved oxygen with chironomid-based transfer functions. The results of the biotic proxy were supplemented with a geochemical analysis. The results demonstrated significant changes in the lake community's structure, its sediment composition, and its redox conditions due to increased eutrophication, water level fluctuations, and erosion. The additional nutrient load, particularly phosphorus, increased the abundance of planktonic eutrophic–hypereutrophic diatoms, the lake water's transparency decreased, and hypolimnetic anoxia occurred. Cladocera, Chironomidae, and diatoms species indicated a community shift towards eutrophy, while the low trophy species were suppressed or disappeared.

Keywords: eutrophication; water level fluctuation; multi-proxy approach; Cladocera; Chironomidae; diatoms; Northern Europe

1. Introduction

Eutrophication strongly influences the functioning of freshwater ecosystems by changing their water qualities, such as oxygen availability, light conditions, and increasing the production of algae, which results in a reduction of the water's self-purification capacity. The process of nutrient enrichment of water bodies is a part of a lake's natural lifecycle. However, the introduction of sewage water, fertilizer, and detergent to lake systems greatly accelerates eutrophication and results in significantly increased biological productivity. Therefore, cultural eutrophication continues to be ranked as the most common water-quality problem in the world [1–5].

Not only intensified cultivation and clear-cut logging, but also activities such as artificial water replenishment into lakes, can strongly affect lake ecosystems. There are several reasons for taking such actions, such as increasing the flow of water into lakes for restoration (particularly relevant in arid regions due to intense evaporation), in connection to the hydropower industry [6,7], or increasing the groundwater level to secure the operations of water pumping stations. Such activities can cause significant environmental issues since the physical, chemical, and biological characteristics of the lake can be changed.

Water was artificially replenished to increase the water level in Lake Sekšu, located in the vicinity of Riga city (Latvia, Baltic Region, Northern Europe). This lake is a part of the drinking water supply system and enriches the groundwater horizons near the "Baltezers" drinking water pumping station. The pumping station "Baltezers" began to operate in 1904 as an extension to the pre-existing water supply system meant to solve the problem of water shortages in the Riga city. In addition to the existing drinking water source (the river Daugava), the new water pumping station was designed to use groundwater. However, alongside the construction of residential and public buildings, the area's population and industrial activity increased rapidly after World War I. The size of the water supply network developed proportional to urban growth, but during World War II, the water supply system was seriously damaged. However, by 1948, the pre-war level of industrial activity was again reached [8]. In the late 1950s, the suburbs of Riga were developed for housing purposes. Natural biotopes in the vicinity of the city were replaced by dense residential areas and small kitchen gardens [9]. The consumption of water continued to increase, and in 1953, an artificial groundwater recharge system went into operation. Between 1953 and 1965, the water supply from an adjacent eutrophic lake to Lake Sekšu was established through a pipe and ditch [10].

In this study, we hypothesized that even the relatively short-term pumping of water from the nearby eutrophic lake could have changed the trophic conditions in Lake Sekšu and could have led to persistent shifts in the lake's ecosystem functioning. We analyzed sediment core representing the time period ~1935–2018 to investigate how water replenishment affected the lake's ecosystem functioning and to determine if the lake system showed recovery after the water replenishment activities were terminated. We applied a multi-proxy approach and developed a quantitative reconstruction of the total amount of phosphorus using diatoms and hypolimnetic dissolved oxygen with chironomid-based transfer functions along with the indicative properties of Cladocera. The plant succession in the lake and catchment was reconstructed using pollen analysis. The results were supplemented with a geochemical analysis, which helped to detect changes in the relative supply of organic and inorganic sediment material, as well as variability in the organic matter sources. The geochemical analysis also provided further evidence of changes in the lake's trophic state.

2. Materials and Methods

2.1. Study Site

Lake Sekšu (57°03′ N, 24°35′ E, Figure 1) is a small (surface area 7.9 ha), shallow (the average and maximum depth is 2.5 m and 6 m, respectively) lake at an elevation of 2.5 m a.s.l., located in the vicinity of the capital city of Riga, central Latvia, Northern Europe [11,12]. The average annual air temperature (1981–2010) in areas close to the Baltic Sea coast is +6.8 to +7.4 °C. July is the warmest month of the year, with an average air temperature +17.4 °C (average maximum +22.3 °C). The coldest month of the year is February, with an average air temperature of −3.7 °C. The annual rainfall is 692 mm. According to the data on climate change, the air temperature and precipitation in the area are increasing [13].

The lake is mostly surrounded by inland dune forest and dominated by pine growing on sandy soil. The southern part of the lake is dominated by birches growing on organic soils [14]. The lake has no runoff apart from a small, shallow ditch that transports humic substances to the lake. In this area, there is also a peat soil-based, meliorated forest [9,13].

According to the EU Water Framework Directive criteria (total phosphorus, Secchi depth, and chlorophyll *a*), the lake's current ecological status is good. The latest macrozoobenthos studies confirmed the lake's high biodiversity. Following Carlson's trophic state index, in terms of water transparency (SD), Lake Sekšu is a mesotrophic lake, while its chlorophyll *a* concentration (CA) indicates a eutrophic lake status. The average value of the indices corresponds to a eutrophic lake. Nevertheless, the lake still features low eutrophication. The main problem for such lakes is a loss of transparency [15].

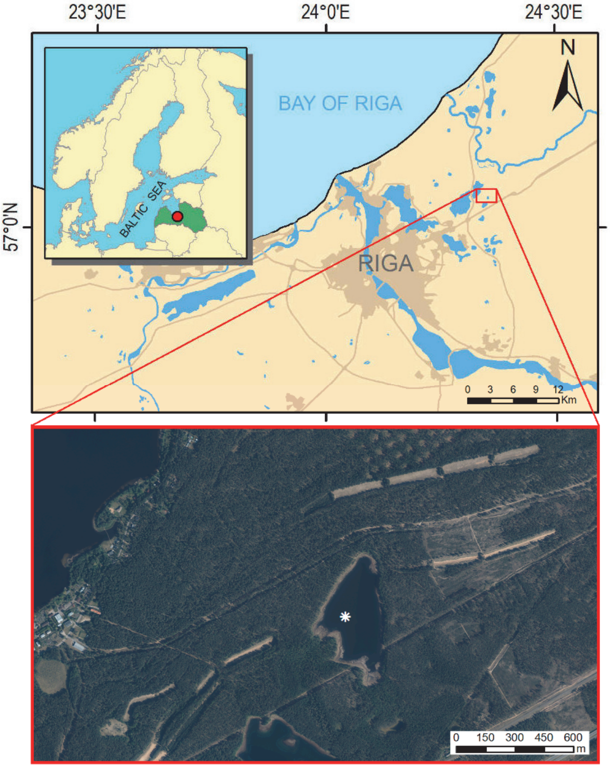


Figure 1. Lake Sekšu location on map. Asterisk indicates deepest part of the lake where sampling occurred.

2.2. Materials and Methods

2.2.1. Lake Sediment Coring

A 46 cm sediment core from the deepest part of Lake Sekšu was taken on 13th February 2019 using a Kayak/HTH gravity-type corer. The sediment core was divided in the field into 1 cm sections and stored in a cold room. In the laboratory, 1 cm^3 subsamples of fresh sediment from each section were taken for analysis of the biological (Cladocera, Chironomidae, diatoms, pollen) and spheroidal carbonaceous particles (SCPs). Dried material was used for ^{137}Cs/^{210}Pb dating, as well as chemical and physical analysis.

2.2.2. Core Chronology

A sediment core from Lake Sekšu was dated with ^{137}Cs and ^{210}Pb at the Geochronology Laboratory at the Gdańsk University according to the standard procedure [16]. The activity of ^{137}Cs and ^{226}Ra was determined directly by gamma-ray spectrometry. Gamma measurements were carried out using a HPGe well-type detector (GCW 2021, Canberra) coupled to a multi-channel analyzer and shielded by a 15 cm thick layer of lead. Counting efficiency was determined using reference materials (CBSS-2 for ^{137}Cs at 661.6 keV, and RGU-1 for ^{226}Ra via ^{214}Pb at 352 keV) with the same measurement geometry as the samples. The counting time for each sediment sample was 24 h.

The activity of total ^{210}Pb was determined indirectly by measuring ^{210}Po using alpha spectrometry. Dry and homogenized sediment samples of 0.2 g were transferred into Teflon containers, spiked with a ^{209}Po yield tracer, and digested with concentrated HNO_3, $HClO_4$, and HF at a temperature of 100 °C using a CEM Mars 6 microwave digestion system. After 24 h, the solution was transferred into a Teflon beaker, evaporated with 6 M HCl to dryness, and then dissolved in 0.5 M HCl. Polonium isotopes were spontaneously deposited within 4 h on silver discs. After deposition, the discs were analyzed for ^{210}Po and ^{209}Po using a 7200-04 APEX Alpha Analyst integrated alpha-spectroscopy system (Canberra) equipped with PIPS A450-18AM detectors. The samples were counted for 24 h. A certified mixed alpha source (^{234}U, ^{238}U, ^{239}Pu, and ^{241}Am; SRS 73833-121, Analytics, Atlanta, Georgia, USA) was used to check the detector counting efficiencies, which varied from 30.9% to 33.9% for the applied geometry.

In addition, an abundance of spheroidal carbonaceous particles (SCPs) was estimated throughout the sediment sequence following the methodology of Rose [17] and Alliksaar [18]. The analysis was performed in the Department of Geography, University of Latvia. According to the black carbon combustion continuum model of Hedges et al. [19] and Masiello [20], SCPs only form during industrial fuel combustion at high temperatures (greater than 1000 °C). Therefore, the peak followed the fuel combustion pattern: 1950—the rise of SCPs, 1982—the peak of SCPs, and 1991—the decrease of SCPs. The peak SCP emissions were previously established for Latvia at 1982 ± 10 years [21].

In the final step, we combined the results from the radionuclides and the SCP analyses to build an age-depth model using the Clam 2.2 deposition model [22] with a 95.4% confidence level in the R environment [23].

2.2.3. Physical and Chemical Sediment Analyses

Sediment geochemical characteristics were determined using loss on ignition (LOI) combustion analysis and inductively coupled plasma-optical emission spectrometry (ICP-OES). Altogether, 45 subsamples at 1 cm intervals were analyzed, but only the topmost two sediment samples were merged into one sample representing depths from 0 to 2 cm. The sediment organic matter and carbonate content were investigated using the LOI method [24]. A measure of 0.1–0.2 g of fresh sub-sample sediment was weighed in a crucible and dried at 105 °C for 12 h; then, it was combusted at 550 °C for 4 h and, finally, at 950 °C for 2 h. Between each step, the samples were cooled with an exicator and weighed. The organic matter (OM) content was measured as the LOI from the combusted samples at 550 °C, and the carbonate matter (CM) was calculated as the difference between the LOI at 950 °C and the LOI at 550 °C multiplied by 1.36 [24]. Non-carbonate siliciclastic matter, here referred to as minerogenic matter (MM) content, was obtained by subtracting OM and CM from the total sample weight after final combustion. MM also includes biogenic silica (opal). However, siliciclastic matter here mainly represents terrigenous clastic matter.

A set of homogenized sub-samples was freeze dried and powdered using an agate mortar. The total carbon (TC) and total nitrogen (TN) contents were analyzed using thermal combustion elemental analyses (Element Analyzer Vario EL III) with an uncertainty of ±5%. Approximately 7–8 mg of prepared material was weighed into tin cups for analyses that were performed at an accredited laboratory (ISO/IEC/17025).

For the ICP-OES analyses, 0.1–0.2 g of dry sediment powder was weighed in Teflon vials, and 5 mL of 65% HNO_3 was added. The vials were closed loosely, and digestion was carried out at 160 °C for 30 min. Gases and volatiles from the digestion were allowed to escape through the cap. Following digestion, 10 mL H_2O was added to dilute the remaining acid, and the vials were weighed to determine the dilution factor. A measure of 1 mL of the resulting solution was then pipetted into 15 mL centrifuge tubes, and 9 mL 0.5 mol/l HNO_3 was added. These steps were performed to give the samples a final acid concentration of approximately 1 mol/l HNO_3 and to have the element concentrations in a suitable range for the ICP-OES analysis. The sulfur (S) concentration was determined by ICP-OES (Thermo Scientific iCAP 6000) using a concentric nebulizer. Certified control samples and blank samples were used to ensure the quality of the analytical process.

2.2.4. Pollen and Non-Pollen Palynomorphs

Samples of known volume for the pollen analysis were processed using standard procedures [25]. Known quantities of *Lycopodium* spores were added to each sample to allow the calculation of pollen concentrations [26]. At least 500 terrestrial pollen grains per sample were counted under a light microscope (400× magnification). Taxa were identified to the lowest possible taxonomic level using the reference collection at the Department of Geography at the University of Latvia along with published pollen keys [27]. The percentage of dry-land taxa was estimated using arboreal and non-arboreal pollen sums (excluding the sporomorphs of aquatic and wetland plants). Counts of spores were calculated as the percentages of the total sum of terrestrial pollen. Non-pollen palynomorphs were recorded throughout the pollen analysis and identified using the published literature listed in Miola [28], as well as from the descriptions of Sweeney [29] and Finsinger and Tinner [30]. Non-pollen palynomorphs were expressed as presence or concentrations. The pollen diagram was compiled using TILIA software [31].

2.2.5. Diatom Analysis

Samples were prepared according to the standard methods [32]. The material was treated with 10% HCl to remove calcareous matter, washed with distilled water, and then treated with 30% H_2O_2 in a water bath to remove organic matter. The material was repeatedly washed with distilled water, and a known number of microspheres in a solution (concentration 8.02×10^6 microspheres/cm^3) was added to the diatom suspensions to estimate the diatom concentrations [33]. A few drops of diatom suspension were dried on a cover glass. At least 300 diatom valves per sample were analyzed using oil immersion at 1000× magnification under a light microscope. For identification, a selection of published keys was used [34–41].

The diatom ecological groups were determined using the OMNIDIA software (Version 4.2) [42]. Next, the resulting groups were distinguished according to Denys [43] and van Dam [44]. We considered the following indicator parameters: habitat category [43], dominant taxa (abundance over 2%) and preference for pH, saprobic level (OM contamination), and trophy [44]. The percentage diatom diagram was prepared with the Tilia software [31].

The total phosphorus (TP) concentration was reconstructed based on changes in the diatom species composition (DI-TP). The reconstruction was performed using the European Diatom Database (EDDI) in the ERNIE software [45]. A model based on inverse regression had a root mean square error of prediction (RMSEP) of 0.33 $\mu g\ L^{-1}$ and a coefficient of determination (r^2) of 0.64. The reconstruction of the TP was based on the diatom taxa present at more than 2% abundance. The DI-TP was calculated using the combined TP dataset (derived from nine datasets with 347 samples in total), covering a TP range of 2–1189 $\mu g\ L^{-1}$, with a mean of 98.6 $\mu g\ L^{-1}$. The weighted averaging (WA) method with good empirical predictive ability was used [45].

2.2.6. Cladocera Analysis

The 46 fresh sediment samples were prepared in a laboratory according to the standard procedures [46], heated in 10% KOH, and sieved using a 38 µm mesh size. Microscope slides were prepared from 0.1 mL of each sample and examined with a light microscope under magnifications of ×100, ×200, and ×400. For each sample, 1–3 slides were scanned, and all skeletal elements (head shields, shells, and postabdomens) were counted until 70–100 individuals were found, which is regarded as an adequate number to characterize the assemblages [47]. Identification of the cladoceran remains was based on the key by Szeroczyńska and Sarmaja-Korjonen [46]. The stratigraphic diagrams presenting the results were prepared using C2 freeware [48].

The Cladocera composition is presented in the stratigraphic diagrams with percentage values. For trophic state reconstruction, we used changes in the percentage of species regarded as indicators for the eutrophic state, which, according to Flössner [49], are *Alona rectangula* and *Chydorus* cf. *sphaericus*. Lake water level changes were reconstructed by using the added percentage values of planktonic and littoral cladocerans.

2.2.7. Chironomidae Analysis

Standard methods were applied in the fossil Chironomidae analysis [50]. The wet sediment was sieved through mesh (100 µm), and the residue was examined under a stereomicroscope for larval head capsule extraction using a target counting sum of 50 per sample. The head capsules were mounted with Euparal on microscope slides for taxonomic identification following Brooks et al. [50] under a light microscope (400× magnification).

Hypolimnetic dissolved oxygen (DO) was reconstructed using a Finnish 30-lake chironomid-based calibration model [51,52]. The calibration sites range from anoxic ($O_2 = 0.5$ mg L^{-1}) to hypersaturated sites ($O_2 = 18.1$ mg L^{-1}). The weighted averaging partial least squares (WA-PLS) model had an r^2 (leave-one-out cross-validation) of 0.74 and an RMSE P of 2.3 mg L^{-1}.

3. Results

3.1. Core Chronology

The depth profile of ^{137}Cs activity is long and smooth, with only one wide maximum between a 28 and 38 cm sediment depth (Figure 2). The sharp decrease below 41 cm indicates the presence of sediments older than 1950 below this depth. The lack of two independent peaks indicating global fallout during 1961–1965 and the Chernobyl peak in 1986 might suggest the deep mixing of surface sediments.

However, the excess ^{210}Pb activities decrease regularly with mass depth, which demonstrates no significant disturbance of the sediment column and relatively stable mass accumulation rates. Thus, we used the CFCS (Constant Flux Constant Sedimentation) model to calculate the mean value of the mass accumulation rate (MAR) for the entire core. The mean MAR value is 34.5 ± 2.2 mg/cm^2/yr and allows us to estimate a maximum age of 84 ± 5 yrs (1935 ± 5) at a 45.5 cm sediment depth. The age of the depth interval with the greatest ^{137}Cs activities (37–32 cm) is 1956–1965 according to the CFCS model, which is consistent with global fallout history. This comparison suggests that the lack of a Chernobyl peak is related to ^{137}Cs migration within the sediment column rather than physical sediment mixing.

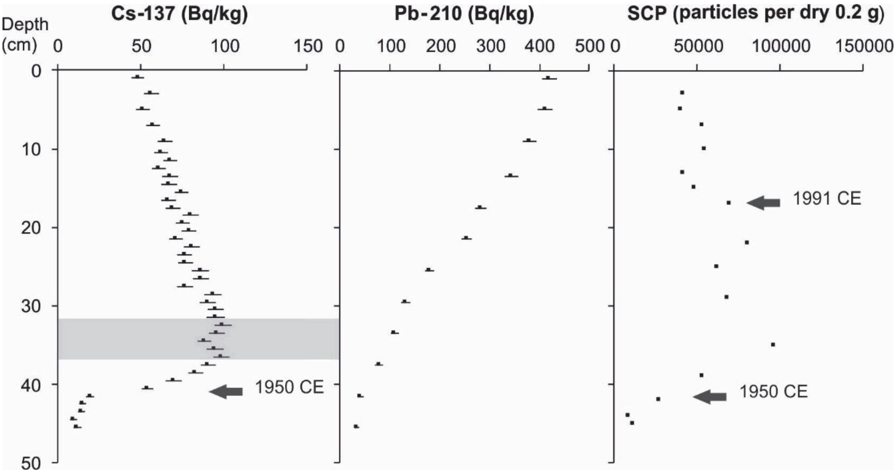


Figure 2. Downcore distribution of ^{137}Cs and ^{210}Pb activities as well as spheroidal carbonaceous particles (SCP) concentrations in the Lake Sekšu topmost sediments. The grey shaded area on the caesium diagram indicates time period 1956–1965 CE.

Based on the SCP results, it was possible to define the years 1950 and 1991 with an error of +/− 10 years at depths 42 and 17 cm, respectively. The locations of these peaks are, with relative certainty, consistent with the ^{137}Cs and ^{210}Pb data.

The final age-depth model, including the radionuclide and SCP data, shows relatively stable sedimentation rates with only a moderate increase in the topmost part of the profile (Figure 3). The maximum age of sediment at a depth of 46 cm is 84 ± 9 yrs (95%). The mean sedimentation rate is 0.6 cm per year.

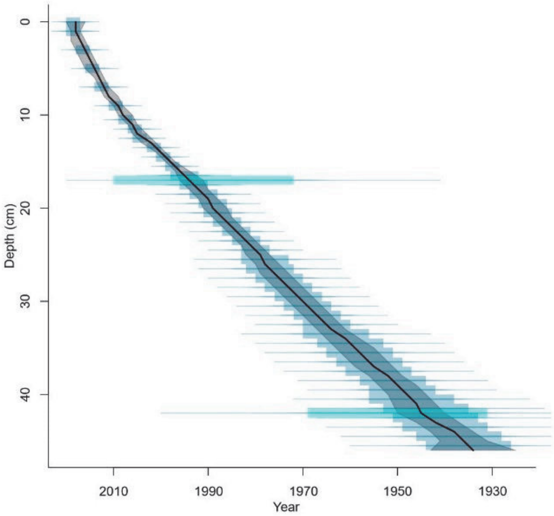


Figure 3. Lake Sekšu age depth model. The black solid line shows the weighted mean ages of all depths, whereas the grey area indicates a reconstructed 95% chronological uncertainty band. Dates of ^{210}Pb (pale blue boxes) and spheroidal carbonaceous particles (electric blue boxes) with their error margin and associated age-depth model uncertainties are displayed.

3.2. Sediment Composition

The Lake Sekšu sediment composition is dominated by organic matter (50%–61%) with a significant component of minerogenic matter (35%–46%, Figure 4). The sediments contain 2%–5% carbonate matter. Based on sediment composition and the variation in element concentrations, the sedimentary data are divided into two zones, Zones I and II, which correspond to the approximate time period before 1950 and between 1950 and 2018. Within Zone II, short-lived events can be distinguished.

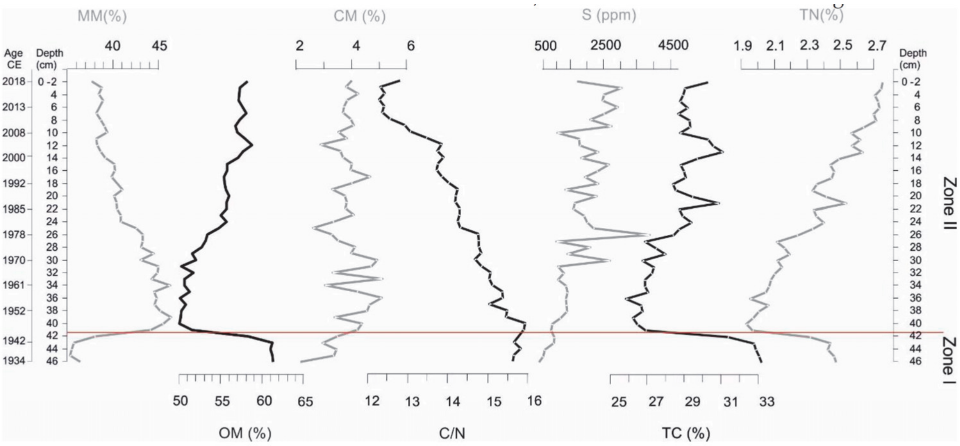


Figure 4. Lake Sekšu Sediment composition: minerogenic matter (MM), organic matter (OM), carbonate matter (CM), C/N expressed as atomic ratio, sulfur (S), carbon (TC), nitrogen (TN), and the division in two zones based on major changes in sedimentary composition.

Zone I

The relative organic matter (OM), total carbon (TC), and total nitrogen (TN) content show high values in this time period (Figure 4). The OM is around 61%, while TC is around 32%, and TN is around 2.5%. The C/N value, expressed as the atomic ratio, is around 15.7. The sulfur (S) content is approximately 500 ppm. The relative minerogenic matter (MM) (36%) displays the lowest values, while approximately 3.5% is carbonate matter (CM).

Zone II

At the boundaries of Zone I and Zone II, a large change occurs. The OM content shows a sudden drop from 61% to 51% accompanied by a fall in TC and TN content from 33% to 27% and from 2.45% to 1.95%, respectively. Simultaneously, the MM content increases from 36% to 45%. After this rapid change, a steady gradient emerges from 41 cm to the sediment surface, during which MM, OM, and TC gradually reset towards their Zone I value. However, TN increases over the same period to values far exceeding those of Zone I (approximately 2.8% at the sediment surface, Figure 4). Consequently, C/N displays a continuous gradient towards lower values throughout the entire core. Similarly, S content increases gradually throughout the entire core, with some pronounced variability within Zone II.

3.3. Pollen and Non-Pollen Palynomorphs

There is no significant change in surrounding vegetation before or after the pipe installation. The vegetation includes the stable dominance of pine (*Pinus*), birch (*Betula*), spruce (*Picea*), and alder (*Alnus*) over the studied period (Figure 5). The presence of conifer stomata in the lake sediment supports local abundance of spruce and pine. Although, the surrounding landscape is forested, there is continuous evidence of human-activities in the vicinity. For instance, the presence of pollen of flax (*Linum*), rye (*Secale cereale*), barley (*Hordeum*), and wheat/oat (*Triticum*/*Avena*) is a direct indication of agricultural practices. Our results also underline that there have not been agricultural fields directly at the Sekšu lake shores, but only further away, as evidenced by the high (nearly 85–90%) forest pollen component in the landscape. It is interesting that the rye pollen accumulation rates above 1000 cm^{-2} year^{-1} (Figure 6) point to cereal fields within a 2 km radius of Lake Sekšu [53,54]. Based on USSR topographic maps from the time period of 1941–1991, the cereal fields could be present in the northwest and east of the Sekšu Lake where pastoral activities have also been evident. It is, however, possible that the high concentration of rye pollen can be partially a result of soil erosion and water pumping (enlarging the pollen source area outside the watershed) into the Lake Sekšu. This assumption is further supported by a strong increase of fungi hyphae and corroded pollen grains.

Regarding in-lake vegetation, lake quillwort/Merlin's grass (*Isoëtes lacustris*) was recorded throughout the sediment sequence. The highest relative abundance of *I. lacustris* was recorded prior the pipe installation, after which values continuously declined and did not reach previous values. Sporadically, the pollen of water lilies (*Nymphaeaceae*), bulrush (*Typha*), spiked water-milfoil (*Myriophyllum spicatum*), pondweed (*Potamogeton*), and bur-reed (*Sparganium*) were found.

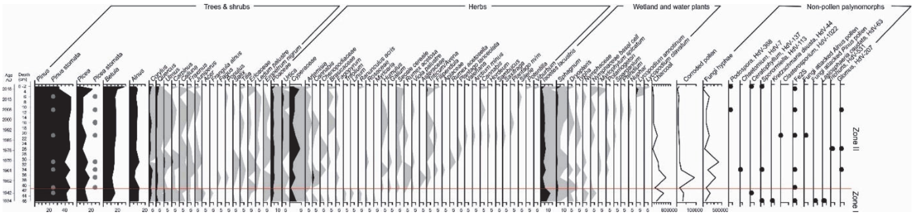


Figure 5. Pollen and non-pollen palynomorphs of Lake Sekšu. Trees, shrubs, herbs, crops, ruderal plants, bryophytes, and water plants expressed in percentages. Non-pollen palynomorphs and charcoal expressed as microscopic object accumulation rate cm^{-2} year^{-1}. Grey shaded areas indicate ×10 time exaggeration to underline the presence of microscopic remains.

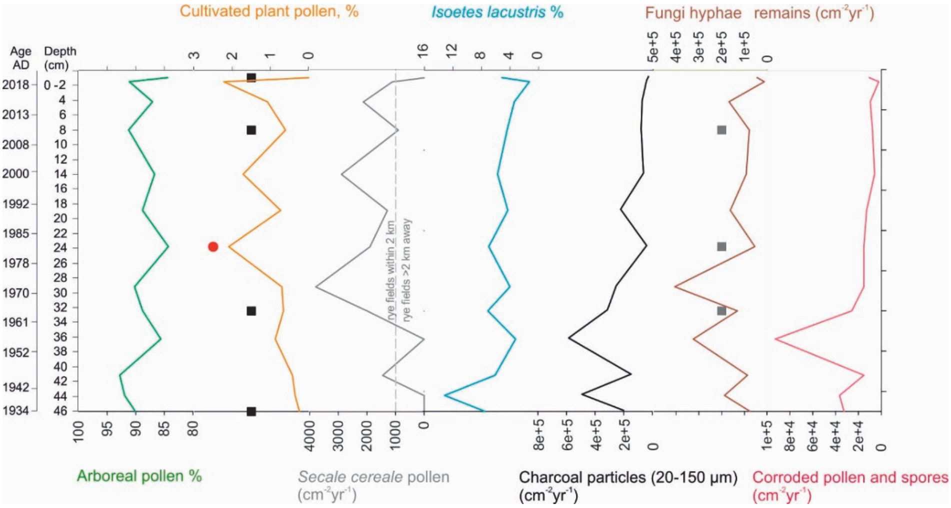


Figure 6. Selection of pollen and non-pollen palynomorphs, from the left: arboreal pollen (%), cultivated plant pollen (%), secale-cereale pollen (cm^{-2} yr^{-1}), *Isoëtes lacustris* (%), charcoal particles (cm^{-2}yr^{-1}), fungi hyphae remains (cm^{-2}yr^{-1}), and corroded pollen grains and spores (cm^{-2} yr^{-1}). The presence of whipworm in the sample is marked with a red circle, the presence of herbivores with black squares and the presence of *Glomus* spores indicating erosion with grey squares.

3.4. Diatom Analysis

The results show a medium to deplorable state for the diatom frustules, with numerous traces of destruction and dissolution. In total, 178 species of diatoms were identified. There were 47 dominant taxa, whose share was more than 2% of the relative abundance. Based on the changes in species composition and the proportions between the ecological diatom groups, the data are divided into two zones, Zones I and II, which closely correspond to the geochemical zones (Figures 7 and 8). Species were classified according to their habitat category, preference for pH, saprobic state, and trophic state (Figure 7). The total phosphorous (TP) reconstruction presented values between 21.43 and 102.14 μg L^{-1} (Figure 11).

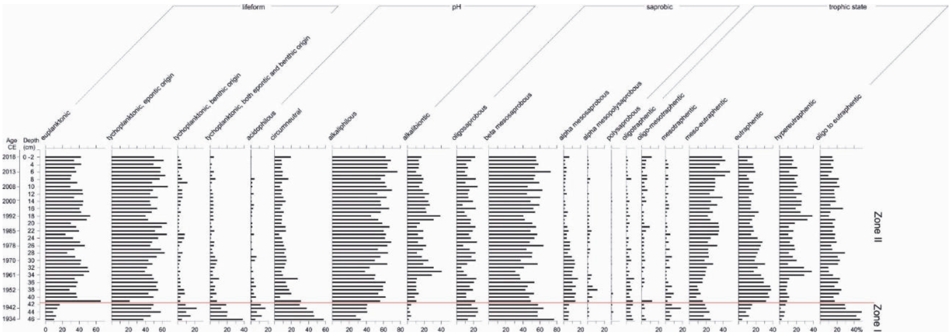


Figure 7. Relative abundance of the diatom group in Lake Sekšu according to habitat category (lifeform), pH, OM contamination (saprobic), and trophy preference.

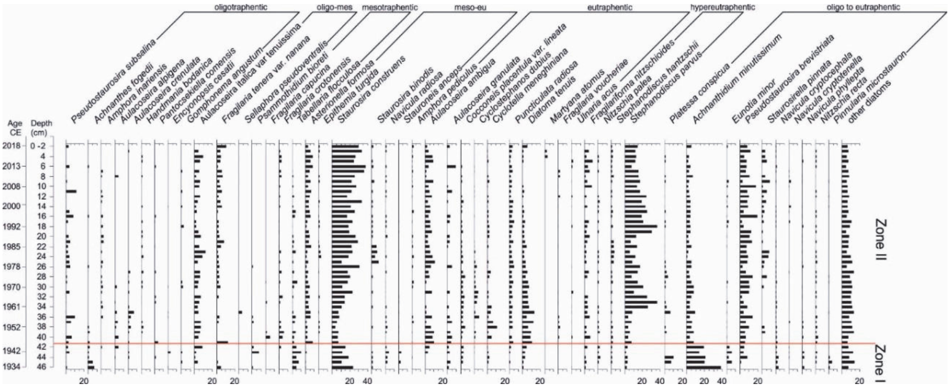


Figure 8. Relative abundance of dominant diatom species in Lake Sekšu (species with values >2%).

Zone I

This zone was characterized by the dominance of tychoplanktonic taxa, especially *Staurosira construens* and *Achnanthidium minutissimum* (Figure 8). In terms of pH, circumneutral taxa dominated. At the beginning of the phase, we observed an increase in alkaliphilous diatoms. The analysis of saprobic preferences revealed the domination of β-mesosaprobous diatoms. In terms of its trophic state, a high proportion of oligo to eutraphentic taxa was observed. The TP reconstruction remained low, between 21.43–57.66 μg L^{-1} (Figure 11).

Zone II

Several short-term fluctuations in species composition were observed. Around 1950, the planktonic taxa (euplanktonic) increased by up to 65%, represented by *Asterionella formosa, Aulacoseira ambigua, A. granulata, Diatoma tenuis, Fragilaria nanana*, *Cyclotella planktonica*, *Handmania bodanica,* and *Pantocsekiella comensis* (Figure 8). The alkaliphilous species dominated the pH group, with an abundance between 38.7 and 76.5 R. Around 1950, the α-mesosaprobous species increased by 0.3%–17.0%. An increase in eutrophic and hypereutrophic taxa was also observed (Figure 7). The TP reconstruction values increased up to 102.14 μg L^{-1} (Figure 11).

3.5. Cladocera Analysis

The remains of 44 cladoceran species were found (Figure 9). Throughout the core, the dominant planktonic species were *Bosmina (Eubosmina)* spp. and *Bosmina (Bosmina) longirostris*, while among the littoral species, *Chydorus* cf. *sphaericus*, *Alona quadrangularis* and *Alonella nana* dominated. The overall species composition changes, as well as the indicator species appearance and continuation, allowed us to distinguish between Zones I and II, which correspond to the time before and after the pipe started to operate (Figure 9).

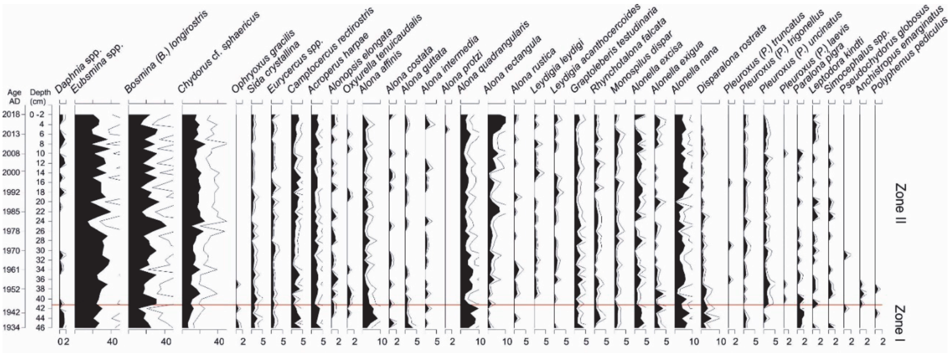


Figure 9. Relative abundance of the Cladocera species in Lake Sekšu.

Zone I

The littoral cladocerans comprised more than 50% of all species, among which *Alona affinis*, *A. quadrangularis,* and *Alonella nana* dominated. The Cladocera eutrophic indicator, which is based on the littoral species, showed the lowest values in the sequence. The rare species *Ophryoxus gracilis* was present almost continuously. Among the pelagic species, *Bosmina (E.)* spp. dominated, and *Daphnia* spp. remains were constantly present.

Zone II

During this time, several fluctuations in the species share and Cladocera indicator are observable. The pelagic species constitute more that 50% of all species until 2014 CE. However, an increase in the littoral taxa share was noted at the beginning of 1950, 1960, 1980, and ~1995. Next, *Chydorus* cf. *sphaericus* becomes the dominant littoral species. After 2014 CE, a clear decrease of pelagic species and an increase of littoral species occurred, and littoral *A. rectangula* started to dominate. The trophic indicator increased from around 1950 CE, but even more visibly from the ~1978 (Figure 9). The highest values of the indicator species were observed almost continuously from ~2010 until present.

3.6. Chironomidae Analysis

In the 45 sediment samples, 52 different chironomid taxa were observed. None of the taxa occurred in all the samples. The *Polypedilum nubeculosum*-type was the most frequent, as it was observed in 40 samples. The highest maximum abundance values belonged to *Procladius* (35.3%), *P. nubeculosum*-type (31.4%), and *Heterotanytarsus apicalis* (30.0%). The *P. nubeculosum*-type also had the highest mean abundance (9.3%), followed by the *Psectrocladius sordidellus*-type (7.9%) and the *Tanytarsus pallidicornis*-type (6.6%) (Figure 10). The hypolimnetic oxygen reconstruction showed values between 0.2 and 15.7 mg L^{-1} (Figure 11).

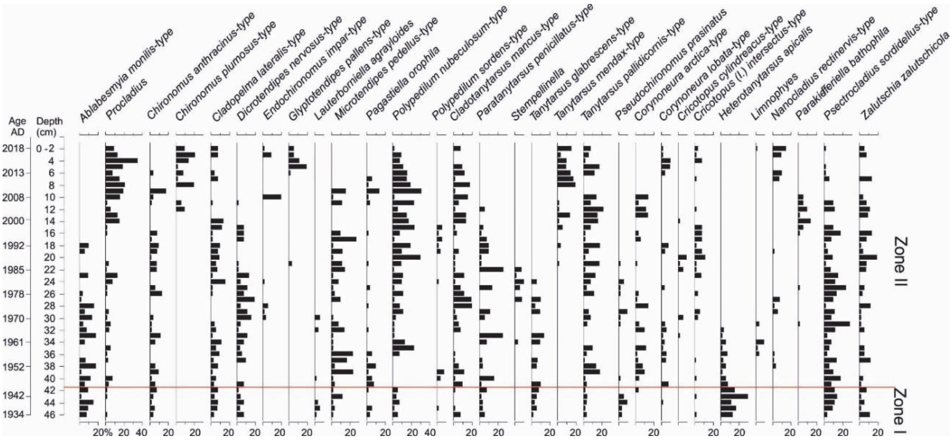


Figure 10. Relative abundance of Chironomidae in Lake Sekšu sediment.

Zone I

The initial part of the sediment profile (before ~1950 CE) was dominated by oligotrophic taxa, such as *H. apicalis* and the *Ablabesmyia monilis*-type. The hypolimnetic oxygen reconstructed values remained high at ~10 mg L^{-1}.

Zone II

In the middle portion of the sediment profile (1950–1990 CE), the *P. sordidellus*-type, which is a common species, was the most abundant. From 2000 CE onwards, *Procladius*, which prefers nutrient enriched waters, began to dominate. During the most recent years, the eutrophy indicating the *Chironomus plumosus*-type and *Glyptotendipes pallens*-type also significantly increased. From the 1950s until the 1980s, the oxygen values decreased to a level of ~4–8 mg L^{-1}. The hypolimnetic oxygen reconstructed values remained at ~4 mg L^{-1} from the late 1980s until 2010, after which the values further decreased to anoxic levels in recent years.

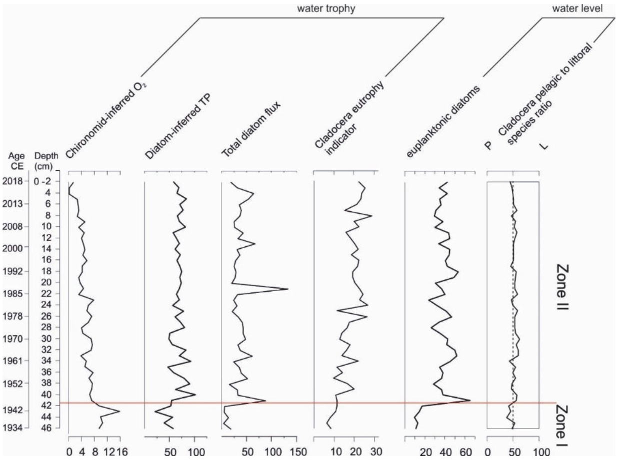


Figure 11. Comparison of indicators used to reconstruct trophic state changes: chironomid-inferred hypolimnetic oxygen reconstruction (O_2) mg L^{-1}, diatom-inferred total phosphorus reconstruction (TP) µg L^{-1}, total diatom flux (frustules × 10^6 /cm^2/yr^{-1}), Cladocera based eutrophy indicators, and water-level changes indicators, such as the euplanktonic diatoms (%) and pelagic (P) to littoral (L) Cladocera species ratio (%).

4. Discussion

Lake Sekšu exemplifies how environmental changes have occurred, in this case, as a result of artificial water pumping station activities, and also shows how such changes at the trophic level can have a lasting influence on lake functioning. In 1953 CE, the pipe was built and for 12 years (1953–1965) pumped water to Lake Sekšu from the large eutrophic lake, Mazais Baltezers. Our results clearly show that this action persistently changed the lake's ecosystem by causing increased eutrophication.

A major cause of eutrophication is an increase in the nutrient supply, particularly phosphorus [55]. Besides excessive plant production, algal blooms, and anoxia, the lake community structure changes through cascading trophic effects and benthic-pelagic coupling [56,57]. Another stressor controlling ecosystem functioning is water level fluctuations, which are essential for aquatic–terrestrial shared boundary processes. The physical and biological effects are especially pronounced in the littoral zone and in shallow water ecosystems in general (e.g., erosion, sedimentation, habitat alterations, and biota changes) [58]. Furthermore, erosion is a source of enhanced nutrient supply, and a greater sediment load decreases water quality. An increase of suspended solids reduces water transparency and increases turbidity, which negatively affects the photosynthesis processes but may also reduce the density of fish and invertebrates [56,59].

The Time Before ~1950

Before the pipe started to operate in 1953 CE, Lake Sekšu was a low productivity lake. However, the Cladocera community composition found in our research and in a study by Kuptsch [60] shows that already at the beginning of our core (~1935), the lake trophy had increased compared to 1924. This increase is indicated by a disappearance of the oligotrophy indicating *Holopedium gibberum* and the appearance of the increasing trophy indicator, *Bosmina (Bosmina) longirostris* [61–65].

The oldest available investigations from 1924 report a transparency of 5.8 m in the middle of June [60], i.e., almost throughout the lake. It was also reported that Lake Sekšu is one of the 14 lakes located in the vicinity of Latvia's capital city, Riga, that are *Lobelia–Isoëtes* population dominated lakes [66]. At the beginning of 20 century, there were at least three species typical for *Lobelia–Isoëtes* lakes found in Lake Sekšu—*L. dortmanna*, *Isoëtes lacustris,* and *Juncus bulbosus* [67]. Our research revealed the presence and high share of lake quillwort pollen *Isoëtes lacustris*, as well as Cladocera species *Ophryoxus gracilis*, around 1935 (Figure 9). *Ophyroxus gracilis* is a species characteristic of deep, transparent lakes, indicating low/moderate trophy [64,68]. Flössner [49] considers *O. gracilis* a species typical for *Lobelia–Isoëtes* lakes.

The diatom-based total phosphorus (TP) reconstruction for Lake Sekšu indicates values between 25–50 μg L^{-1} before the pipe started to operate (Figure 11), which, according to the OECD (Organisation for Economic Cooperation and Development) classification, indicates a meso- to eutrophic type lake [69]. However, this reconstruction seems to overestimate the TP values when considering the other paleoindicators. This might be due to weak diatom assemblage analogues [70–73]. Nevertheless, the diatom-inference model closely reflected a significant trend in the measured TP, namely, declining TP values before pipe installation and increasing TP values after pipe installation.

The low trophy status is confirmed by the high share of oligotraphentic diatoms and dominance of Chironomidae oligotrophic taxa [74,75]. The well oxygenated hypolimnetic water (values 9–16 mg L^{-1}, Figure 11) was inferred by chironomid-based reconstruction and supports a low trophic status. The chironomid-inferred oxygen values remained at a high level (>8 mg L^{-1}) from the beginning of the record until the mid-1940s, when a step change to a lower level (4–8 mg L^{-1} between the 1950s and early 1980s) occurred. The relative oxygen saturation exceeded 50% [56]. Lake Sekšu was slightly acidic to neutral at that time, indicated by the dominance of acidophilous and circumneutral diatoms [76–79].

The geochemical results support the conclusion of low trophy before the construction of the pipe. However, at that time, the sediment was dominated by organic matter (OM) (Figure 4) with a very high concentration of carbon compared to other lakes in the region [80–83]. The high carbon/nitrogen (C/N) values suggest a significant contribution of terrigenous OM. Atomic C/N values of phytoplankton vary between 4 and 10, while cellulose-rich vascular plants have C/N ratios of more than 20 [84,85].

Therefore, high C/N rates are expected for oligotrophic lakes with low autochthonous production, and the values observed here are consistent with those of the densely forested catchment of Lake Sekšu. The low water levels of this period due to water pumping, and the subsequent water level decreases as early as 1930, may also have led to the concentration of OM in the coring location due to erosion from exposed organic rich littoral sediments from the lake. The water level in 1930 was reported to be very shallow at 1 m a.s.l [86]. The dominance of littoral over planktonic Cladocera confirms this information [87]. In addition, we reconstructed the high hypolimnetic water's oxygen values (Figure 11), which suggest that the sediment was exposed for efficient bioturbation. Water mixing is also confirmed by the dominance of tychoplanktonic diatoms, i.e., random planktonic diatoms, which require turbulent waters to remain suspended within the photic zone [77,88,89].

The Time Between ~1950–2018

The Lake Sekšu water level was artificially increased by pumping water from Lake Mazais Baltezers starting in 1953 CE in order to elevate the ground water level. Apart from the physical changes caused by an increased water level, this action also caused significant changes to the lake's ecology and functioning. The lake became eutrophic according to the diatom-inferred TP values around 100 μg L^{-1} [69]. During the period of artificial water pumping, until 1965, a high P concentration existed at the water column. After the pipe operation was terminated, the TP decreased to about 70 μg L^{-1} until the present, indicating that elevated trophy continued. According to our results, the additional nutrient load increased the presence of planktonic eutrophic–hypereutrophic diatoms (Figure 7), which, in turn, decreased water transparency. For instance, in August 2013, the Secchi depth was 2.1 m [15], while in 2019, in April, June, and October, it was 1.6 m, 1.6 m, and 1 m, respectively [90].

The total diatom flux (Figure 11) shows an increase, suggesting higher primary production [91–93]. As a result, the *I. lacustris* population greatly decreased. In turn, eutrophic-indicating macrophyte species, such as pondweed (*Potamogeton*), reed (*Typha*), and water lily (*Nuphar)*, started to flourish in the lake (Figure 6). *Lobelia–Isoëtes* lakes indicating species have disappeared from Lake Sekšu according to botanical observations [67].

Further evidence of the rapid shift towards higher trophy during artificial water pumping is provided by the other biological and geochemical results. The Cladocera eutrophic indicator, based on the species living in the littoral zone (*Alona rectangula* and *Chydorus* cf. *sphaericus*), increased, thereby indicating eutrophic conditions until the most recent sample (Figure 11). Simultaneously, the higher trophy in the pelagic zone is indicated by the increase of the *Bosmina (B.) longirostris* share. This species is associated with higher concentrations of TP [65,94].

The sudden change in the relative minerogenic matter and OM input coincides with the implementation of the pipeline and water pumping from Lake Mazais Baltezers to Lake Sekšu. The increased MM content of around 10% indicates substantial changes in the sediment sources. The pipe was installed tens of meters from today's lake shore, and flowing waters likely eroded the substrate—sandy soil that is prone to erosion. A comparable increase occurred in carbonate content, which also suggests intensified catchment erosion. The coeval decrease in OM accumulation, as well as carbon and nitrogen content, is likely a result of dilution by an excess MM supply (Figure 4). Despite the prominent relative changes in sediment composition, no evidence of significant increases in the total sedimentation rate are observable. This could be explained by a sudden change from the erosion of previous littoral sediments at a low-water level stage to channel erosion of the ditch, as well as erosion higher on the shore where no former lake sediments exist. Another indicator of the highly dynamic environment after the pipe started to operate is the increased share of corroded pollen grains [95]. The erosion of the shores is also indicated by the presence of herbivores (via coprophilous fungal spores), Fungi hyphae remains, and *Glomus* spores [54,96].

Pumping caused a significant elevation of the water level from 1 m a.s.l up to 4.5 m a.s.l [86], which is also reflected in the paleolimnological results. The higher water stand is expressed by the larger share of euplanktonic diatoms [97,98] and the dominance of pelagic over littoral Cladocera species [87] (Figures 9 and 11). However, the fluctuation of water level during the whole 12-year period can be deduced from the different share of the Cladocera pelagic/littoral taxa [87]. Both the increasing and decreasing water levels are related to increased catchment erosion [99–101]. The variable MM and carbonate matter (CM) content during the period of external water pumping indicate that fluctuating water levels enhanced catchment erosion in addition to channel erosion of the ditch from the pipe-end to the lake.

The C/N ratio (Figure 4) began to decrease soon after the major sedimentary change occurred, which suggests a steadily increasing proportion of phytoplankton in the total organic matter up to the present day. This is consistent with the gradual eutrophication of the lake, as indicated by the microfossil data. The sediment sulfur (S) profile also provides indirect evidence of eutrophication. Sulfur in lake sediments may be derived from natural processes, such as the weathering of sulfur-bearing rocks and the oxidation of organic sulfur in the catchment [102]. However, changes in S contents in recently deposited lake sediments generally indicate the balance between anthropogenic inputs and the rate of sulfate reduction leading to iron sulfide precipitation in sediments [103]. The steady increase in sedimentary S towards the present day suggests an additional input of sulfate from Lake Mazais Baltezers during the period of pumping, followed by enhanced iron sulfide precipitation in anoxic, OM-rich sediments during subsequent eutrophication. Eutrophication due to sewage water input from Lake Mazais Baltezers was suggested by Leinerte [10] (p.2) and is further supported by the high abundance of α-mesosaprobous diatoms [104,105]. This diatom group flourishes under the lower oxygen saturation in the water column [44].

In the middle part of the sediment record, representing the early 1980s, a threshold change can be observed in the chironomid-inferred hypolimnetic oxygen values (Figure 11). At this point, the values decreased from the previous level of 4–8 mg L^{-1} (between ~1945 and 1980) to a constant level of 4 mg L^{-1}, which prevailed until the 2010s. This is supported by the rapid decrease in hypolimnetic oxygen levels reconstructed from the chironomid data and recent measurements in April and June 2019, when the hypolimnetic oxygen concentration was 4.0 mg L^{-1} and 0.1 mg L^{-1}, respectively [90]. Jansons [9] (p. 27) and Zarina [15] (p.41) reported an amount of oxygen close to zero or zero in the hypolimnion of the deepest part of the basin, which agrees well with our reconstruction. Oxygen depletion was likely also favored by the water depth increase from <3 meters to 8 meters. Deeper waters reduced wind-driven mixing and enabled efficient thermal stratification.

From around 2000 CE, the water level lowered, reaching 2.5 m a.s.l. at present. This might have increased sedimentary nutrient release, further favoring eutrophication [58]. This higher productivity is indicated by the increase of the Chironomidae species *Procladius*, which prefers nutrient-rich waters [106] (Figure 10), but is also evidenced by the higher values of diatom-inferred TP (Figure 11). The lowering of the water level inferred from the Cladocera pelagic/littoral species ratio was also confirmed by the local authority [107]. The water level decrease and water trophy increase resulted in oxygen depletion in the hypolimnion, which was revealed by the chironomid reconstruction and recent measurements. Another threshold change based on the chironomid reconstruction occurred during the most recent decade, when the values decreased from a level of 4 mg L^{-1} (between the ~1940s and 2010s) to <2 mg L^{-1} (Figure 11). Such a decrease in oxygen concentration is ecologically highly significant for chironomid larvae [108].

The lake continues to be significantly overgrown with water plants, which is evidenced by the slight increase in the abundance of the Cladocera phytophilous species, *Alonella exigua*, and *A. excisa* [49,109,110]. More sand and mud associated species (*Rhynchotalona falcata*, *Leydigia* spp., and *Ilyocryptus* sp.) have joined the existing community since 1924 [58]. The lake surface pH in 2019 varied within a season from 7.9 to 8.4 [88], which is consistent with previous studies [9,15].

Due to inappropriate water resource management, many lakes in Riga and its vicinity have lost their high ecological quality. The pumping of water from the eutrophic Lake Mazais Baltezers into the low trophic Lake Sekšu increased nutrient inflow and pushed the lake over the threshold, causing eutrophication. Presently, Lake Sekšu continues to be overgrown with macrophytes such as *Phragmites australis*, *Nuphar* sp., and *Nymphaea* sp. [15]. Phytoplankton blooms can be observed in the lake. In 1995/1996, the majority of the cyanobacterial mass contained toxic species [111], while in 2002, Balode et al. [112] found no toxic species.

The "Baltezers" water pumping station is still in use. However, its contribution to the drinking water supply is not as significant as it was in previous years because other pumping stations were established, and additional resources for water supply were found [8].

5. Conclusions

The pumping of water from the eutrophic lake changed the water level and contributed to faster eutrophication in Lake Sekšu. Before the pipe began operations, the lake was shallow with low productivity and could be defined as a *Lobelia–Isoëtes* population-dominated biotope. The core studied represents the time period ~1935–2018. In 1953, the water level was artificially increased by pumping water from another lake. The sudden nutrient load increased the abundance of planktonic eutrophic–hypereutrophic diatoms, causing the lake water transparency to decrease and inducing hypolimnetic anoxia. The deterioration of the lake's ecological state, as indicated by the results of the biological analysis, was also confirmed by the geochemical results. Cladocera species indicating low trophy became suppressed or disappeared.

Reducing external nutrient loading is known as an important approach to improve the environmental state in small shallow lakes suffering from eutrophication. Nevertheless, in Lake Sekšu, after the water replenishment activities were terminated, the disturbance effect caused by the pumping continued to occur over decades, slowly changing assemblages of keystone species and the foodweb. This highlights the long legacy effects of eutrophication in lacustrine systems. Artificial restoration measures may, therefore, be considered as a strategy to accelerate the recovery of Lake Sekšu.

Author Contributions: Conceptualization, I.Z. and I.D.-D.; methodology, I.Z., T.P.L., S.S., N.S., W.T., T.J.; software NO; validation, NO; formal analysis, I.Z., T.P.L., M.R., S.S., N.S., W.T., T.J.; investigation, I.Z., I.D.-D., S.S., A.L., M.R.; resources, I.D.-D.; data curation, I.Z., T.P.L., M.R., S.S., N.S.; writing—original draft preparation, I.Z., I.D.-D., T.P.L., M.R., S.S., N.S., W.T., A.L., M.R., T.J.; writing—review and editing, I.Z., I.D.-D., M.R., S.S., N.S., W.T.; visualization, I.Z., N.S., W.T., M.R.; supervision, NO.; project administration, I.D.-D.; funding acquisition, I.D.-D., I.Z., N.S. All authors have read and agreed to the published version of the manuscript.

Funding: Research was funded by the European Regional Development Fund, 1.1.1.2 Post-doctoral project No.1.1.1.2/VIAA/2/18/359 and Latvian Institute of Aquatic Ecology. The effort of Izabela Zawiska was supported by a grant from Polish National Science Centre No.2016/23/D/ST10/03071. The work of Normunds Stivrins was supported by grants founded by Estonian Research Council grant PRG323 and the Latvian Council of Science Project No. LZP-2018/1-0171 and performance-based funding of the University of Latvia within the "Climate change and sustainable use of natural resources" program. Funding for Tomi P. Luoto was provided by the Kone Foundation (grant number 090140).

Acknowledgments: Our special thanks to lab assistants Juris Tunens, Nina Sunelika and all who participated in sampling. In particular, we would like to acknowledge Timo Saarinen for organizing sampling campaign, storyteller Pauls Timrots from Riga Water Supply Museum for providing historical background of the study site and expert in lake plants Uvis Susko from Latvian Fund for Nature for sharing his notes on historical observations.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Haas, M.; Baumann, F.; Castella, D.; Haghipour, N.; Reusch, A.; Strasser, M.; Eglinton, T.I.; Dubois, N. Roman-driven cultural eutrophication of Lake Murten, Switzerland. *Earth Planet Sci. Lett.* **2019**, *505*, 110–117. [CrossRef]
2. Wassmann, P. Cultural eutrophication: Perspectives and prospects. In *Drainage Basin Nutrient Inputs and Eutrophication: An Integrated Approach*; Wassmann, P., Olli, K., Eds.; University of Tromsø: Tromsø, Norway, 2005; pp. 224–234.
3. Hasler, A.D. Eutrophication of lakes by domestic drainage. *Ecology* **1947**, *28*, 383–395. [CrossRef]

4. Elmgren, R.; Larsson, U. Eutrophication in the Baltic Sea area: Integrated coastal management issues. In *Science and Integrated Coastal Management*; von Bodungen, B., Turner, R.K., Eds.; University Press: Berlin, Germany, 2001; pp. 15–35.
5. Smol, J.P. *Pollution of Lakes and Rivers. A Paleoenvironmental Perspective*, 2nd ed.; Blackwell Publishing Ltd.: Oxford, UK, 2008; pp. 1–396.
6. Yuksel, I.; Arman, H.; Ceribasi, G. Water Resources Management of Hydropower and Dams as Sustainable Development. In Proceedings of the International Conference on Sustainable Systems and the Environment (ISSE), Sharjah, UAE, 23–24 March 2011.
7. Chen, J.; Qian, H.; Gao, Y.; Wang, H.; Zhang, M. Insights into hydrological and hydrochemical processes in response to water replenishment for lakes in arid regions. *J. Hydrol.* **2020**, *581*. [CrossRef]
8. Dziluma, M. *Riga Water and the Riga Water Supply Museum*; Riga Water: Riga, Latvia, 2003; pp. 1–86.
9. Jansons, E. *Rīgas Dzeramais ūdens un tā Resursu Aizsardzība. Baltezeru un to Apkaimes Izpēte*; Rīgas Ūdens: Rīga, Latvija, 1997; pp. 1–53.
10. Krutofala, T.; Levins, I. *Pazemes ūdeņu Atradnes "Baltezers", Iecirkņa "Akoti" Pase. Pazemes ūdeņu Ekspluatācijas Krājumu Novērtējums. Atradne "Baltezers", iecirknis "Akoti". Gruntsūdens Horizonts*; Latvijas Vides, ģeoloģijas un Meteoroloģijas Aģentūra: Rīga, Latvija, 2006; pp. 1–38.
11. Pastors, A. Sekšu ezers. In *Latvijas Daba: Enciklopēdija*; Kavacs, G., Ed.; Latvijas Enciklopēdija: Rīga, Latvija, 1995; Volume 5, pp. 12–13.
12. Bauze-Krastiņš, M.G. *Garkalnes novada teritorijas plānojums 2009–2021. Gadam. Paskaidrojuma Raksts*; Garkalnes novads: Rīga, Latvija, 2009; pp. 1–169.
13. Latvijas Klimats. Latvijas Vides, ģeoloģijas un Meteoroloģijas Centrs. Available online: https://www.meteo.lv/lapas/laika-apstakli/klimatiska-informacija/latvijas-klimats/latvijas-klimats?id=1199&nid=562 (accessed on 10 March 2020).
14. Natural Data Management System OAK, Meža Valsts Reģistra Informācija. Available online: http://ozols.daba.gov.lv/pub/Life/ (accessed on 10 March 2020).
15. Zarina, D. Sekšu Ezera, Sudrabezera un Venču Ezera Ekoloģiskais Stāvoklis. Master's Thesis, Latvijas Universitāte, Riga, Latvija, 2014.
16. Tylmann, W.; Bonk, A.; Goslar, T.; Wulf, S.; Grosjean, M. Calibrating 210Pb dating results with varve chronology and independent chronostratigraphic markers: Problems and implications. *Quat. Geochronol.* **2016**, *32*, 1–10. [CrossRef]
17. Rose, N. A method for the selective removal of inorganic ash particles from lake sediments. *J. Paleolimnol.* **1990**, *4*, 61–68. [CrossRef]
18. Alliksaar, T. Spatial and temporal variability of the distribution of spherical fly-ash particles in sediments in Estonia. Ph.D. Thesis, Tallinn Pedagogical University, Tallinn, Estonia, 2000.
19. Hedges, J.I.; Eglinton, G.; Hatcher, P.G.; Kirchman, D.L.; Arnosti, C.; Derenne, S.; Evershed, R.P.; Kögel-Knabner, I.; de Leeuw, J.W.; Littke, R.; et al. The molecularly-uncharacterized component of non-living organic matter in natural environments. *Org. Geochem.* **2000**, *31*, 945–958. [CrossRef]
20. Masiello, C.A. New directions in black carbon organic geochemistry. *Mar. Chem.* **2004**, *92*, 201–213. [CrossRef]
21. Stivrins, N.; Wulf, S.; Wastegård, S.; Lind, E.M.; Allisaar, T.; Gałka, M.; Andersen, T.J.; Heinsalu, A.; Seppä, H.; Veski, S. Detection of the Askja AD 1875 cryptotephra in Latvia, Eastern Europe. *J. Quat. Sci.* **2016**, *31*, 437–441. [CrossRef]
22. Blaauw, M. Methods and code for 'classical' age-modelling of radiocarbon sequences. *Quat. Geochronol.* **2010**, *5*, 512–518. [CrossRef]
23. R Core Team. *R: A Language and Environment for Statistical Computing*; R Foundation: Vienna, Austria, 2018.
24. Heiri, O.; Lotter, A.F.; Lemcke, G. Loss on ignition as a method for estimating organic and carbonate content in sediments, reproducibility and comparability of results. *J. Paleolimnol.* **2001**, *25*, 101–110. [CrossRef]
25. Berglund, B.E.; Ralska-Jasiewiczowa, M. Pollen analysis and pollen diagrams. In *Handbook of Holocene Palaeoecology and Palaeohydrology*; Berglund, B., Ed.; John Wiley & Sons: Chichester, UK, 1986; pp. 455–484.
26. Stockmarr, J. Tablets with spores used in absolute pollen analysis. *Pollen Spores* **1971**, *13*, 615–621.
27. Fægri, K.; Iversen, J. *Textbook of Pollen Analysis*; John Wiley & Sons: Chichester, UK, 1986.
28. Miola, A. Tools for non-pollen palynomorphs (NPPs) analysis: A list of quaternary NPP types and reference literature in English language (1972–2011). *Rev. Palaeobot. Palynol.* **2012**, *186*, 142–161. [CrossRef]

29. Sweeney, C.A. A key for the identification of stomata of the native conifers of Scandinavia. *Rev. Palaeobot. Palynol.* **2004**, *128*, 281–290. [CrossRef]
30. Finsinger, W.; Tinner, W. New insights on stomata analysis of European conifers 65 years after the pioneering study of Werner Trautmann (1953). *Veg. Hist. Archaeobotany* **2019**. [CrossRef]
31. Grimm, E.C. *TILIA Software*; Illinois State Museum, Research and Collection Center: Springfield, IL, USA, 2012.
32. Battarbee, R.W. Diatom analysis. In *Handbook of Holocene Paleoecology and Paleohydrology*; Berglund, B.E., Ed.; John Wiley and Sons Ltd.: Chichester, UK, 1986; pp. 527–570.
33. Battarbee, R.W.; Kneen, M.J. The use of electronically counted microsphere sin absolute diatom analysis. *Limnol. Oceanogr.* **1982**, *27*, 184–188. [CrossRef]
34. Krammer, K.; Lange-Bertalot, H. Bacillariophyceae 4. Achnanthaceae. In *Süsswasserflora von Mitteleuropa*, 3rd ed.; Ettl, H., Gärtner, G., Gerloff, J., Heyning, H., Mollenhauer, D., Eds.; Fisher: Stuttgardt, Germany, 2011; Volume 2, p. 437.
35. Krammer, K.; Lange-Bertalot, H. Bacillariophyceae 1. Naviculaceae. In *Süsswasserflora von Mitteleuropa*, 4th ed.; Ettl, H., Gerloff, J., Heyning, H., Mollenhauer, D., Eds.; Fisher: Stuttgardt, Germany, 2010; Volume 2, p. 876.
36. Krammer, K.; Lange-Bertalot, H. Bacillariophyceae 2. Ephitemiaceae. Bacillariaceae. Surirellaceae. In *Süsswasserflora von Mitteleuropa*, 4th ed.; Ettl, H., Gerloff, J., Heyning, H., Mollenhauer, D., Eds.; Fisher: Stuttgardt, Germany, 2008; Volume 2, p. 596.
37. Krammer, K.; Lange-Bertalot, H. Bacillariophyceae 3. Centrales. Fragilariaceae. Eunotiaceae. In *Süsswasserflora von Mitteleuropa*, 3rd ed.; Ettl, H., Gerloff, J., Heyning, H., Mollenhauer, D., Eds.; Fisher: Stuttgardt, Germany, 2008; Volume 2, pp. 1–577.
38. Lange-Bertalot, H.; Hofmann, G.; Werum, M. *Diatomeen im Süßwasser-Benthos von Mitteleuropa*; A.R.G. Gantner Verlag, K.G.: Ruggell, Liechtenstein, 2011; pp. 1–908.
39. Lange-Bertalot, H.; Metzeltin, D. Indicators of Oligotrophy. 800 taxa representative of three ecologically distinct lake types. In *Iconographia Diatomologica: Annotated Diatom Micrographs*; Lange-Bertalot, H., Ed.; A.R.G. Gantner Verlag, K.G.: Ruggel, Liechtenstein, 1996; pp. 1–390.
40. Lange-Bertalot, H.; Bąk, M.; Witkowski, A.; Tagliaventi, N. *Eunotia* and related genera. In *Diatoms of Europe*; A.R.G. Gantner Verlag, K.G.: Ruggell, Liechtenstein, 2011; Volume 6, pp. 1–747.
41. AlgaeBase. Available online: https://www.algaebase.org/ (accessed on 19 February 2020).
42. Lecointe, C.; Coste, M.; Prygiel, J. "Omnidia": Software for taxonomy, calculation of diatom indices and inventories management. In *Twelfth International Diatom Symposium*; Springer: Dordrecht, The Netherlands, 1993; pp. 509–513.
43. Denys, L. *A Check-List of the Diatoms in the Holocene Deposits of the Western Belgian Coastal Plain with a Survey of their Apparent Ecological Requirements*; Service Geologique de Belgique: Brussels, Belgium, 1991; Volume 1, pp. 1–2.
44. Van Dam, H.; Mertens, A.; Sinkeldam, J. A coded checklist and ecological indicator values of freshwater diatoms from the Netherlands. *Neth. J. Aquat. Ecol.* **1994**, *28*, 117–133.
45. Juggins, S. *Version 1.0. User Guide. The European Diatom Database*; Newcastle University: Newcastle upon Tyne, UK, 2001.
46. Szeroczyńska, K.; Sarmaja-Korjonen, K. *Atlas of Subfossil Cladocera from Central and Northern Europe*; Friends of Lower Vistula Society: Świecie, Poland, 2007; pp. 1–84.
47. Kurek, J.; Korosi, J.B.; Jeziorski, A.; Smol, J.P. Establishing reliable minimum count sizes for cladoceran subfossils sampled from lake sediments. *J. Paleolimnol.* **2010**, *44*, 603–612. [CrossRef]
48. Juggins, S. *C2 Version 1.5. User Guide. Software for Ecological and Palaeoecological Data Analysis and Visualisation*; Newcastle University: Newcastle upon Tyne, UK, 2007.
49. Flössner, D. *Die Haplopoda und Cladocera (ohne Bosminidae) Mitteleuropas*; Backhuys Publishers: Leiden, The Netherlands, 2000; p. 428.
50. Brooks, S.J.; Langdon, P.G.; Heiri, O. *The Identification and Use of Palaearctic Chironomidae Larvae in Palaeoecology*; Quaternary Research Association: Edinburgh, UK, 2007.
51. Luoto, T.P.; Nevalainen, L. Inferring reference conditions of hypolimnetic oxygen for deteriorated Lake Mallusjärvi in the cultural landscape of Mallusjoki, southern Finland using fossil midge assemblages. *Water Air Soil Pollut.* **2011**, *217*, 663–675. [CrossRef]

52. Luoto, T.P.; Salonen, V.P. Fossil midge larvae (Diptera: Chironomidae) as quantitative indicators of late-winter hypolimnetic oxygen in southern Finland: A calibration model, case studies and potentialities. *Boreal Environ. Res.* **2010**, *15*, 1–18.
53. Meltsov, V.; Poska, A.; Odgaardd, B.V.; Sammula, M.; Kull, T. Palynological richness and pollen sample evenness in relation to local floristic diversity in southern Estonia. *Rev. Palaeobot. Palynol.* **2011**, *166*, 344–351. [CrossRef]
54. Stivrins, N.; Kołaczek, P.; Reitalu, T.; Seppä, H.; Veski, S. Phytoplankton response to the environmental and climatic variability in a temperate lake over the last 14,500 years in eastern Latvia. *J. Paleolimnol.* **2015**, *54*, 103–119. [CrossRef]
55. Schindler, D.W. The Dilemma of Controlling Cultural Eutrophication of Lakes. *Proc. R. Soc. B* **2012**, *279*, 4322–4333. [CrossRef] [PubMed]
56. Lampert, W.; Sommer, U. *Limnoecology*; Oxford University Press: Oxford, UK, 1997; pp. 1–382.
57. Schindler, D.W. Recent advances in the understanding and management of eutrophication. *Limnol. Oceanogr.* **2006**, *51*, 356–363. [CrossRef]
58. Leira, M.; Cantonati, M. Effects of water-level fluctuations on lakes: An annotated bibliography. *Hydrobiologia* **2008**, *613*, 171–184. [CrossRef]
59. Koralay, N.; Kara, O. Effects of Soil Erosion on Water Quality and Aquatic Ecosystem in a Watershed. In Proceedings of the 1st International Congress on Agricultural Structures and Irrigation, Antalya, Turkey, 26–28 September 2018; pp. 20–29.
60. Kuptsch, P. Die Cladoceren der Umgegend von Riga. *Arch. Hydrobiol.* **1927**, *18*, 273–315.
61. Hakkari, L. Zooplankton species as indicators of environment. *Aqua Fenn.* **1972**, *1*, 46–54.
62. Lyche, A. Cluster analysis of plankton community structure in 21 lakes along a gradient of trophy. *Verh. Internat. Verein Limnol.* **1990**, *24*, 586–591. [CrossRef]
63. Urtane, L. Cladocera as indicators of lake types and trophic state in Latvian lakes. Ph.D. Thesis, University of Latvia, Riga, Latvia, 1998.
64. Walseng, B.; Halvorsen, G. Littoral microcrustaceans as indices of trophy. *Verh. Internat. Verein Limnol.* **2005**, *29*, 827–829. [CrossRef]
65. Jensen, T.C.; Dimante-Deimantovica, I.; Schartau, A.K.; Walseng, B. Cladocerans respond to differences in trophic state in deeper nutrient poor lakes from Southern Norway. *Hydrobiologia* **2013**, *715*, 101–112. [CrossRef]
66. Umja Ezera Dabas Aizsardzības Plāns. Available online: https://www.daba.gov.lv/upload/File/DAPi_apstiprin/DL_Ummis-06.pdf (accessed on 20 March 2020).
67. Susko, U.; Latvian Fund for Nature, Riga, Latvia. Personal communication, 2020.
68. Sloka, N. *Latvijas PSR Dzīvnieku Noteicējs. Latvijas Kladoceru (Cladocera) Fauna un Noteicējs*; P. Stučkas Latvijas valsts universitāte: Rīga, Latvia, 1981; p. 146.
69. *Eutrophication of Waters, Monitoring, Assessment and Control*; OECD (Organisation for Economic Cooperation and Development): Paris, France, 1982.
70. Andrén, E. Changes in the Composition of the Diatom Flora During the Last Century Indicate Increased Eutrophication of the Oder Estuary, South-western Baltic Sea. *Estuar. Coast. Shelf Sci.* **1999**, *48*, 665–676. [CrossRef]
71. Andrén, E.; Clarke, A.L.; Telford, R.J.; Wesckström, K.; Vilbaste, S.; Aigars, J.; Conley, D.; Johnsen, T.; Juggins, S.; Korhola, A. *Defining Reference Conditions for Coastal Areas in the Baltic Sea*; TemaNord Series; Nordic Council of Ministers: Copenhagen, Denmark, 2007.
72. Andrén, E.; Shimmield, G.; Brand, T. Environmental changes of the last three centuries indicated by siliceous microfossil records from the southwestern Baltic Sea. *Holocene* **1999**, *9*, 25–38. [CrossRef]
73. Weckström, K. Assessing recent eutrophication in coastal waters of the Gulf of Finland (Baltic Sea) using subfossil diatoms. *J. Paleolimnol.* **2006**, *35*, 571–592. [CrossRef]
74. Milecka, K.; Bogaczewicz-Adamczak, B. Zmiany żyzności trofii w ekosystemach miękkowodnych jezior Borów Tucholskich. *Przegl. Geol* **2006**, *54*, 81–86.
75. Christensen, K.K.; Sand-Jensen, K. Precipitated iron and manganese plaques restrict root uptake of phosphorus in Lobelia dortmanna. *Can. J. Bot.* **1998**, *76*, 2158–2163.

76. Battarbee, R.W.; Simpson, G.L.; Shilland, E.M.; Flower, R.J.; Kreiser, A.; Yang, H.; Clarke, G. Recovery of UK lakes from acidification: An assessment using combined palaeoecological and contemporary diatom assemblage data. *Ecol. Indic.* **2014**, *37*, 365–380. [CrossRef]
77. Battarbee, R.W.; Jones, V.J.; Flower, R.J.; Cameron, N.G.; Bennion, H.; Carvalho, L.; Juggins, S. Diatoms. In *Tracking Environmental Change Using Lake Sediments. Terrestrial, Algal, and Siliceous Indicators*; Smol, J.P., Birks, H.J.B., Last, W.M., Eds.; Kluwier Academic Publishers: Norwell, MA, USA, 2001; Volume 3, pp. 155–202.
78. Battarbee, R.W.; Charles, D.F.; Dixit, S.S.; Renberg, I. Diatoms as indicators of surface water acidity. In *The Diatoms: Applications for the Environmental and Earth Sciences*; Stoermer, E.F., Smol, J.P., Eds.; Cambridge University Press: Cambridge, UK, 1999; pp. 85–127.
79. Battarbee, R.W.; Charles, D.F. Diatom-based pH reconstruction studies of acid lakes in Europe and North America: A synthesis. *Water Air Soil Pollut.* **1986**, *30*, 347–354. [CrossRef]
80. Klavins, M.; Kokorite, I.; Jankevica, M.; Mazeika, J.; Rodinov, V. Trace elements in sediments of lakes in Latvia. In Proceedings of the 4th WSEAS International Conference on Energy and Development—Environment—Biomedicine, Corfu Island, Greece, 14–16 July 2011.
81. Kļaviņš, M.; Briede, A.; Kļaviņa, I.; Rodinov, V. Metals in sediments of lakes in Latvia. *Environ. Int.* **1995**, *21*, 451–458. [CrossRef]
82. Liiv, M.; Alliksaar, T.; Amon, L.; Freiberg, R.; Heinsalu, A.; Reitalu, T.; Saarse, L.; Seppä, H.; Stivrins, N.; Tõnno, I.; et al. Late glacial and early Holocene climate and environmental changes in the eastern Baltic area inferred from sediment C/N ratio. *J. Paleolimnol.* **2019**, *61*, 1–16. [CrossRef]
83. Terasmaa, J.; Puusepp, L.; Marzecová, A.; Vandel, E.; Vaasma, T.; Koff, T. Natural and human-induced environmental changes in Eastern Europe during the Holocene: A multi-proxy palaeolimnological study of a small Latvian lake in a humid temperate zone. *J. Paleolimnol.* **2013**, *49*, 663–678. [CrossRef]
84. Meyers, P.A.; Ishiwatari, R. Lacustrine organic geochemistry—An overview of indicators of organic matter sources and diagenesis in lake sediments. *Org. Geochem.* **1993**, *20*, 867–900. [CrossRef]
85. Meyers, P.A.; Teranes, J.L. Sediment Organic Matter. In *Tracking Environmental Change Using Lake Sediments: Physical and Geochemical Methods, Developments in Paleoenvironmental Research*; Last, W.M., Smol, J.P., Eds.; Springer: Dordrecht, The Netherlands, 2001; pp. 239–269.
86. Buzajevs, V.; Levina, N.; Levins, I. *Pazemes ūdeņu bilance un kvalitāte Baltezera ūdensgūtnēs*; Valsts Ģeoloģijas Dienests: Riga, Latvia, 1997; pp. 1–56.
87. Sarmaja-Korjonen, K. Correlation of fluctuations in cladoceran planktonic: Littoral ratio between three cores from a small lake in southern Finland: Holocene water-level changes. *Holocene* **2001**, *11*, 53–63. [CrossRef]
88. Cooper, J.T.; Steinitz-Kannan, M.; Kallmeyer, D.E. Bacillariophyta: The Diatoms. In *Algae: Source of Treatment*; Ripley, M.G., Ed.; American Water Works Association: Denver, CO, USA, 2010; pp. 207–215.
89. Zelnik, I.; Balanč, T.; Toman, M. Diversity and Structure of the Tychoplankton Diatom Community in the Limnocrene Spring Zelenci (Slovenia) in Relation to Environmental Factors. *Water* **2018**, *10*, 361. [CrossRef]
90. Dimante-Deimantovica, I.; Latvian Institute of Aquatic Ecology, Riga, Latvia. Personal communication, 2020.
91. Ardiles, V.; Alcocer, J.; Vilaclara, G.; Oseguera, L.A.; Velasco, L. Diatom fluxes in a tropical, oligotrophic lake dominated by large-sized phytoplankton. *Hydrobiologia* **2012**, *679*, 77–90. [CrossRef]
92. Romero, O.E.; Thunell, R.C.; Astor, Y.; Varela, R. Seasonal and interannual dynamics in diatom production in the Cariaco Basin, Venezuela. *Deep-Sea Res.* **2009**, *56*, 571–581. [CrossRef]
93. Ryves, D.B.; Jewson, D.H.; Sturm, M.; Battarbee, R.W.; Flower, R.J.; Mackay, A.W.; Granin, N.G. Quantitative and qualitative relationships between planktonic diatom communities and diatom assemblages in sedimenting material and surface sediments in Lake Baikal, Siberia. *Limnol. Oceanogr.* **2003**, *48*, 1643–1661. [CrossRef]
94. Ceirans, A. Zooplankton indicators of trophy in Latvian lakes. In *Acta Universitatis Latviensis. Biology*; University of Latvia: Riga, Latvia, 2007; Volume 723, pp. 61–69.
95. Veski, S.; Amon, L.; Heinsalu, A.; Reitalu, T.; Saarse, L.; Stivrins, N.; Vassiljev, J. Lateglacial vegetation dynamics in the eastern Baltic region between 14,500 and 11,400 cal yr BP: A complete record since the Bolling (GI-1e) to the Holocene. *Quat. Sci. Rev.* **2012**, *40*, 39–53. [CrossRef]
96. Kołaczek, P.; Zubek, S.; Błaszkowski, J.; Mleczko, P.; Włodzimierz, M. Erosion or plant succession—How to interpret the presence of arbuscular mycorrhizal fungi (Glomeromycota) spores in pollen profiles collected from mires. *Rev. Palaeobot. Palynol.* **2013**, *189*, 29–37. [CrossRef]

97. Wang, L.; Mackay, A.W.; Leng, M.J.; Rioual, P.; Panizzo, V.N.; Lu, H.; Gu, Z.; Chu, G.; Han, J.; Kendrick, C.P. Influence of the ratio of planktonic to benthic diatoms on lacustrine organic matter δ13C from Erlongwan maar lake, northeast China. *Org. Geochem.* **2013**, *54*, 62–68. [CrossRef]
98. Wolin, J.A.; Stone, J.R. Diatoms as Indicators of Water-Level Change in Freshwater Lakes. In *The Diatoms Applications to the Environmental and Earth Sciences*; Stoermer, E.F., Smol, J.P., Eds.; Cambridge University Press: Cambridge, UK, 2010; pp. 174–185.
99. Carmignani, J.R.; Roy, A.H. Ecological impacts of winter water level drawdowns on lake littoral zones: A review. *Aquat. Sci.* **2017**, *79*, 803–824. [CrossRef]
100. Magny, M.; Arnaud, F.; Billaud, Y.; Marguet, A. Lake-level fluctuations at Lake Bourget (eastern France) around 4500–3500 cal. a BP and their palaeoclimatic and archaeological implications. *J. Quat. Sci.* **2012**, *27*, 494–502. [CrossRef]
101. Theuerkauf, E.J.; Braun, K.N.; Nelson, D.M.; Kaplan, M.; Vivirito, S.; Williams, J.D. Coastal geomorphic response to seasonal water-level rise in the Laurentian Great Lakes: An example from Illinois Beach State Park, USA. *J. Great Lakes Res.* **2019**, *45*, 1055–1068. [CrossRef]
102. Holmer, M.; Storkholm, P. Sulphate reduction and sulphur cycling in lake sediments: A review. *Freshw. Biol.* **2001**, *46*, 431–451. [CrossRef]
103. Couture, R.M.; Fischer, R.; Van Cappellen, P.; Gobeil, C. Non-steady state diagenesis of organic and inorganic sulfur in lake sediments. *Geochim. Cosmochim. Acta* **2016**, *194*, 15–33. [CrossRef]
104. Aasif, A.; Nilli, A.; Aasif, L.; Hema, A.; Rayees, S. Diatom Diversity and Organic Matter Sources in Water Bodies around Chennai, Tamil Nadu, India. *MOJ Ecol. Environ. Sci.* **2017**, *2*, 141–146.
105. Rosińska, A.; Rakocz, K. Rola biodegradowalnej materii organicznej w procesie dezynfekcji wody. *Inż. Ochr. Środ.* **2013**, *16*, 511–521.
106. Brodersen, K.P.; Quinlan, R. Midges as palaeoindicators of lake productivity, eutrophication and hypolimnetic oxygen. *Quat. Sci.* **2006**, *25*, 1995–2012. [CrossRef]
107. Timrots, P.; Riga Water Supply Museum, Riga, Latvia. Personal communication, 2019.
108. Brodersen, K.P.; Pedersen, O.; Lindegaard, C.; Hamburger, K. Chironomids (Diptera) and oxy-regulatory capacity: An experimental approach to paleolimnological interpretation. *Limnol. Oceanogr.* **2004**, *49*, 1549–1559.
109. Kacalova, O.; Laganovsla, R. *Zivju Barības Bāze Latvijas PSR Ezeros*; Latvijas PSR Zinātņu akadēmijas izdevniecība: Rīga, Latvija, 1961; pp. 17–23.
110. Bledzki, L.A.; Rybak, J.I. *Freshwater Crustacean Zooplankton of Europe Cladocera and Copepoda (Calanoida, Cyclopoida), Key to Species Identification, with Notes on Ecology, Distribution, Methods and Introduction to Data Analysis*; Springer: New York, NY, USA, 2016; pp. 1–918.
111. Lielā un Mazā Baltezera Eitroficēšanās Izpēte. Available online: https://www.google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=1&ved=2ahUKEwiPufXQp7_oAhXpxIsKHfMmDOcQFjAAegQIBRAB&url=https%3A%2F%2Fwww.ezeri.lv%2Fblog%2FDownloadAttachment%3Fid%3D347&usg=AOvVaw1qjWh6fVLl6-JGxc-_EbzG (accessed on 10 March 2020).
112. Balode, M.; Purina, I.; Strake, S.; Purvina, S.; Pfeifere, M.; Barda, I.; Povidisa, K. Toxic cyanobacteria in the lakes located in Rīga (the capital of Latvia) and its surroundings: Present state of knowledge. *Afr. J. Mar. Sci.* **2006**, *28*, 225–230. [CrossRef]

Appendix 4

Manuscript I
Bakumenko, V., **Lanka, A.**, Belle, S., Poska, A., Vassiljev, J., Alliksaar, T., Heiri, O., Veski, S.
A 14 500 - year multi-proxy reconstruction of climate and environment change in Eastern Baltics: case study from Southern Estonia.

A 14 500-year multi-proxy reconstruction of climate and environmental change in Eastern Baltics

Varvara Bakumenko[a*], Anna Lanka[a], Anneli Poska[a,b], Jüri Vassiljev[a], Oliver Heiri[v], Simon Belle[d], Tiiu Alliksaar[a], Siim Veski[a]

[a] Department of Geology, Tallinn University of Technology, Ehitajate tee 5, 19086, Tallinn, Estonia

[b] Department of Physical Geography and Ecosystem Science, Lund University, Lund, Sweden

[c] Department of Environmental Sciences, University of Basel, Basel, Switzerland

[d] Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

[*]varvara.bakumenko@taltech.ee

Keywords: Paleolimnology, Cladocera, Chironomidae, pollen, continentality

Abstract

This study presents a 14,500-year high-resolution multi-proxy reconstruction of past climate and environmental changes from Lake Nakri in Southern Estonia. Estonia's geographical position at the intersection of maritime and continental climate zones and boreal and nemoral biomes makes it a highly suitable location for studying past small climate fluctuations. We used Cladocera, Chironomidae, pollen, and loss-on-ignition analyses to reconstruct mean July air temperatures, explore changes in continentality expressed in annual temperature range (ATR), to track environmental changes (trophy, pH, etc.) and lake ecosystem dynamics throughout the late glacial and Holocene. Using Cladocera remains to infer past changes in nutrient status, we found no evidence of significant shifts. Therefore, we conclude that the chironomid-based reconstruction was not biased by such changes. Chironomidae and pollen analysis results were used to reconstruct July air temperatures. The reconstruction curves are coherent and consistently reveal climate events, happened around the 8.2 ka, 7.5 ka, 5.5 ka cold events, Medieval Warm Period, and Little Ice Age. The exception to the otherwise consistent proxy pattern is that Chironomidae data reveal an earlier onset of Early Holocene

warming compared with the pollen record. This discrepancy may be attributed to low local pollen productivity and delayed postglacial vegetation development. The chironomid-based reconstructions show that the Younger Dryas climate was marked by a 3°C drop in summer temperature and increased ATR. The chironomid-based continentality (difference in summer and winter temperatures) reconstruction approach is still under development. We have produced the first tentative chironomid-inferred ATR reconstruction showing trends similar to ones already published. The resulting reconstructions provide critical insights into past regional climate variability and ecosystem responses in eastern temperate-boreal ecotones. New climate curves can serve as a reference for future regional climate studies.

1. Introduction

Transitional regions, characterized by changing climates and biomes, are particularly sensitive to climate variability (Fu, 1992). The Eastern Baltic region exemplifies such a transitional zone, lying along the north-south gradient between boreal and temperate vegetation zones and exhibiting a pronounced west-east shift from oceanic to continental climates (Team, 2008; Heikkilä and Seppä, 2010; Edvardsson et al., 2016). Furthermore, Stonevicius et al. (2018) reported significant change in continentality expressed in annual temperature range (ATR) over the last 50 years. Given that recent climate change in Europe has already led to warmer temperatures and reduced precipitation during the growing season—and these trends are expected to continue—it is important to understand how such changes may impact sensitive ecosystems in transitional climate zones.

Pollen are excellent indicators of regional and local land cover and human impact changes and are one of the most commonly used proxies in past climate reconstructions (Ilyashuk et al., 2009; Salonen et al., 2012; Chevalier et al., 2020), as well as the most abundant type of climate reconstruction in the region (e.g. (Niinemets and Saarse, 2009; Poska et al., 2022; Saarse and Veski, 2001; Seppä and Poska, 2004), with just a few examples of usage of other biotic proxies (Heiri et al., 2014; Stansell et al., 2017; Druzhinina et al., 2020; Šeirienė et al., 2021). However, for Quaternary climate reconstruction in northern and eastern Europe the method also has some limitations. For instance, it has been shown that immigration of plants after deglaciation may lag climate change (Väliranta et al., 2015), and some intervals, such as the Younger Dryas, may presently have no analogues in modern vegetation (Magny et al., 2001). Furthermore, boreal forest can be resistant to minor climate changes (Stralberg et al., 2020) implying that pollen-based climate reconstructions in the boreal region may not be sensitive to minor changes. Therefore, there is an urgent need for long-term multi-proxy climate and environmental reconstructions using independent climate proxies in Northern Europe and particularly in the Eastern Baltic region, where such studies are currently lacking.

Subfossil chironomids, non-biting midges from the family Chironomidae, are widely used as a proxy to reconstruct past July air temperatures (Tóth et al., 2015; Hájková et al., 2016; Jiménez-Moreno et al., 2023; Rigterink et al., 2024), and have revealed some potential for continentality changes assessment (Self et al., 2011). However, chironomids can be sensitive to changes in other in-lake factors, such as trophic state, pH and oxygen concentration (Brooks et al., 2001; Luoto, 2011; Nazarova et al., 2011; Ursenbacher et al., 2020). Therefore, it is helpful to account for these potential confounding influences using complementary proxies to support chironomid-based climate reconstructions. Cladocera analysis is a well-established palaeolimnological method for detecting past environmental changes within lakes (Van Damme and Kotov, 2016; Pastukhova et al., 2024), as cladocerans are sensitive to changes in lake water pH, trophic state and conductivity (Lanka et al., 2024; Zawiska et al., 2025) as well as lake water depth (Wang et al., 2024). Loss-on-ignition (LOI) is commonly used in the multi-proxy research (Hamerlík et al., 2016; Yao et al., 2017; Sapelko et al., 2019), provides data on the organic and inorganic carbon content of sediments and can be used a waterbody trophic state evaluation. Combining chironomid-, pollen-, cladoceran- and loss on ignition analysis results will allow us to produce critical quantitative and qualitative palaeoecological datasets often used to complement Chironomide-based palaeoclimate reconstructions (Lotter et al., 1997; Mirosław-Grabowska et al., 2015; Veski et al., 2015; Druzhinina et al., 2020; Šeirienė et al., 2021).

We selected the Lake Nakri (Southern Estonia) palaeo-sequence, which covers the last 14.5 ka cal BP—from the time of ice retreat to the present day— to perform the palaeo-environment reconstruction using Chironomidae, Cladocera, pollen and LOI analysis and compared the results other records from eastern and northern Europe. The objectives of the current study is to (I) present a new high-resolution multiproxy based palaeolimnological record from Eastern Baltic region (II) reconstruct the late glacial and Holocene climate and environmental dynamics (III) compare the responses of different proxies in respect to July air temperature, annual temperature range and environment changes, and (IV) evaluate the reconstructed fluctuations within the framework of known regional and global climatic and environmental changes.

The outcome of this paper contributes to our overall understanding of past global climate change patterns, produces a novel high resolution environmental change record for the Baltic region, and documents the response of local environments and ecosystems to changing climate aiding in assessments the potential effects of future changes. The resulting climate reconstructions have the potential to serve as a reference for Eastern Europe.

2. Study site description

Lake Nakri (0.9 ha, 48.5 m a.s.l., 57° 53.703′ N, 26° 16.389′ E), is situated in Southern Estonia (Fig. 1). It is a small shallow (up to 3 m depth) lake with ca 0.25 km^2 catchment area. Based on modern limnological measurements and observations, Lake Nakri has been classified as an eutrophic lake (Secchi depth 1.6 m) with slightly alkaline pH (Lanka et al., 2024) and brownish water color. The lake has a low swampy shoreline and is surrounded by natural mixed spruce-pine dominated boreal forest with fairly low modern land use in catchment. With an average annual air temperature of 5.5°C, mean July temperature of 18°C, mean January temperature of −4°C, and annual precipitation of 675 mm, the region exhibits climatic conditions that are transitional between oceanic and continental climates (Estonian Environment Agency).

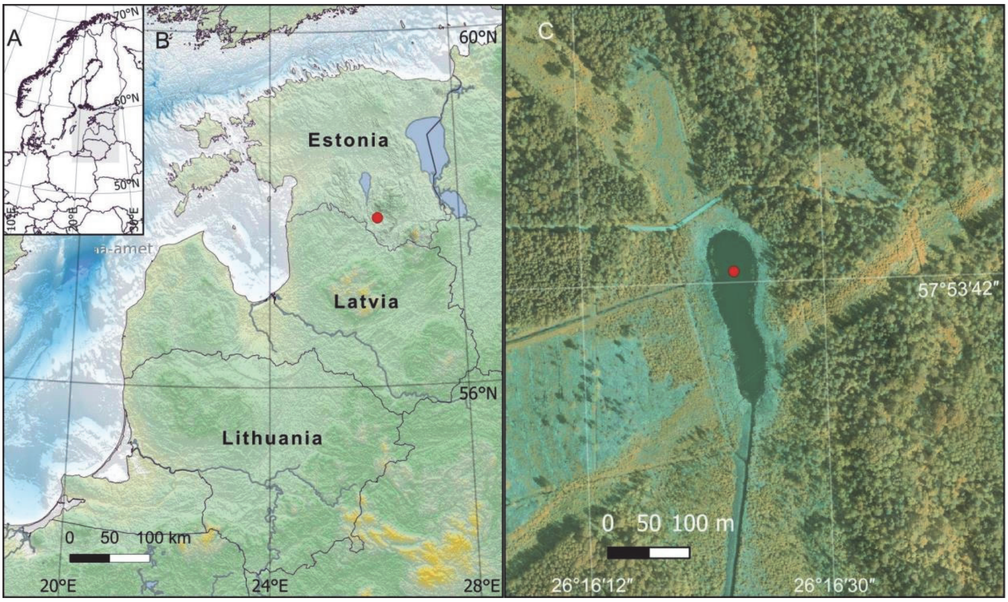


Fig.1 - Overview map (A) and EOTOPO 2022 map (NOAA National Centers for Environmental Information, 2022) of the eastern Baltic (B) and false-color forestry orthophoto (Republic of Estonia Land and Spatial Development Board, 2025) for Lake Nakri (C). Red dot marks the sampling point.

3. Methods

3.1. Sampling strategy

Parallel overlapping sets of 1 m long segments of the lake sediment sequence, covering 1346 cm, were taken using a Russian corer. The coring was conducted from the deepest part of the lake in 2007, 2009 and 2018. The uppermost 58 cm unconsolidated sediments were retrieved with a Wilner sediment sampler. Sediment cores were correlated according to loss-on-ignition curves and radiocarbon dates. Samples for analysis from depths of 0–587 cm were taken from the 2018 core, while deeper samples were obtained from the 2007 and 2009 cores..

The core was described and photographed in the field and subsequently transported to the laboratory for further analysis and documentation. The full sediment sequence (0—1346 cm) was sampled for pollen analysis (163 samples), Chironomidae analysis (149 samples), and LOI analysis (1340 samples). The upper part of the core (0—1028 cm) was also analysed for Cladocera communities (68 samples). Samples for all types of analysis were taken from the same levels if possible.

Lower part of the sequence covering 14.0-9.0 ka cal BP has been published in detail by Amon et al. (2012, 2014).

3.2. Chronology

The chronology of the Lake Nakri sediments was established by the OxCal 4.4 deposition model (Bronk Ramsey, 2009; Ramsey, 2008), where lithological boundaries, coring time (top of the sediment), radiocarbon dating and age determinations derived from spheroidal fly ash particle (SFAP) analysis (Renberg and Wik, 1985; Alliksaar, 2000; Heinsalu et al., 2007) were used. The radiocarbon ages were determined at the Poznan Radiocarbon Laboratory in Poland. The radiocarbon dates were calibrated using the IntCal20 calibration curve (Reimer et al., 2020). For radiocarbon dating, terrestrial plant macrofossils (mainly small branches, *Dryas* leaves, and *Betula* catkin scales). Levels lacking macrofossils were dated using bulk sediment samples.

SFAPs, incomplete combustion products of high-temperature fossil-fuel burning emitted to the environment with flue-gases, are successfully used for dating sediments of post-industrial era (Renberg and Wik, 1985; Rose, 2002). The method has been well-established for Estonia since the beginning of the 20th century (Alliksaar, 2000). Heinsalu et al. (2007) show that the SFAP analysis determined ages are in good correlation with the ^{210}Pb based ages. To count SFAP in sediments the subsamples were subject to sequential pre-treatment with 30% H_2O_2 and 2,7M HCl to remove organic and carbonate matter. The SFAP were counted under the light microscope at 250x magnification together with added Lycopodium spores to calculate SFAP concentration in sediments. The SFAP analysis derived ages were used for the upper 50 cm part of the sediment. The lower part of the sediment was dated by the radiocarbon method.

All ages used in this study are given as median calibrated kiloannum before 1950 CE (ka cal BP). The zonation of all presented proxies follows the formal tripartite subdivision of the Holocene (Walker et al., 2012).

3.3. Lithostratigraphy

To reconstruct changes in sediments organic matter dynamics, organic, carbonate and mineral matter contents of the sediment was determined by loss-on-ignition (LOI) analysis procedure described by Heiri et al. (2001). Measurements were performed on continuous 1 cm thick sediment samples of 1 cm^3 volume. The sediment samples were dried for 24 hours at 105 °C and then burned for 4 hours at 525 °C to determine organic matter (OM) content. The residue was thereafter burned for 2 hours at 950 °C and the weight loss was multiplied by 1.36 to express the amount of carbonaceous matter as carbonate ions (CO_3^{2-}) content (Bengtsson and Enell, 1986). The remaining fraction was deemed as mineral matter.

3.4. Pollen analysis

To reconstruct terrestrial landcover and July air temperatures, pollen analysis was applied. Pollen subsamples of known volume (0.5 cm^3 in the Holocene and 2 cm^3 in the late glacial) and thickness (1 cm) were taken at 5–10 cm intervals. Pollen sample preparation followed a standard acetolysis method (Berglund and Ralska-Jasiewiczowa, 1986) combined with hot HF treatment with 40% and 75% acids to remove inorganic matter (Bennett and Willis, 2001). Lycopodium spores were added to calculate pollen concentration and subsequently the pollen accumulation rate (PAR) (Stockmarr, 1971). At least 500 terrestrial pollen grains were counted at each subsample level, except for the four lowest level samples, where only about 200 grains were observed due to low pollen concentrations. Pollen data were expressed as percentages of the total terrestrial pollen sum. Counts of spores, green algae, charcoal, and other microfossils were calculated as percentages of the total sum of terrestrial pollen.

3.5. Cladocera analysis

To reconstruct lake environmental parameters (trophic state, pH, water depth fluctuations), Cladocera analysis was applied. Sediment subsamples of known volume (1 cm^3) and thickness (1 cm) were taken from the sediment core with an interval of 10-20 cm. Samples for subfossil Cladocera analysis were prepared according to standard procedure (Frey, 1986), heating them for 30 minutes in 10% KOH solution at 85 °C water bath. Afterwards samples were filtered through a sieve with a mesh size of 40 µm and thereafter remains were diluted with 10 ml of water and coloured with Safranin O.

Microscope slides were prepared from 100 µl of the diluted, homogenized subsample and examined under a light microscope at 100x-400x magnification. We examined as many slides as was necessary to find at least 70 subfossil Cladocera individuals and examined one extra slide for each sample to identify any previously undetected species (Kurek et al., 2010). Subfossil Cladocera species were identified based on the key by Szeroczynska and Sarmaja-Korjonen (2007). *Daphnia* spp. and *Ceriodaphnia* spp. remains were dominated by postabdominal claws, from which it can be difficult to distinguish between these two groups. Therefore, they were merged under the *Daphnia* spp. group. *Alona gutatta* and *Coronatella rectangula* were counted as separate species based on the postabdomen findings but merged in group *C. rectangula*/*A. gutatta* if the head shields or shells were found.

3.6. Chironomidae analysis

To reconstruct July air temperatures, ATR and environmental changes (trophy, water level fluctuations), Chironomidae analysis was applied. Chironomidae subsamples of standardized volume (1 cm^3) and thickness (1 cm) were taken at 10 cm intervals. Subsamples were treated according to standard procedures (Brooks et al., 2007). Sediments were water-sieved with a 100-µm mesh size sieve to remove fine particles. In case coarse sediment particles remained, additional deflocculation in the hot KOH (70 ºC) for 10 minutes was applied. After deflocculation the sample was water-washed on the 100-µm mesh size. Further, each sample was transferred into a Petri dish from which Chironomidae head capsules were collected with fine forceps under a stereomicroscope at 25X magnification. The obtained head capsules were air-dried and mounted in Aquatex® mounting medium.

Taxonomic identification was conducted under the light microscope at 100x–400x magnification. The Nakri lake fossil Chironomidae assemblages' collection is stored in Tallinn University of Technology.

Identification of the Chironomidae subfossil head capsules was done by OH (late glacial-early Holocene) and VB (Holocene) with 0.5 ka cal BP (3 samples) of overlap using the same taxonomic approximation according to Brooks et al. (2007) and using identification keys by Klink and Pillot (2003), Andersen et al. (2013) and Larocque-Tobler (2014). All identifications at genus or subfamily taxonomic level (Tanytarsini, *Tanytarsus* spp., *Paratanytarsus* spp., Tanypodinae, Chironomini, Orthocladiinae) were excluded from the Nakri lake dataset to avoid including broad groups of Chironomidae species with different ecological preferences. *Cricotopus intersectus*-type was merged with *Cricotopus laricomalis*-type into one type due to the high chance of misidentification of these morphotypes. Morphotype-level identifications for the genera *Ablabesmyia*, *Einfeldia*, *Zalutschia*, *Eukiefferiella*, and *Dicrotendipes* were combined into their respective genus-level groups to align with the varying identification resolutions used elsewhere.

3.7. Training sets for the climate reconstruction

Pollen-based July mean air temperature reconstruction was done based on the modern pollen-climate analogue dataset described by Seppä and Birks (2001).

Chironomid-based mean July air temperature reconstruction proceeded using two training sets: a region specific Finno-Baltic-Polish (FBP) dataset described in detail in Bakumenko et al. (2024) and a Swiss-Norwegian dataset (Heiri et al., 2011), that has been widely used across Europe for reconstructing late Quaternary July air temperature change (e.g. Oliver Heiri et al., 2014; Lapellegerie et al., 2024). Comparing the performance of the two training sets will help determine whether a local training set improves the accuracy of chironomid-based climate reconstructions.

A novel tentative reconstruction of chironomid-based continentality, expressed as ATR (difference in the mean temperature of the coldest and the warmest months) was performed using FBP training seta. The geographic area of the training set includes clear ATR gradient (18.6–27.1 ºC; Fig. 2) as well as a mean July air temperature one (12.1–19.2 ºC; Fig. 2). Moreover, gradients of these climate variables are distributed in different patterns across the region (Fig. 2). While July air temperature continuously increases from North to South, ATR has the highest values in the central Fennoscandia and decreases towards the seas. This difference in distribution makes it potentially possible to calibrate the TS for mean July temperature and ATR independently and separate signals from these two variables.

Modern climate data for the samples in the FBP chironomid calibration dataset sites was extracted from the ERA5 dataset with hourly temporal and 0.25° x 0.25° spatial resolution (Hersbach et al., 2020), downloaded as July and January months mean temperature in °C from the Copernicus Climate Data Store

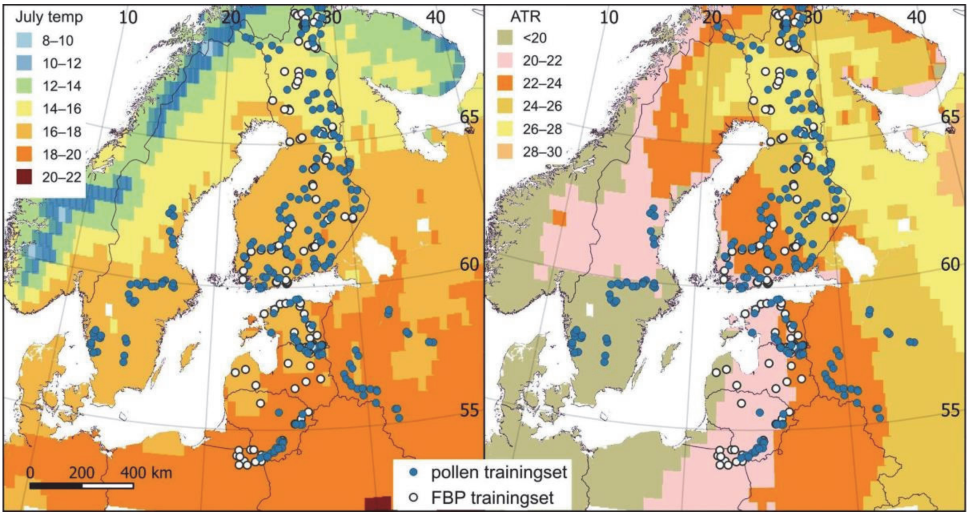


Fig. 2. Location of pollen and Finno-Baltic-Polish (FBP) chironomid training sets. Maps display July mean air temperature (Hersbach et al., 2020) and annual temperature range (ATR).

3.8. Data analysis

Cladocera were grouped based on their habitat preference according to Bledzki and Rybak (2016). Redundancy analysis (RDA; Birks et al., 1997) was used to test the influence of ATR on the Chironomidae assemblages of the FBP training set.

Principal Component Analysis (PCA) was applied to the fossil assemblages of Chironomidae, pollen, and Cladocera to identify potential drivers of assemblages patterns. Pearson correlations were used to examine the relationships between the first two PCA axes of each proxy and with other environmental indicators, including LOI, herbs percentages in the pollen spectra, oxygen isotopes inferred from the Greenland ice sheet (GRIP; Rasmussen et al., 2023) and Cladocera *Bosmina longirostris* as an additional marker of trophic change.

The weighted averaging–partial least squares (WA-PLS) regression and calibration (ter Braak and Juggins, 1993) with bootstrapping (9999 permutations; Birks and Birks, 1998) was used for both pollen and chironomid-based climate reconstructions. The best transfer functions were selected as those producing the lowest cross-validated root mean squared error of prediction (RMSEP). The values of R^2, root mean squared error (RMSE), and both maximum and average bias were used to assess the reliability of the interpolation model. The WA-PLS coefficients for the best performing component of FBP-based reconstruction were used to divide climate dependent Chironomidae taxa, according to Brooks et al. (2007) and Bakumenko et al. (2024), into three groups (typical for cold, moderate, and warm conditions) in respect to the mean July air temperature. The rare taxa deletion (abundance more than 2% at least in one sample) was done for Lake Nakri chironomid assemblages to reduce the influence of random appearances and to increase performance of the WA-PLS (Walker, 2001).

Software program R version 4.1.1. was used to perform numerical analysis and plots. The following packages were used: ‘tidyverse’ for data visualisation (Wickham et al., 2019), ‘dplyr’ for data restructuring and basic calculations (Wickham et al., 2022), ‘vegan’ for ordination (Oksanen et al., 2022). The program C2 (Juggins, 2003) was used to perform pollen- and chironomid-based reconstructions. Stratigraphic diagrams were prepared in Tilia 3.0.1 software.

4. Results

4.1. Litho- and chronostratigraphy

Lake Nakri age-depth model (Fig. 3) is based on 17 radiocarbon dates (Table 1). Radiocarbon date Poz-124700 is considered too old and not used in the age-depth model. Radiocarbon dates Poz-124704 and Poz-124705 from the bulk sediment are not used in the age-depth model as there are nearby dated macro remains which are preferred; however the omitted dates show similar ages with dated macro remains. The ages for the uppermost sediments were corrected according to the SFAP analysis's derived ages, so that 30 cm deth corresponds to 1950±5 CE.

Table 1 - Lake Nakri ^{14}C dates. * marks the outliers not used in the age-depth model.

	Lab code	**^{14}C age**	**Calibrated ages cal yr BP**		**Dated material**
Depth from the sediment surface cm		**yr BP**	**at 95.4%**	**median**	
98-99	Poz-124700*	2625±30	2590–2490	2540	gyttja
188-189	Poz-124701	3420±35	3730–3560	3630	gyttja
498-499	Poz-124703	6370±40	7060–6990	7030	gyttja
591	Poz-34547	6620±35	7670–7530	7570	wood
682-683	Poz-124704*	7440±50	8380–8170	8260	gyttja
685	Poz-29987	7760±50	8640–8440	8550	wood (branch)
751	Poz-29986	8150±50	9240–9010	9110	bark, seeds, catkins
797-798	Poz-124705*	8770±50	10120–9550	9770	gyttja

859	Poz-20611	8870±50	10190–9940	10100	wood, seeds, catkins
931	Poz-20612	9610±60	11020–10680	10810	seeds, catkins
962	Poz-20076	10150±50	11890–11600	11750	wood
1112.5	Poz-22639	10510±60	12610–12470	12540	wood
1152	Poz-20077	10800±40	12830–12710	12750	wood
1187	Poz-20526	11430±70	13470–13240	13360	plant macro
1210	Poz-20528	11660±70	13600–13400	13510	plant macro
1235	Poz-20613	11810±80	13700–13510	13610	Dryas leaves
1320	Poz-20529	12060±70	14080–13790	13950	plant macro

The lowermost part of the sequence (1346–952 cm; 14–11.5 ka cal BP), roughly coinciding with the late glacial, is composed of silt and silty clay with mineral content about 77–91%. There is an increase of organic matter content (up to 7%) in the depth interval 1190–1154 cm (about 13.4–12.8 ka cal BP) (Fig. 3). The Holocene part of the sequence starts with detritius gyttja (952–930 cm; 11.5–10.8 ka cal BP) where organic matter content increases from 8 to 30%, overlain with distinctly laminated gyttja (930–897 cm; 10.8–10.5 ka cal BP). The uppermost part (897–0 cm) of the sediments is homogeneous gyttja with increasing content of organic matter (up to 60%). Carbonate content is fluctuating but does not in general exceed 20% throughout the sediment sequence (Fig. 3).

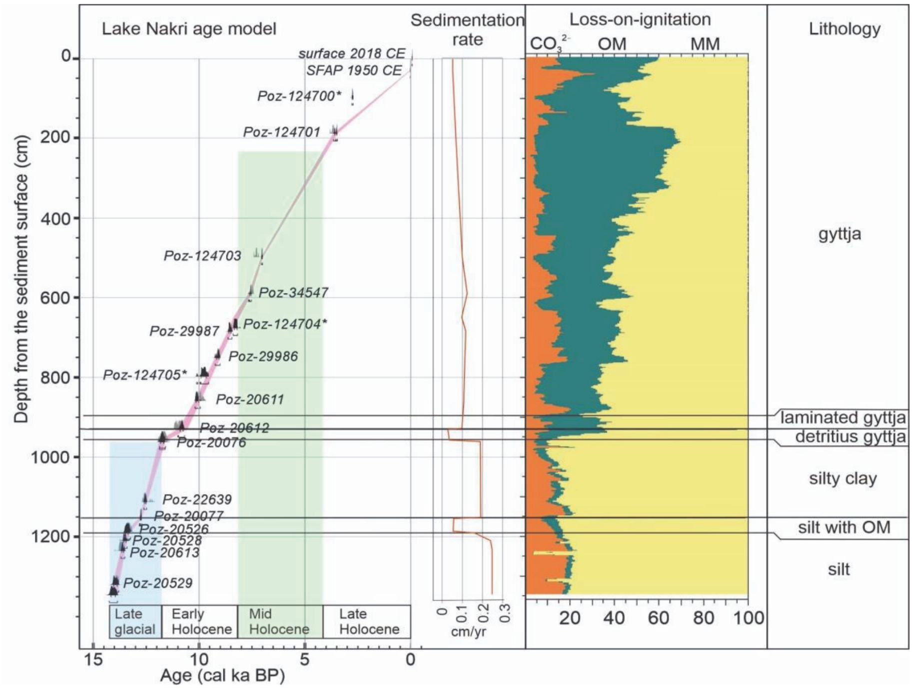


Fig. 3. Lake Nakri age-depth model at 95% probability range (pink curve), sedimentation rate, loss-on-ignition and lithology. The graphs on the age-depth curve show the likelihood (gray) and posterior (black) probability distribution of the calibrated radiocarbon dates. Radiocarbon dates with * are not used in the model.

4.2. Pollen analysis

108 microfossil types were identified in Lake Nakri pollen record (Fig. 4). Late glacial is characterised by high herb pollen values and has considerable input of redeposited temperate broadleaved tree pollen. Between 13.5–12.85 ka cal BP the amount of redeposited pollen is lower, and cold tolerant trees like *Betula* (birch) and *Pinus* (pine) expand. The local presence of both is confirmed by finds of *Pinus* stomata and *Betula* macrofossils from the same sediment interval (Amon et al., 2012).

The tree succession at the beginning of the Early Holocene is typical for the area – first *Betula* and then *Pinus* culminate. The first thermophilous trees *Ulmus* (elm) and *Corylus* (hazel) appear ca. 1000 years later. *Alnus* (alder) expands rapidly all over Estonia around 9.5 ka cal BP. Just before the end of Early Holocene ca 8.5 ka cal BP *Tilia* (lime) expands, and the amount of temperate broadleaved trees rises rapidly just to collapse at the Early Holocene – Middle Holocene boundary around 8.2 ka cal BP. The 8.2 ka cooling event is very clear in

Lake Nakri pollen data: most of the broadleaved trees alongside with *Alnus* and *Corylus* show a clear drop in relative abundances, *Betula* in contrast flourishes.

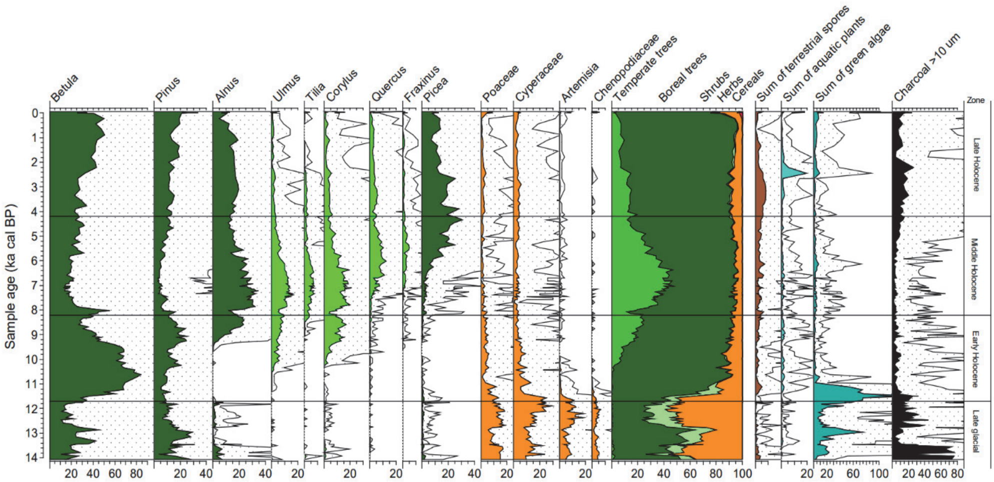


Fig. 4. Subfossil pollen diagram of selected taxa. The relative abundance of taxa is expressed in %. The abundance of charcoal particles is expressed in % of charcoal particles against pollen total sum.

During the Middle Holocene the temperate broadleaved trees maximum (up to ca 45%) is visible around 8–6 ka cal BP, showing the typical succession for Estonia with subsequent culminations of *Ulmus*, *Tilia*, *Quercus* (oak) and *Fraxinus* (ash). *Picea* (spruce) expands during the second half of the Middle Holocene and culminates around 4.2 ka cal BP. Low amount and taxonomic richness of herb pollen indicates dense forest cover. Still, first scattered finds of cultivated plants (*Triticum* (wheat) and *Hordeum* (barley)) accompanied by well-known anthropohores like *Plantago lanceolata* (narrowleaf plantain) and an increase in charcoal appear since 5 ka cal BP.

During the Late Holocene, the vegetation was characterized by mixed boreal forests dominated by *Betula*, *Pinus*, *Alnus*, and *Picea*, with a noticeable decline in temperate broadleaved trees. The weak signs of anthropogenic deforestation in the surroundings of Lake Nakri are observable as a slight increase in herb pollen and its taxonomic diversity since 1 ka cal years BP. Sporadic presence of cultivated plants (*Secale* (rye), *Hordeum*, *Triticum* and *Cannabis* (hemp)) suggests small-scale arable farming in the largely natural vicinity of Lake Nakri.

4.3. Cladocera analysis

In total 49 cladocera species were identified within the core, with *Bosmina longispina* and *Bosmina longirostris* as the main dominant species (Fig. 5).

The late glacial period is characterised by low total cladocera flux, and changing species composition as in almost each sample a new dominant species emerges.

In the Early Holocene *B. longispina* is the dominant species and several new macrophyte associated species appear. In the Middle Holocene between 8 and 6 ka cal BP *Bosmina longirostris* became the dominant species and an increase of Cladocera flux can be observed. About 5.5 ka cal BP *B. longirostris* is replaced by *Daphnia* spp. as the dominant species.

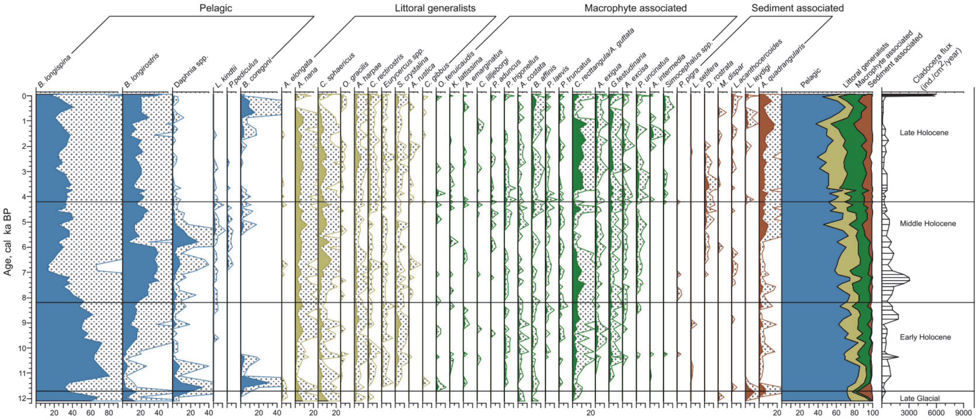


Fig. 5. Subfossil Cladocera diagram of selected taxa. The relative abundance of taxa is expressed in %.

At the end of the Middle Holocene and throughout the Late Holocene *B. longispina* and *B. longirostris* dominate. The relative abundance of sediment associated species increases, but that seems to be mainly connected to the increase of *Alona quadrangularis* relative abundances. We also observed a slight increase in the relative abundances of macrophyte associated species. Within the last millennium there seems to be a time period, where Cladocera flux reduces almost to the late glacial level, and several species for a time disappear, just to re-appear in the uppermost sediment layers. The highest Cladocera flux was observed in the few uppermost sediment samples that correspond with the time period from 1950 CE forward.

While most of the species appear throughout the core, there are some that seem to be present in some periods and missing in others. Most of the littoral species appear for the first time at the beginning of the Holocene. Species that appear during late glacial and beginning of the Early Holocene but then disappear until the end of Middle Holocene are *Bosmina coregoni, Leydigia leydigi* and *Alona intermedia*. *Alonopsis elongata* appears in almost every sample of late glacial and beginning of the Early Holocene but afterwards appears rather sporadically. *Leptodora kindtii, Polyphemus pediculus,* and *Disparalona rostrata* are predominantly found in the Middle Holocene, with their presence also marking the transition periods at the end of the Early Holocene and the beginning of the Late Holocene.

Species that mostly appear in the Middle Holocene and the Late Holocene are *Alona rustica* and *Leydigia acanthocercoides* and the most characteristic taxon for the Late Holocene is *Simocephalus* spp..

4.4. Chironomidae analysis

44 chironomid head capsules were counted per sample on average with the counting range 30–127 (38 samples counts were under 50). 155 chironomid taxa were identified in the Lake Nakri sequence (Fig. 6), from which 94 taxa were left after rare species removal.

The late glacial period is characterised by the dominance of the widely distributed *Microtendipes pedellus*-type, *Tanytarsus mendax*-type and *Chironomus anthracinus* which were assessed as cool-climate related taxa. Cold-related taxa abundant in the late glacial period include *Tanytarsus lugens*-type, *Psectrocladius septentrionalis*-type, *Micropsectra insignilobus*-type and *Heterotrissocladius grimshawi*-type (overall dominant at 13.5–14.5 ka cal BP). Also, not climate dependent *Procladius* and *Psectrocladius sordidellus*-type and *Cricotopus intersectus*-type were presented.

Throughout the Early Holocene period, cool-related *Dicrotendipes nervosus*-type and *Cladopelma lateralis*-type and temperate-related *Chironomus plumosus*-type and *Corynoneura scutellata*-type are present, as well as generalistic *Psectrocladius sordidellus*-type and *Cricotopus intersectus*-type. Cold-related *Tanytarsus lugens*-type appeared only at the start of the zone. temperate-related *Glyptotendipes pallens*-type, *Neozavrelia* and *Endochironomus albipennis*-type dominate since 10 ka cal BP.

In the Middle Holocene period taxa composition is similar to the Early Holocene one, but with increased counts of cool-related *Cladotanytasus mancus*-type and temperate-related *Polypedilum sordens*-type, as well not climate dependent *Lauterborniella* and *Nanocladius* *rectinervis*-type. Also, here cold-related *Sergentia coracina*-type and *Micropsectra insignilobus*-type reappear at low abundances.

The Late Holocene period is marked by peaks of temperate-related *Chironomus plumosus*-type, *Neozavrelia, Tanytarsus pallidicornis*-type and cool-related *Cladopelma lateralis*-type, *Cladotanytarsus mancus*-type. Cool-climate related *Polypedilum nubeculosum*-type becomes overwhelmingly dominant around 0.5 ka cal BP. Cold-related taxa are almost not present in the Late Holocene. Not climate dependent *Psectrocladius sordidellus*-type and *Cricotopus intersectus*-type increased.

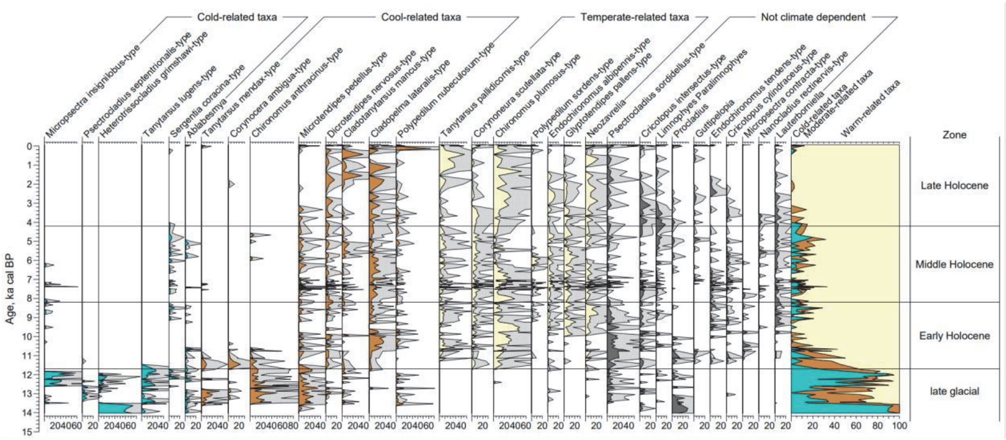


Fig. 6. Subfossil Chironomidae diagram of selected taxa. The relative abundance of taxa is expressed in %. Taxa are sorted by the corresponding WA-PLS coefficients for component 1 of the Finno-Baltic-Polish dataset.

4.5. Climate reconstructions

The chironomid-based July air temperature reconstruction of the Lake Nakri sequence showed similar trends and performance values based on two different training sets (FBP, Swiss-Norwegian, Fig. 9; Table 2), although the FBP-based one revealed the smallest error of reconstruction ($RMSEP_{boot} = 0.7$ °C). Dicrotendipes, Endochironomus, Cladopelma morphotypes were grouped together for Swiss-Norwegian TS-based reconstruction, accounting to following average abundances in the Nakri record: 3.3%, 5.4%, 7.55%. In the FBP training set these taxa are identified to a higher taxonomic resolution (*Dicrotendipes notatus*-type (0.3% in average), *Dicrotendipes nervosus*-type (3%), *Endochironomus albipennis*-type (3.4%), *Endochironomus tendens*-type (1.4%), Endochironomus impar-type (0.6%), Cladopelma lateralis-type (7.5%), Cladopelma laccophila-type (0.05%)).

The pollen-based July air temperature reconstruction of the Lake Nakri sequence shows in general values similar to the chironomid-based reconstruction using the FBP training set.

ATR explained 11 % of variation in the FBP training set based on RDA (p = 0.001; λ1: λ2 = 1; Fig. 7). The chironomid-based ATR reconstruction performed with the Finno-Baltic-Polish training set revealed RMSEP of 1.4 ºC and R^2 of 0.8 (Table 2).

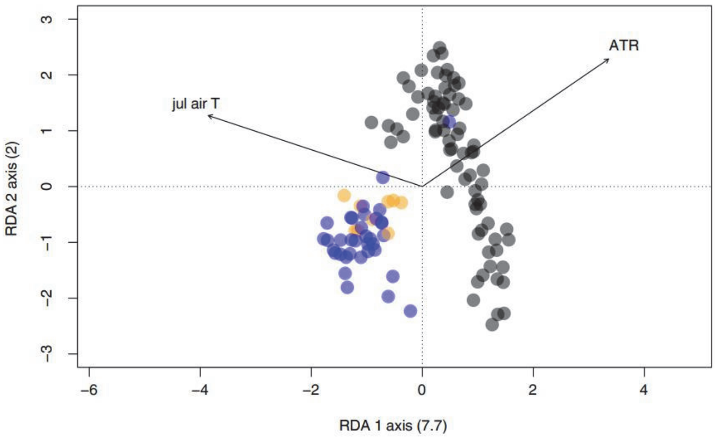


Fig. 7. Redundancy analysis (RDA) of Finno-Baltic-Polish training set using July air temperatures (Jul T; °C) and annual temperature range (ATR; °C). Blue dots indicate lakes from Eastern Baltic (Estonia, Latvia, Lithuania), yellow dots indicate Polish lakes, black dots indicate Finnish lakes.

The PCA1 of both chironomid and pollen assemblages from the Lake Nakri record exhibits significant correlations with each other and with GRIP oxygen isotope data (r >0.8; S1). This suggests that both chironomid and pollen assemblages are primarily influenced by climatic factors.

The PCA2 of chironomid assemblage suggests that chironomid and pollen assemblage are both driven by the same driver. The strongest correlation of chironomid PCA2 (r =0.42; S1) is the herb's proportion in the pollen spectrum, which revealed drastic change in Younger Dryas/Holocene boundary (Fig. 9). The Cladocera PCA1 scores had the strongest correlation with herb cover and organic matter curve (correlation index around 0.6; S1), suggesting that Cladocera communities were significantly influenced by changes in vegetation and nutrient availability.

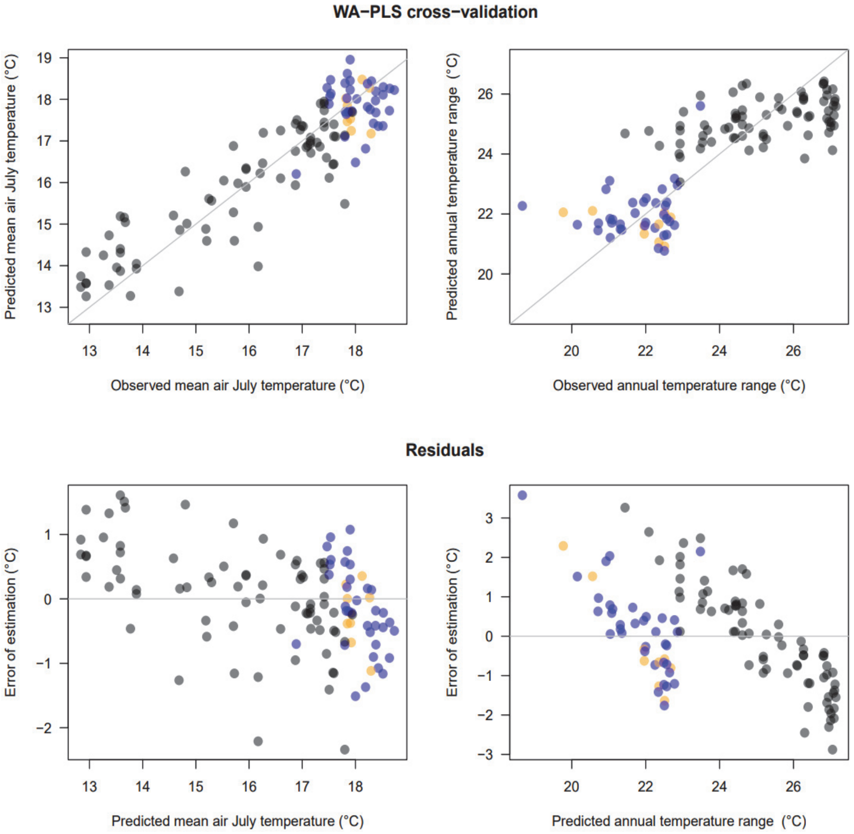


Fig. 8. Diagnostic plots of cross-validated estimates and prediction residuals compared with observed values of the Finno–Baltic–Polish training set calculated with a WA-PLS-based model based on two components using July air temperatures (°C) and annual temperature range (°C). Blue dots indicate lakes from Eastern Baltic (Estonia, Latvia, Lithuania), yellow dots indicate Polish lakes, black dots indicate Finnish lakes.

Table 2. WA-PLS Chironomid- and pollen-based training sets cross-validation and reconstructions outcome.

	Finno-Baltic-Polish training set - July air temperature (Bakumenko et al., 2024)	**Swiss-Norwegian training set - July air temperature (Heiri et al., 2011)**	**Pollen-based reconstruction - July air temperature (Seppä and Birks, 2001)**	**Finno-Baltic-Polish training set - annual temperature range**
Gradient range (°C)	12.1–19.2	3.5–18.4	7.5–17.5	18.6–27.1
% of explanatory power	14.4 (RDA-based)	5.6 (CCA-based)	11.4 (RDA-based)	11.0 (RDA.based)
$RMSEP_{boot}$ (°C)	0.7	1.5	0.7	1.4
RMSE (°C)	0.6	1.3	0.6	0.8
$R2_{boot}$	0.9	0.9	0.8	0.8
Average $Bias_{boot}$ (°C)	0.02	–0.03	–0.03	0.04
Maximum $Bias_{boot}$ (°C)	0.7	1	2.9	3.1

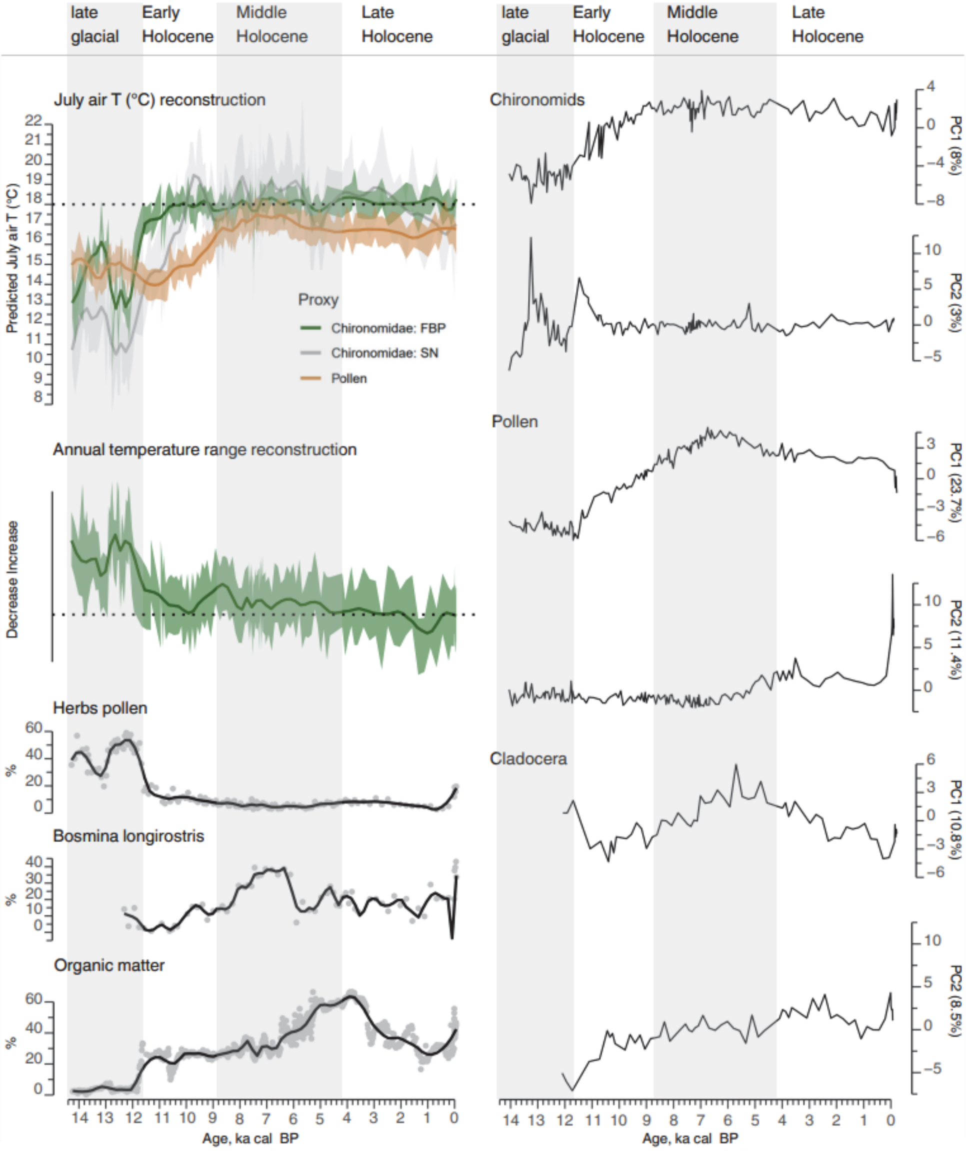


Fig. 9. Chironomid-based July air temperature (ºC) and annual temperature range (ºC) reconstructions from Lake Nakri together with the percentages of herb pollen (indicator of vegetation openness), *Bosmina longirostris* and organic matter (indicators of trophic changes) and PCAs of the Chironomids, Cladoceran and pollen Lake Nakri subfossil assemblages. The horisontal grey dotted line indicates modern values of July air temperature and annual temperature range.

5. Discussion

5.1. Lake environment and climate reconstruction validation

5.1.1. Trophic state

Lake trophic state can influence chironomid-based temperature reconstructions, with more eutrophic lakes being reconstructed as warmer in comparison to oligotrophic lakes (Heiri et al., 2003; Heiri et al., 2014; Tóth et al., 2015). Chironomid taxa that indicate oligotrophic conditions are typically cold-water species, while those associated with eutrophic environments tend to prefer warmer waters, reflecting a positive co-tolerance to both eutrophication and climate change. The research from contemporary lake ecosystems and mesocosm experiments have shown that the zooplankton and phytoplankton communities have a similar reaction to warming as it is to nutrient enrichment (Visconti et al., 2008; Jeppesen et al., 2009; Moss, 2011). This can lead to difficulties distinguishing between the influence of climate and nutrient availability for aquatic organisms in palaeolimnology. At the same time lake trophic state is expected to change with temperature, as changing climate can affect weathering, nutrient mobilization and primary productivity in lakes (Brodersen and Quinlan, 2006; Velle et al., 2010; Eggermont and Heiri, 2012). Therefore, to some extent, shifts in trophic status can be expected during climate changes. In this case trophic state changes would not bias the Chironomidae based climate reconstructions. However, variations in trophic state and productivity unrelated to temperature (e.g., from human activity) may introduce errors and distort chironomid-derived temperature records.

5.1.2. Proxy choice for climate reconstructions

The performance statistics of the pollen-based transfer function applied to the Nakri record are comparable to those of the chironomid-based reconstructions (Table 2). Climate is usually one of primary drivers of terrestrial vegetation composition is importance of climate for Nakri dataset, was confirmed by the significant correlation of PCA1 of pollen, and chironomids with GRIP ice core oxygen isotopes data (Rasmussen et al., 2023; S1). However, the pollen-based reconstruction suggests warmer temperatures during the late glacial, an absence of major cooling during the Younger Dryas and a significant delay in Early Holocene warming compared to the chironomid-based reconstructions (Fig. 9). The latter can be explained by the migration delays of the terrestrial vegetation during the late glacial and Early Holocene which can influence the quality of the pollen-based reconstructions, especially in formerly glaciated areas of northern and eastern Europe (Rao et al., 2022; Väliranta et al., 2015; Zani et al., 2023). The Younger Dryas vegetation on the other hand may lack suitable modern analogues in contemporary ecosystems (Magny et al., 2001), due to the dry and high continental climate, potentially explaining the warmer temperatures reconstructed from pollen records in the region (Fig. 9).

5.1.3. Chironomid training set choice

WA-PLS based Chironomid-based July air temperature transfer functions using the FBP and Swiss-Norwegian training sets had similar cross-validated performance statistics, such as RMSEP, maximum bias and average bias (Table 2). Additionally, both temperature reconstructions generally reflected similar climate patterns (Fig. 9) and resemble the temperature development of the GRIP ice core (Rasmussen et al., 2023; Fig. 10). However, the Swiss-Norwegian-based reconstruction indicated colder values during the late glacial and Early Holocene along with more pronounced temperature fluctuations during 9.0-8.0, 7.0-7.5, 6.5-5.5 ka cal BP compared to the FBP-based reconstruction. The causes of differences in reconstructions using different training sets have been previously discussed in the literature (Luoto, 2011; Engels et al., 2014; Kotrys et al., 2020; Bakumenko et al., 2024). These can be attributed to two primary reasons: (1) systematic differences in the estimated values between geographically distinct training sets (Engels et al., 2014; Bakumenko et al., 2024) and (2) mismatches in Chironomidae taxonomic resolution (Heiri and Lotter, 2010). In the Swiss-Norwegian training set, morphotypes optima tend to be lower than those in the FBP-based training set due to the presence of cooler modern analogues (Bakumenko et al., 2024). In the Swiss-Norwegian training set, certain genera are grouped at a broader taxonomic level, whereas in the FBP training set, these taxa are identified with higher taxonomic resolution. Improving taxonomic resolution can enhance the performance and sensitivity of transfer functions by capturing more ecological details, but also carry a risk of reduced training set reliability if misidentifications occur (Heiri and Lotter, 2010). In this study, we minimized such risks by consistently using established identification keys for modern Chironomidae and rigorously comparing them with fossil specimens from Lake Nakri (see Methods). We suggest that for Nakri the FBP-based training set and transfer function may provide more realistic results, as it encompasses the distribution patterns of the modern Chironomidae taxa from the Baltic lowlands area. However, the general agreement between the two chironomid-based reconstructions based on different calibration data supports that the July air temperature records presented here have successfully captured the major patterns of late glacial and Holocene summer temperature change in the region.

Our tentative reconstruction of ATR based on the FBP calibration dataset features a cross-validated RMSEP of 1.4, which, compared to the ATR range in the dataset (18.6–27.7 ºC) is relatively small. Although the distributions of Chironomidae taxa and assemblages have been observed to correspond to continentality changes (Self et al., 2011) a fully functional training set for the Baltic area has not been developed yet, and the approach has not been tested in downcore reconstructions or on surface sediments from other regions. It has to be kept in mind that chironomid-based continentality reconstructions can be biased by numerous collinear climatic and environmental factors, including July air temperatures (Self et al., 2011) and should be treated with caution. Therefore, we have presented the results of the ATR reconstruction as a change in trend rather than absolute values.

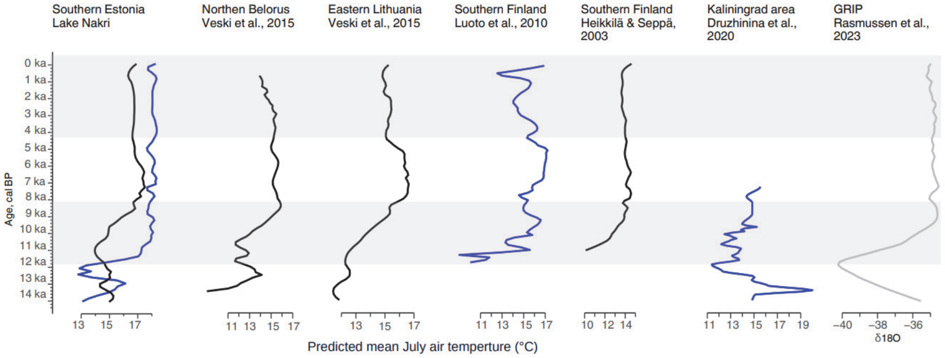


Fig. 10. Lake Nakri Chironomid-based temperature reconstruction based on the Baltic-Finish-Polish calibration data and pollen-based temperature reconstruction in comparison with already published climate reconstructions from Northern and Northeastern Europe and Greenland.The gray shading indicates time periods: late glacial (14.5-11.7 ka cal. BP), Early Holocene (11.7 − 8.2 ka cal. BP), Middle Holocene (8.2 − 4.2 ka cal. BP), Early Holocene (4.2 − 0 ka cal. BP). Black lines indicate pollen-based reconstructions, black lines indicate chironomid-based reconstructions, gray line indicates δ18O-based reconstruction.

5.2. Lake Nakri palaeoclimate and palaeoenvironment history

5.2.1. Late glacial (14.5–11.7 ka cal BP)

Deglaciation of Estonia took place around 14.7−12.7 ka cal BP (Kalm et al., 2011; Lasberg and Kalm, 2013; Amon et al., 2016; Hughes et al., 2016). The oldest ^{14}C radiocarbon date in the Nakri record is dated to 14.0–13.8 ka cal BP, and the oldest sediments estimated to an age of 14.5 ka cal BP. This represents an extraordinary sedimentary archive, directly capturing conditions during the ice retreat from the region and providing a valuable window into deglaciation dynamics. Based on previous pollen-based studies, late glacial climate and environment in Eastern Baltic revealed two distinct events: the Bölling/Alleröd warming followed by the Younger Dryas cooling (Seppä and Poska, 2004; Laumets et al., 2014). Immigration of plant and animal taxa followed shortly after the ice retreat and the late glacial open tundra biome was dominated by herbs and cold-tolerant shrub species (Amon et al., 2016; Poska et al., 2022). Modern chironomids are known to be sensitive to the presence or absence of vegetation (Ólafsson et al., 2002). This, combined with the significant correlation between PCA2 of the Lake Nakri fossil chironomid assemblages and the percentage of herb pollen (S1), highlights the drastic ecological shifts which occured in the region during the late glacial period.

During the late glacial period the ecosystem of Lake Nakri was characterised by the presence of green algae with a peak 13 ka cal. BP. Green algae are an important group of primary producers in lakes, and although other algae groups are not represented in pollen slides, the high abundance of green algae suggests increased productivity in the lake. This event coincides with temporal extirpation of oligotrophic and cold-related chironomids *Heterotrissocladius grimshawi*-type, *Tanytarsus lugens*-type and *Micropsectra insignilobus*-type and appearance of eutrophic aquatic vegetation-related chironomids *Cricotopus cylindraceus*-type (single appearance in the late glacial) and *Polypedilum nubeculosum*-type (sporadic in late glacial). The trophic increase appears linked to the Bølling-Allerød event, consistent with chironomid records indicating warmer July air temperatures and lower ATR.

Previously, the Younger Dryas was mainly characterised by the cold winters and the summer temperature were supposed to be relatively similar to the modern one (Borisova, 1997; Davis et al., 2003). Theuerkauf and Joosten (2012) pointed out the uncertainty whether Younger Dryas winters were cold and climate was continental or not. Our data supports the hypothesis that the Younger Dryas cooling also affected summer temperatures (Lotter et al., 2000), and is similar to many chironomid-based summer temperature reconstructions across Europe (Heiri et al., 2014). Besides cold summers, our results suggest that the Younger Dryas period was also characterized by an increase in ATR (Fig. 9) which aligns with reconstructed increase in seasonality based on cryogenic cave carbonates from Great Britain (Töchterle et al., 2024), as well as with model-based reconstructions of Younger Dryas climate (e.g. Renssen et al., 2001). It was also hypothesized that the establishment of tundra biomes, indicated in the Younger Dryas from Lake Nakri sediments, was encouraged by an increase in continentality (Sher et al., 2003; Kienast et al., 2008). The Younger Dryas summer cooling resulted in an increase of cold- and oligotrophic- conditions related to chironomids taxa (*Micropsectra insignilobus*-type, *Tanytarsus lugens*-type).

5.2.2. Early Holocene (11.7–8.2 ka cal BP)

At the start of the Early Holocene, Characeae disappeared from Lake Nakri (Amon et al., 2012), and green algae abundance reached its highest peak around 11.5 ka cal BP (Fig. 4). Such a regime shift does not necessarily mean increase in nutrients (Scheffer and Van Nes, 2007). Considering the chironomid-inferred rapid warming from 13 up to 18 ºC (Fig. 9) and the connection between climate and productivity (Jeppesen et al., 2009) it is possible that the algae dominated state is a result of temperature increase. At the same time, we observed new macrophyte associated chironomids morphotypes (*Cricotopus cylindraceus*-type, *Lauterborniella*; Fig. 6). While Characeae that were present during the late glacial period (Amon et al., 2012) can easily grow on mineral matter rich sediments (Holzhausen, 2024), this is not the case for many other macrophyte species. Around 11 cal ka BP we observed an increase in organic matter from approximately less than 7% to more than 20% (Fig. 9) and an abrupt decrease in green algae (Fig. 4). When considering these results together with presence of macrophyte associated with Cladocera and Chironomidae taxa (Figs. 5 and 6), it suggests that around this time a new macrophyte dominated lake stage was established. However, it is unlikely that during this time the lake was highly eutrophic, as Cladocera *Bosmina longispina* - a species associated with mesotrophic lakes (Jensen et al., 2013; Lanka et al., 2024) dominates (Fig. 5). Chironomids *Chironomus plumosus*-type, *Procladius*, *Psectrocladius sordidellus*-type are common in the sediments from 11.8 ka cal BP onwards are usually considered indicators for low oxygen concentrations in bottom waters (Brooks et al., 2007) and often occur in eutrophic lakes.

Warmer and more stable climate conditions of Early Holocene led to the replacement of tundra biomes with boreal forests, as evidenced by the Lake Nakri pollen record and similar findings from other parts of the Eastern Baltics (Amon et al., 2016; Poska et al., 2022). Later, ca 8.5 ka cal BP the boreal forests were gradually replaced by temperate broad-leaved ones (Saarse and Veski, 2001; Niinemets and Saarse, 2009; Poska et al., 2022) with a distinct effect of 8.2 ka cold event apparent in the vegetation records (Seppä and Poska, 2004; Niinemets and Saarse, 2009; Seppä et al., 2009; Veski et al., 2015). The cold event is also visible in the chironomid-based reconstruction as a cooling of approximately 1 ºC, reappearance of cold-related oligotrophic taxa (*Micropsectra insignilobus*-type, *Sergentia coracina*-type) and decline in warm-related eutrophic ones (*Chironomus plumosus*-type, *Neozavrelia*) around 9.0–8.5 ka cal BP. In the Cladocera assemblages this event is associated with general reduction in Cladocera flux since 9.0 ka cal BP. Decrease in Cladocera abundance (represented by Cladcoera flux) can be related to cooling or oligotrophication (Manca et al., 2007; Zawiska et al., 2017). However, in the case of the 8.2 event in Lake Nakri, this change is most likely climate driven, as no changes in Cladocera assemblages that would be indicative of oligotrophication, can be observed (Fig. 5). The pollen-based reconstructions (Heikkilä and Seppä, 2003; Veski et al., 2015) mainly indicate short cooling event around 8.2 ka cal BP and indicate quick recovery of the ecosystem thereafter. However, chironomid-based reconstruction from South Finland and Central Poland support the hypothesis that in our region the 8.2 ka event may have been embedded into a longer summer cooling episode starting at 9.0 ka cal BP (Luoto et al., 2010; Płóciennik et al., 2011). Based on globally distributed multi-proxy data, Mayewski et al. (2004) interprets the interval 9.0–8.0 ka cal BP as a partial return toward more glacial conditions following an orbitally driven delay in Northern Hemisphere deglaciation.

Summarized by (Davis et al., 2003), pollen-based reconstructions from Northern and Eastern Europe suggest that cooling 9.0–8.0 ka cal BP was more pronounced during the winter than during summer. Our data indicated an increase of ATR between 9.0 and 8.0 ka cal BP, which aligns with these findings. A reconstruction based on phosphorus concentrations in stalagmite calcite from western Ireland suggests also an increased temperature seasonality during the 8.2 ka cal BP event (Baldini et al., 2002). Additionally, evidence points to heightened seasonality of precipitation and severe arid events between 9 and 8 ka cal BP across the Northern Hemisphere (Shuman, 2012; Andersen et al., 2017). These events may have been triggered by the weakening of the meridional overturning circulation due to reduced Atlantic meridional overturning circulation, decline in summer insolation and cooling influence of volcanic aerosols (Mayewski et al., 2004; Carlson et al., 2008).

5.2.3. Middle Holocene (8.2–4.2 ka cal BP)

The Middle Holocene is characterized by a generally warm and stable climate, corresponding to the Holocene Thermal Maximum, during which, based on pollen data, temperate broadleaved trees became abundant in the Eastern Baltic area.

At the same time we can observe an increase in productivity in Lake Nakri. Whether this is solely due to rising temperatures, or a combination of warming and nutrient enrichment remains uncertain. In the Cladocera record this period is marked by the increase in relative abundance of *Bosmina longirostris* (8.2–5.8 ka cal BP) and increase in Cladocera influx (8.2–7 ka cal BP). While the first is a well-established indicator for eutrophic conditions (Chen et al., 2010; Adamczuk, 2016), the latter is considered to be representative of either warming or eutrophication (Manca et al., 2007; Zawiska et al., 2017). This phase aligns with a period of warmest temperatures in the pollen- and chironomid- based temperature reconstructions. Rising surface water temperatures can enhance water column stratification, potentially leading to hypolimnetic oxygen depletion (Nickus et al., 2010). Such conditions can facilitate phosphorus release from sediments (Hupfer and Lewandowski, 2008), which may be the case for Lake Nakri, as indicated by the disappearance of the oxygen-sensitive Chironomidae morphotype *Micropsectra contracta*-type (Fig. 6; Brooks et al., 2007). Therefore, during the Holocene thermal maximum, both temperature and nutrient enrichment could have contributed to the increase in productivity.

Short summer cooling events of approximately 0.5–1°C together with the slight ATR oscillations occurred in our chironomid-based temperature reconstruction around 7.0–7.5 ka and 6.5–5.5 ka cal BP (Fig. 9). A cooling around 7–7.5 ka cal BP was also observed in a chironomid record from Southern Finland (Fig. 6; Luoto et al., 2010), however, no pollen based reconstruction indicates this event. Even though pollen-based reconstructions from eastern Baltic did not reveal any climate changes in this period, pollen-based reconstruction from Sweden indicated winter cooling and increase in continentality 7 ka cal BP (Seppä et al., 2005).

The 6.5-5.5 chironomid-inferred cooling trend aligns with an increase in Cladocera *Daphnia* spp. abundancy, which is considered indicative of cooler climate (Nevalainen et al., 2014). A peak in this taxon occurs in Lake Nakri 5.8–5.2 ka cal BP together with decline in *Bosmina longirostris*. This point towards decrease of productivity, which was probably caused by climate. The 6.5–5.5 ka cal cold spell BP has also been observed in pollen-based records from Northern Belarus and Eastern Latvia, as well as in the chironomid-based reconstruction from Southern Finland (Fig. 10; Luoto et al., 2010; Veski et al., 2015). Also, cooling periods with similar age have been reported from the North Atlantic and central Europe (O'Brien et al., 1995; Oppo et al., 2003; Moros et al., 2004; Vollweiler et al., 2006). The average 5.5 ka cal BP summer cooling across North America and Europe was estimated to be at least 0.5°C (Marsicek et al., 2018). The identified possible cause of the described cooling event is a decrease in solar activity, primarily summer insolation, driven by changes in orbital forcing (Mayewski et al., 2004; Shuman, 2012). This reduction led to lower mid-latitude temperatures, glacier advances, a rise in the treeline limit in Scandinavia (Liu et al., 2000; Clement et al., 2000; Braconnot et al., 2004; Mayewski et al., 2004; Liu et al., 2007). Therefore, this event can be described as a complex response to peak rates of insolation change, involving feedback interactions among multiple components (Shuman, 2012).

5.2.4. Late Holocene (4.2–0 ka cal BP)

After 4.2 ka cal BP the development of southern mixed boreal forests where late successional temperate taxa are replaced by early successional ones happened in Eastern Baltic (Niinemets and Saarse, 2009; Poska et al., 2022). This coincides with stable chironomid-inferred July air temperatures around 18°C. The relatable stable Cladocera species composition throughout the Late Holocene suggests that by the end of the Middle Holocene, Lake Nakri had reached conditions similar to those observed today. This also aligns with our knowledge that the area has experienced modest, compared to average in Estonia, anthropogenic impact.

Despite the generally stable conditions, some minor climate events were observed in the Late Holocene: 0.5°C July air temperature increase approximately 1–0.5 ka cal BP, followed by a subsequent drop. This period corresponds to the Medieval Warm Period and following cooling can be associated with the Little Ice Age (Diaz et al., 2011; Płóciennik et al., 2011). Similar amplitude changes connected with the Medieval Warm Period and Little Ice Age have been observed from the pollen records in Eastern Latvia and Southern Finland (Heikkilä and Seppä, 2003; Luoto et al., 2010; Veski et al., 2015). The Medieval Warm Period revealed almost no ATR fluctuations (Fig. 9). The data from Southern Finland reports it as a dry and warm period in the Baltic area (Seppä et al., 2009).

The Little Ice Age was indicated by a cooling pattern together with ATR decrease. Also, possible decrease of productivity might have occurred during the Little Ice Age, where several littoral species disappeared, and Cladocera influx was reduced to values similar to the late glacial period (Fig. 5). The chironomid-based reconstruction from Southern Finland (Fig. 7; Luoto et al., 2010) shows more pronounced cooling than observed in Lake Nakri record, which can possibly be attributed to its more northern location. The ATR decrease which aligns with study of Jones et al. (2014), revealing that this event is characterized predominantly by snowy winters with periodic episodes of cool and humid summers. Together, these conditions contributed to a positive glacier mass balance and the advance of glaciers across the Northern Hemisphere (Steiner et al., 2008; Solomina et al., 2015). Several factors may have contributed to this cooling, including a decrease in solar insolation in northern hemisphere (Wanner et al., 2008) and the atmospheric effects of frequent volcanic eruptions, which often led to cool, humid summers due to increased dust and aerosols (Büntgen et al., 2016; Owens et al., 2017; Strandberg et al., 2023). Additional contributing factors include due to anthropogenic deforestation increased surface albedo (Owens et al., 2017), as well as sea-ice export from the Arctic Ocean (Miles et al., 2020).

6. Conclusions

This study presents a high-resolution, multi-proxy reconstruction of postglacial climate and environmental dynamics from Lake Nakri. The site is situated in the transitional from continental to maritime climate Eastern Baltic region and represents the record of the past 14.5 ka cal BP - from the last deglaciation until modern days. The multi-proxy approach, applied to lake Nakri records included Chironomidae, Cladocera, pollen, and LOI analyses, which made it possible to estimate both climate and environmental changes of the site.

Chironomid- and pollen-based climate reconstructions generally infer the same July air temperature trends. However, pollen-based reconstruction revealed evident lag likely related to postglacial migration dynamics and the absence of modern analogues for late glacial climates. The trophic changes, estimated from Cladocera assemblages, are assessed as relatively minor and not expected to influence the chironomid-based reconstructions drastically.

The chironomid-based July temperature reconstructions, developed using two independent training sets, revealed generally similar patterns. However, the usage of the local training set showed its advantages exhibiting lower error of July air temperature estimation. The chironomid-inferred ATR trends aligned well with published literature and vegetation changes, observed in lake Nakri. Thus, the usage of chironomids as a continentality proxy can be justified.

The chironomid-inferred reconstruction captures major and minor climate events, some of which have already been observed in the literature. The Bølling-Allerød was characterised by increased lake productivity, likely driven by warming. During the Younger Dryas, chironomid assemblages suggest colder summers and increased ATR, accompanied by a cold-adapted, oligotrophic cladocera and chironomid taxa and the development of tundra vegetation. On the Holocene boundary the major climate warming event was observed, which resulted in forest expansion, with boreal forests later replaced by temperate ones. The 8.2 ka cold event, expressed in a ~1°C July air temperature decrease and ATR increase, was suggested to be a part of a broader 9.0–8.0 ka cal BP cooling episode. The Middle Holocene climate, which incorporates Holocene Thermal Maximum, was characterised by warm and stable climate and the spread of temperate broadleaved forests in the Eastern Baltic. Also, some minor cooling events were indicated by chironomid-inferred reconstructions at ~7.0–7.5 and 6.5–5.5 ka cal BP. The Late Holocene was characterised by warm July air temperatures and development of southern mixed boreal forests in the Eastern Baltic. The Medieval Warm Period was reflected as a July air temperature increase of approximately 0.5 °C with almost no ATR changes. It was followed by the Little Ice Age, which was marked by cooling, decreased ATR. After it, the reconstructed values were close to the modern ones.

The new findings contribute to a broader understanding of how ecosystems of the Eastern Baltic region have responded to past climate forcing and provide a valuable context for anticipating future environmental trajectories under ongoing climate change.

CRediT authorship contribution statement

Varvara Bakumenko: conceptualisation; data curation; investigation; formal analysis; software; visualisation; writing – original draft; writing – review & editing. **Anna Lanka**: conceptualisation; data curation; investigation; formal analysis; software; visualisation; writing – review & editing. **Anneli Poska:** supervision; conceptualisation; data curation; validation; writing – review & editing. **Jüri Vassiljev**: investigation; conceptualisation; formal analysis; software; writing – review & editing. **Oliver Heiri**: investigation; supervision; writing – review & editing. **Tiiu Alliksaar**: investigation; formal analysis; software; writing – review & editing. **Simon Belle**: supervision; conceptualisation; writing –

review & editing. **Siim Veski**: supervision; investigation; conceptualisation; writing – review & editing; funding acquisition; resources.

Acknowledgments

This study was financially supported by the Estonian Research Council grants PRG1993 and TK215. Varvara Bakumenko and Anna Lanka was supported by the Doctoral School of Earth Sciences and Ecology, supported by the European Union, European Regional Development Fund (ASTRA "TTÜ arenguprogramm aastateks 2016–2022"). Anneli Poska was supported by Swedish strategic research area BECC (Biodiversity and Ecosystem Services in a Changing Climate); MERGE (ModElling the Regional and Global Earth system at Lund University).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References

Adamczuk, M., 2016. Past, present, and future roles of small cladoceran Bosmina Adamczuk, M., 2016. Past, present, and future roles of small cladoceran Bosmina longirostris (O. F. Müller, 1785) in aquatic ecosystems. Hydrobiologia 767, 1–11. https://doi.org/10.1007/s10750-015-2495-7

Alliksaar, T., 2000. Application of spherical fly-ash particles to study spatial deposition of atmospheric pollutants in north-eastern Estonia. Oil Shale 4, 335–50.

Amon, D.J., Ziegler, A.F., Dahlgren, T.G., Glover, A.G., Goineau, A., Gooday, A.J., Wiklund, H., Smith, C.R., 2016. Insights into the abundance and diversity of abyssal megafauna in a polymetallic-nodule region in the eastern Clarion-Clipperton Zone. Sci Rep 6, 30492. https://doi.org/10.1038/srep30492

Amon, L., Veski, S., Heinsalu, A., Saarse, L., 2012. Timing of Lateglacial vegetation dynamics and respective palaeoenvironmental conditions in southern Estonia: evidence from the sediment record of Lake Nakri. J Quaternary Science 27, 169–180. https://doi.org/10.1002/jqs.1530

Amon, L., Veski, S., Vassiljev, J., 2014. Tree taxa immigration to the eastern Baltic region, southeastern sector of Scandinavian glaciation during the Late-glacial period (14,500–11,700 cal. b.p.). Veget Hist Archaeobot 23, 207–216. https://doi.org/10.1007/s00334-014-0442-6

Andersen, N., Lauterbach, S., Erlenkeuser, H., Danielopol, D.L., Namiotko, T., Hüls, M., Belmecheri, S., Dulski, P., Nantke, C., Meyer, H., Chapligin, B., Von Grafenstein, U., Brauer, A., 2017. Evidence for higher-than-average air temperatures after the 8.2 ka event provided by a Central European δ18O record. Quaternary Science Reviews 172, 96–108. https://doi.org/10.1016/j.quascirev.2017.08.001

Andersen, T., Sæther, O., Cranston, P., Epler, J., 2013. The larvae of Orthocladiinae (Diptera: Chironomidae) of the Holarctic region–Keys and diagnoses. Insect Systematics & Evolution.

Bakumenko, V., Poska, A., Płóciennik, M., Gasteviciene, N., Kotrys, B., Luoto, T., Belle, S., Veski, S., 2024. Chironomidae-based inference model for mean July air temperature reconstructions in the eastern Baltic area 53, 401–414. https://doi.org/10.1111/bor.12655

Baldini, J.U.L., McDermott, F., Fairchild, I.J., 2002. Structure of the 8200-Year Cold Event Revealed by a Speleothem Trace Element Record. Science 296, 2203–2206. https://doi.org/10.1126/science.1071776

Bengtsson, L., Enell, M., 1986. Chemical analysis, in: Handbook of Holocene Palaeoecology and Palaeohydrology. John Wiley & Sons Ltd, Chichester, Berglund B.E.(ed.), pp. 423–451.

Bennett, K.D., Willis, K.J., 2001. Pollen, in: Smol, J.P., Birks, H.J.B., Last, W.M., Bradley, R.S., Alverson, K. (Eds.), Tracking Environmental Change Using Lake Sediments: Terrestrial, Algal, and Siliceous Indicators. Springer Netherlands, Dordrecht, pp. 5–32. https://doi.org/10.1007/0-306-47668-1_2

Berglund, E., Ralska-Jasiewiczowa, M., 1986. , in: Handbook of Holocene Palaeoecology and Palaeohydrology. Wiley-Interscience, Chichester.

Birks, H. j. b., Braak, C. j. f. T., Line, J.M., Juggins, S., Stevenson, A.C., Battarbee, R.W., Mason, B.J., Renberg, I., Talling, J.F., 1997. Diatoms and pH reconstruction. Philosophical Transactions of the Royal Society of London. B, Biological Sciences 327, 263–278. https://doi.org/10.1098/rstb.1990.0062

Birks, H.J.B., Birks, H.J.B., 1998. D.G. Frey and E.S. Deevey Review 1: Numerical tools in palaeolimnology – Progress, potentialities, and problems. Journal of Paleolimnology 20, 307–332. https://doi.org/10.1023/A:1008038808690

Bledzki, L.A., Rybak, J.I., 2016. Freshwater Crustacean Zooplankton of Europe: Cladocera & Copepoda (Calanoida, Cyclopoida) Key to species identification, with notes on ecology, distribution, methods and introduction to data analysis. Springer International Publishing, Cham. https://doi.org/10.1007/978-3-319-29871-9

Borisova, O.K., 1997. Younger Dryas landscape and climate in Northern Eurasia and North America. Quaternary International 41–42, 103–109. https://doi.org/10.1016/S1040-6182(96)00041-9

Braconnot, P., Harrison, S.P., Joussaume, S., Hewitt, C.D., Kitoch, A., Kutzbach, J.E., Liu, Z., Otto-Bliesner, B., Syktus, J., Weber, S.L., 2004. Evaluation of PMIP coupled ocean-atmosphere simulations of the Mid-Holocene, in: Battarbee, R.W., Gasse, F., Stickley, C.E. (Eds.), Past Climate Variability through Europe and Africa, Developments in Paleoenvironmental Research. Springer Netherlands, Dordrecht, pp. 515–533. https://doi.org/10.1007/978-1-4020-2121-3_24

Brodersen, K.P., Quinlan, R., 2006. Midges as palaeoindicators of lake productivity, eutrophication and hypolimnetic oxygen. Quaternary Science Reviews, Quaternary beetle research: the state of the art 25, 1995–2012. https://doi.org/10.1016/j.quascirev.2005.03.020

Bronk Ramsey, C., 2009. Bayesian Analysis of Radiocarbon Dates. Radiocarbon 51, 337–360. https://doi.org/10.1017/S0033822200033865

Brooks, S.J., Bennion, H., Birks, H.J.B., 2001. Tracing lake trophic history with a chironomid–total phosphorus inference model. Freshwater Biology 46, 513–533. https://doi.org/10.1046/j.1365-2427.2001.00684.x

Brooks, S.J., Langdon, P.G., Heiri, O., 2007. The identification and use of Palaearctic Chironomidae larvae in palaeoecology. Quaternary Research Association Technical Guide i-vi,1.

Büntgen, U., Myglan, V.S., Ljungqvist, F.C., McCormick, M., Di Cosmo, N., Sigl, M., Jungclaus, J., Wagner, S., Krusic, P.J., Esper, J., Kaplan, J.O., De Vaan, M.A.C., Luterbacher, J., Wacker, L., Tegel, W., Kirdyanov, A.V., 2016. Cooling and societal change during the Late Antique Little Ice Age from 536 to around 660 AD. Nature Geosci 9, 231–236. https://doi.org/10.1038/ngeo2652

Carlson, A.E., LeGrande, A.N., Oppo, D.W., Came, R.E., Schmidt, G.A., Anslow, F.S., Licciardi, J.M., Obbink, E.A., 2008. Rapid early Holocene deglaciation of the Laurentide ice sheet. Nature Geosci 1, 620–624. https://doi.org/10.1038/ngeo285

Chen, G., Dalton, C., Taylor, D., 2010. Cladocera as indicators of trophic state in Irish lakes. J Paleolimnol 44, 465–481. https://doi.org/10.1007/s10933-010-9428-2

Chevalier, M., Davis, B.A.S., Heiri, O., Seppä, H., Chase, B.M., Gajewski, K., Lacourse, T., Telford, R.J., Finsinger, W., Guiot, J., Kühl, N., Maezumi, S.Y., Tipton, J.R., Carter, V.A., Brussel, T., Phelps, L.N., Dawson, A., Zanon, M., Vallé, F., Nolan, C., Mauri, A., de Vernal, A., Izumi, K., Holmström, L., Marsicek, J., Goring, S., Sommer, P.S., Chaput, M., Kupriyanov, D., 2020. Pollen-based climate reconstruction techniques for late Quaternary studies. Earth-Science Reviews 210, 103384. https://doi.org/10.1016/j.earscirev.2020.103384

Clement, A.C., Seager, R., Cane, M.A., 2000. Suppression of El Niño during the Mid-Holocene by changes in the Earth's orbit. Paleoceanography 15, 731–737. https://doi.org/10.1029/1999PA000466

Davis, B.A.S., Brewer, S., Stevenson, A.C., Guiot, J., 2003. The temperature of Europe during the Holocene reconstructed from pollen data. Quaternary Science Reviews 22, 1701–1716. https://doi.org/10.1016/S0277-3791(03)00173-2

Diaz, H.F., Trigo, R., Hughes, M.K., Mann, M.E., Xoplaki, E., Barriopedro, D., 2011. Spatial and Temporal Characteristics of Climate in Medieval Times Revisited. Bull. Amer. Meteor. Soc. 92, 1487–1500. https://doi.org/10.1175/BAMS-D-10-05003.1

Druzhinina, O., Kublitskiy, Y., Stančikaitė, M., Nazarova, L., Syrykh, L., Gedminienė, L., Uogintas, D., Skipityte, R., Arslanov, K., Vaikutienė, G., Kulkova, M., Subetto, D., 2020. The Late Pleistocene–Early Holocene palaeoenvironmental evolution in the SE Baltic region: a new approach based on chironomid, geochemical and isotopic data from Kamyshovoye Lake, Russia. Boreas 49, 544–561. https://doi.org/10.1111/bor.12438

Edvardsson, J., Corona, C., Mažeika, J., Pukienė, R., Stoffel, M., 2016. Recent advances in long-term climate and moisture reconstructions from the Baltic region: Exploring the potential for a new multi-millennial tree-ring chronology. Quaternary Science Reviews 131, 118–126. https://doi.org/10.1016/j.quascirev.2015.11.005

Eggermont, H., Heiri, O., 2012. The chironomid-temperature relationship: expression in nature and palaeoenvironmental implications. Biological Reviews 87, 430–56. https://doi.org/10.1111/j.1469-185X.2011.00206.x

Engels, S., Self, A., Luoto, T., Brooks, S., Helmens, K., 2014. A comparison of three Eurasian chironomid–climate calibration datasets on a W–E continentality gradient and the implications for quantitative temperature reconstructions. Journal of Paleolimnology 51, 529–47. https://doi.org/10.1007/s10933-014-9772-8

Frey, D., 1986. Cladocera Analysis., in: Berglund, B. E. (Ed.),Handbook of Holocene Palaeoecology and Palaeohydrology. John Wiley & Sons Ltd., pp. 667–692.

Hájková, P., Pařil, P., Petr, L., Chattová, B., Matys Grygar, T., Heiri, O., 2016. A first chironomid-based summer temperature reconstruction (13–5 ka BP) around 49°N in inland Europe compared with local lake development. Quaternary Science Reviews 141, 94–111. https://doi.org/10.1016/j.quascirev.2016.04.001

Hamerlík, L., Dobríková, D., Szarlowicz, K., Reczynski, W., Kubica, B., Šporka, F., Bitušík, P., 2016. Lake biota response to human impact and local climate during the last 200 years: A multi-proxy study of a subalpine lake (Tatra Mountains, W Carpathians). Science of The Total Environment 545–546, 320–328. https://doi.org/10.1016/j.scitotenv.2015.12.049

Heikkilä, M., Seppä, H., 2010. Holocene climate dynamics in Latvia, eastern Baltic region: a pollen-based summer temperature reconstruction and regional comparison. Boreas 39, 705–719. https://doi.org/10.1111/j.1502-3885.2010.00164.x

Heikkilä, M., Seppä, H., 2003. A 11,000   yr palaeotemperature reconstruction from the southern boreal zone in Finland. Quaternary Science Reviews 22, 541–554. https://doi.org/10.1016/S0277-3791(02)00189-0

Heinsalu, A., Alliksaar, T., Leeben, A., Nõges, T., 2007. Sediment diatom assemblages and composition of pore-water dissolved organic matter reflect recent eutrophication history of lake peipsi (Estonia/Russia), in: Gulati, R.D., Lammens, E., De Pauw, N., Van Donk, E. (Eds.), Shallow Lakes in a Changing World. Springer Netherlands, Dordrecht, pp. 133–143. https://doi.org/10.1007/978-1-4020-6399-2_13

Heiri, O, Brooks, S., Renssen, H., Bedforf, A., Hazekamp, M., Ilyashuk, B., Jeffers, E., Lang, B., Kirilova, E., Kuiper, S., Millet, L., 2014. Validation of climate model-inferred regional temperature change for late-glacial Europe. Nature Communications 5, 4914. https://doi.org/10.1038/ncomms5914

Heiri, O., Brooks, S.J., Birks, H.J.B., Lotter, A.F., 2011. A 274-lake calibration data-set and inference model for chironomid-based summer air temperature reconstruction in Europe. Quaternary Science Reviews 30, 3445–3456. https://doi.org/10.1016/j.quascirev.2011.09.006

Heiri, Oliver, Brooks, S.J., Renssen, H., Bedford, A., Hazekamp, M., Ilyashuk, B., Jeffers, E.S., Lang, B., Kirilova, E., Kuiper, S., Millet, L., Samartin, S., Toth, M., Verbruggen, F., Watson, J.E., van Asch, N., Lammertsma, E., Amon, L., Birks, H.H., Birks, H.J.B., Mortensen, M.F., Hoek, W.Z., Magyari, E., Muñoz Sobrino, C., Seppä, H., Tinner, W., Tonkov, S., Veski, S., Lotter, A.F., 2014. Validation of climate model-inferred regional temperature change for late-glacial Europe. Nat Commun 5, 4914. https://doi.org/10.1038/ncomms5914

Heiri, O., Lotter, A.F., 2010. How does taxonomic resolution affect chironomid-based temperature reconstruction? J Paleolimnol 44, 589–601. https://doi.org/10.1007/s10933-010-9439-z

Heiri, O., Lotter, A.F., Hausmann, S., Kienast, F., 2003. A chironomid-based Holocene summer air temperature reconstruction from the Swiss Alps. The Holocene 13, 477–484. https://doi.org/10.1191/0959683603hl640ft

Heiri, O., Lotter, A.F., Lemcke, G., 2001. Loss on ignition as a method for estimating organic and carbonate content in sediments: reproducibility and comparability of results. Journal of Paleolimnology 25, 101–110. https://doi.org/10.1023/A:1008119611481

Hersbach, H., Bell, B., Berrisford, P., Hirahara, S., Horányi, A., Muñoz-Sabater, J., Nicolas, J., Peubey, C., Radu, R., Schepers, D., Simmons, A., Soci, C., Abdalla, S., Abellan, X., Balsamo, G., Bechtold, P., Biavati, G., Bidlot, J., Bonavita, M., De Chiara, G., Dahlgren, P., Dee, D., Diamantakis, M., Dragani, R., Flemming, J., Forbes, R., Fuentes, M., Geer, A., Haimberger, L., Healy, S., Hogan, R.J., Hólm, E., Janisková, M., Keeley, S., Laloyaux, P., Lopez, P., Lupu, C., Radnoti, G., de Rosnay, P., Rozum, I., Vamborg, F., Villaume, S., Thépaut, J.-N., 2020. The ERA5 global reanalysis. Quarterly Journal of the Royal Meteorological Society 146, 1999–2049. https://doi.org/10.1002/qj.3803

Holzhausen, A., 2024. What we really know about the dormancy, reproduction, germination and cultivation of charophytes (Characeae). OE 9, e117655. https://doi.org/10.3897/oneeco.9.e117655

Hughes, A.L.C., Gyllencreutz, R., Lohne, Ø.S., Mangerud, J., Svendsen, J.I., 2016. The last Eurasian ice sheets – a chronological database and time-slice reconstruction, DATED-1. Boreas 45, 1–45. https://doi.org/10.1111/bor.12142

Hupfer, M., Lewandowski, J., 2008. Oxygen Controls the Phosphorus Release from Lake Sediments – a Long-Lasting Paradigm in Limnology. International Review of Hydrobiology 93, 415–432. https://doi.org/10.1002/iroh.200711054

Ilyashuk, B., Gobet, E., Heiri, O., Lotter, A.F., van Leeuwen, J.F.N., van der Knaap, W.O., Ilyashuk, E., Oberli, F., Ammann, B., 2009. Lateglacial environmental and climatic changes at the Maloja Pass, Central Swiss Alps, as recorded by chironomids and pollen. Quaternary Science Reviews 28, 1340–1353. https://doi.org/10.1016/j.quascirev.2009.01.007

Jensen, T.C., Dimante-Deimantovica, I., Schartau, A.K., Walseng, B., 2013. Cladocerans respond to differences in trophic state in deeper nutrient poor lakes from Southern Norway. Hydrobiologia 715, 101–112. https://doi.org/10.1007/s10750-012-1413-5

Jeppesen, E., Kronvang, B., Meerhoff, M., Søndergaard, M., Hansen, K.M., Andersen, H.E., Lauridsen, T.L., Liboriussen, L., Beklioglu, M., Özen, A., Olesen, J.E., 2009. Climate Change Effects on Runoff, Catchment Phosphorus Loading and Lake Ecological State, and Potential Adaptations. J of Env Quality 38, 1930–1941. https://doi.org/10.2134/jeq2008.0113

Jiménez-Moreno, G., Heiri, O., García-Alix, A., Anderson, R.S., Jiménez-Espejo, F.J., López-Blanco, C., Jiménez, L., Pérez-Martínez, C., Rodrigo-Gámiz, M., López-Avilés, A., Camuera, J., 2023. Holocene summer temperature reconstruction based on a chironomid record from Sierra Nevada, southern Spain. Quaternary Science Reviews 319, 108343. https://doi.org/10.1016/j.quascirev.2023.108343

Jones, P.D., Harpham, C., Vinther, B.M., 2014. Winter-responding proxy temperature reconstructions and the North Atlantic Oscillation. Journal of Geophysical Research: Atmospheres 119, 6497–6505. https://doi.org/10.1002/2014JD021561

Juggins, S., 2003. Software for ecological and palaeoecological data analysis and visualisation. University of Newcastle, Newcastle upon Tyne.

Kalm, V., Raukas, A., Rattas, M., Lasberg, K., 2011. Pleistocene Glaciations in Estonia, in: Developments in Quaternary Sciences. Elsevier, pp. 95–104. https://doi.org/10.1016/B978-0-444-53447-7.00008-8

Kienast, F., Tarasov, P., Schirrmeister, L., Grosse, G., Andreev, A.A., 2008. Continental climate in the East Siberian Arctic during the last interglacial: Implications from palaeobotanical records. Global and Planetary Change 60, 535–562. https://doi.org/10.1016/j.gloplacha.2007.07.004

Klink, A., Pillot, H., 2003. Chironomidae Larvae: Key to the Higher Taxa and Species of the Lowlands of Northwestern Europe. Expert-Center for Taxonomic Identification.

Kotrys, B., Płóciennik, M., Sydor, P., Brooks, S., 2020. Expanding the Swiss-Norwegian chironomid training set with Polish data. Boreas 49, 89–107. https://doi.org/10.1111/bor.12406

Lanka, A., Poska, A., Bakumenko, V., Dimante-Deimantovica, I., Liiv, M., Stivrins, N., Zagars, M., Veski, S., 2024. Subfossil Cladocera as indicators of pH, trophic state and conductivity: Separate and combined effects in hemi boreal freshwater lakes. Ecological Indicators 167, 112592. https://doi.org/10.1016/j.ecolind.2024.112592

Lapellegerie, P., Millet, L., Rius, D., Duprat-Oualid, F., Luoto, T., Heiri, O., 2024. Chironomid-inferred summer temperature during the Last Glacial Maximum in the Southern Black Forest, Central Europe. Quaternary Science Reviews 345, 109016. https://doi.org/10.1016/j.quascirev.2024.109016

Larocque-Tobler, I., 2014. The Polish sub-fossil chironomids. Palaeontologia Electronica 17, 28. https://doi.org/10.26879/391

Lasberg, K., Kalm, V., 2013. Chronology of L ate W eichselian glaciation in the western part of the E ast E uropean P lain. Boreas 42, 995–1007. https://doi.org/10.1111/bor.12016

Laumets, L., Kalm, V., Poska, A., Kele, S., Lasberg, K., Amon, L., 2014. Palaeoclimate inferred from δ18O and palaeobotanical indicators in freshwater tufa of Lake Äntu Sinijärv, Estonia. J Paleolimnol 51, 99–111. https://doi.org/10.1007/s10933-013-9758-y

Liu, Z., Kutzbach, J., Wu, L., 2000. Modeling climate shift of El Nino variability in the Holocene. Geophysical Research Letters 27, 2265–2268. https://doi.org/10.1029/2000GL011452

Liu, Z., Wang, Y., Gallimore, R., Gasse, F., Johnson, T., deMenocal, P., Adkins, J., Notaro, M., Prentice, I.C., Kutzbach, J., Jacob, R., Behling, P., Wang, L., Ong, E., 2007. Simulating the transient evolution and abrupt change of Northern Africa atmosphere–ocean–terrestrial ecosystem in the Holocene. Quaternary Science Reviews 26, 1818–1837. https://doi.org/10.1016/j.quascirev.2007.03.002

Lotter, A.F., Birks, H.J.B., Eicher, U., Hofmann, W., Schwander, J., Wick, L., 2000. Younger Dryas and Allerød summer temperatures at Gerzensee (Switzerland) inferred from fossil pollen and cladoceran assemblages. Palaeogeography, Palaeoclimatology, Palaeoecology 159, 349–361. https://doi.org/10.1016/S0031-0182(00)00093-6

Lotter, A.F., Birks, H.J.B., Hofmann, W., Marchetto, A., 1998. Modern diatom, cladocera, chironomid, and chrysophyte cyst assemblages as quantitative indicators for the reconstruction of past environmental conditions in the Alps. II. Nutrients. Journal of Paleolimnology 19, 443–463. https://doi.org/10.1023/A:1007994206432

Lotter, A.F., Sturm, M., Teranes, J.L., Wehrli, B., 1997. Varve formation since 1885 and high-resolution varve analyses in hypertrophic Baldeggersee (Switzerland). Aquatic Science 59, 304–325. https://doi.org/10.1007/BF02522361

Luoto, T.P., 2011. The relationship between water quality and chironomid distribution in Finland—A new assemblage-based tool for assessments of long-term nutrient dynamics. Ecological Indicators 11, 255–262. https://doi.org/10.1016/j.ecolind.2010.05.002

Luoto, T.P., Kultti, S., Nevalainen, L., Sarmaja-Korjonen, K., 2010. Temperature and effective moisture variability in southern Finland during the Holocene quantified with midge-based calibration models. J Quaternary Science 25, 1317–1326. https://doi.org/10.1002/jqs.1417

Magny, M., Guiot, J., Schoellammer, P., 2001. Quantitative Reconstruction of Younger Dryas to Mid-Holocene Paleoclimates at Le Locle, Swiss Jura, Using Pollen and Lake-Level Data. Quaternary Research 56, 170–180. https://doi.org/10.1006/qres.2001.2257

Manca, M., Torretta, B., Comoli, P., Amsinck, S.L., Jeppesen, E., 2007. Major changes in trophic dynamics in large, deep sub-alpine Lake Maggiore from 1940s to 2002: a high resolution comparative palaeo-neolimnological study. Freshwater Biology 52, 2256–2269. https://doi.org/10.1111/j.1365-2427.2007.01827.x

Marsicek, J., Shuman, B.N., Bartlein, P.J., Shafer, S.L., Brewer, S., 2018. Reconciling divergent trends and millennial variations in Holocene temperatures. Nature 554, 92–96. https://doi.org/10.1038/nature25464

Mayewski, P.A., Rohling, E.E., Curt Stager, J., Karlén, W., Maasch, K.A., Meeker, L.D., Meyerson, E.A., Gasse, F., Van Kreveld, S., Holmgren, K., Lee-Thorp, J., Rosqvist, G., Rack, F., Staubwasser, M., Schneider, R.R., Steig, E.J., 2004. Holocene climate variability. Quat. res. 62, 243–255. https://doi.org/10.1016/j.yqres.2004.07.001

Miles, M.W., Andresen, C.S., Dylmer, C.V., 2020. Evidence for extreme export of Arctic sea ice leading the abrupt onset of the Little Ice Age. Sci. Adv. 6, eaba4320. https://doi.org/10.1126/sciadv.aba4320

Mirosław-Grabowska, J., Zawisza, E., Jaskółka, A., Obremska, M., 2015. Natural transformation of the Romoty paleolake (NE Poland) during the Late Glacial and Holocene based on isotopic, pollen, cladoceran and geochemical data. Quaternary International, Palaeolandscapes from Saalian to Weichselian: INQUA TERPRO Commission, Peribaltic International Field Symposium, Lithuania 386, 171–185. https://doi.org/10.1016/j.quaint.2015.06.040

Moros, M., Emeis, K., Risebrobakken, B., Snowball, I., Kuijpers, A., McManus, J., Jansen, E., 2004. Sea surface temperatures and ice rafting in the Holocene North Atlantic: climate influences on northern Europe and Greenland. Quaternary Science Reviews, Holocene climate variability - a marine perspective 23, 2113–2126. https://doi.org/10.1016/j.quascirev.2004.08.003

Moss, B., 2011. Allied attack: climate change and eutrophication. IW 1, 101–105. https://doi.org/10.5268/IW-1.2.359

Nazarova, L., Herzschuh, U., Wetterich, S., Kumke, T., Pestryakova, L., 2011. Chironomid-based inference models for estimating mean July air temperature and water depth from lakes in Yakutia, northeastern Russia. J Paleolimnol 45, 57–71. https://doi.org/10.1007/s10933-010-9479-4

Nevalainen, L., Ketola, M., Korosi, J.B., Manca, M., Kurmayer, R., Koinig, K.A., Psenner, R., Luoto, T.P., 2014. Zooplankton (Cladocera) species turnover and long-term decline of Daphnia in two high mountain lakes in the Austrian Alps. Hydrobiologia 722, 75–91. https://doi.org/10.1007/s10750-013-1676-5

Nickus, U., Bishop, K., Erlandsson, M., Evans, C.D., Forsius, M., Laudon, H., Livingstone, D.M., Monteith, D., Thies, H., 2010. Direct Impacts of Climate Change on Freshwater Ecosystems, in: Kernan, M., Battarbee, R.W., Moss, B. (Eds.), Climate Change Impacts on Freshwater Ecosystems. Wiley, pp. 38–64. https://doi.org/10.1002/9781444327397.ch3

Niinemets, E., Saarse, L., 2009. Holocene vegetation and land-use dynamics of south-eastern Estonia. Quaternary International 207, 104–116. https://doi.org/10.1016/j.quaint.2008.11.015

NOAA National Centers for Environmental Information, 2022. ETOPO 2022 15 Arc-Second Global Relief Model. https://doi.org/10.25921/FD45-GT74

O’Brien, S.R., Mayewski, P.A., Meeker, L.D., Meese, D.A., Twickler, M.S., Whitlow, S.I., 1995. Complexity of Holocene Climate as Reconstructed from a Greenland Ice Core. Science 270, 1962–1964. https://doi.org/10.1126/science.270.5244.1962

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O’Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H., Fitzjohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., ter Braak, C., Weedon, J., 2022. vegan: community ecology package. R package version 2.6-4.

Ólafsson, J.S., Adalsteinsson, H., Gíslason, G.M., Hansen, I., Hrafnsdóttir, Th., 2002. Spatial heterogeneity in lotic chironomids and simuliids in relation to catchment characteristics in Iceland. SIL Proceedings, 1922-2010 28, 157–163. https://doi.org/10.1080/03680770.2001.11902566

Oppo, D.W., McManus, J.F., Cullen, J.L., 2003. Deepwater variability in the Holocene epoch. Nature 422, 277–277. https://doi.org/10.1038/422277b

Owens, M.J., Lockwood, M., Hawkins, E., Usoskin, I., Jones, G.S., Barnard, L., Schurer, A., Fasullo, J., 2017. The Maunder minimum and the Little Ice Age: an update from recent reconstructions and climate simulations. J. Space Weather Space Clim. 7, A33. https://doi.org/10.1051/swsc/2017034

Pastukhova, Y., Tsyganov, A., Sapelko, T., Mazei, N., Zharov, A., Mazei, Y., 2024. Paleoecological reconstruction of water level changes in a cascade of lakes on Lunkulansaari Island (Lake Ladoga) based on the analysis of Cladocera remains in lake sediments. Limnology and Freshwater Biology 574–579. https://doi.org/10.31951/2658-3518-2024-A-4-574

Płóciennik, M., Self, A., Birks, H.J.B., Brooks, S.J., 2011. Chironomidae (Insecta: Diptera) succession in Żabieniec bog and its palaeo-lake (central Poland) through the Late Weichselian and Holocene. Palaeogeography, Palaeoclimatology, Palaeoecology 307, 150–167. https://doi.org/10.1016/j.palaeo.2011.05.010

Poska, A., Väli, V., Vassiljev, J., Alliksaar, T., Saarse, L., 2022. Timing and drivers of local to regional scale land-cover changes in the hemiboreal forest zone during the Holocene: A pollen-based study from South Estonia. Quaternary Science Reviews 277, 107351. https://doi.org/10.1016/j.quascirev.2021.107351

Ramsey, C.B., 2008. Deposition models for chronological records. Quaternary Science Reviews, INTegration of Ice-core, Marine and Terrestrial records (INTIMATE): Refining the record of the Last Glacial-Interglacial Transition 27, 42–60. https://doi.org/10.1016/j.quascirev.2007.01.019

Rao, Z., Tian, Y., Guang, K., Wei, S., Guo, H., Feng, Z., Zhao, L., Li, Y., 2022. Pollen Data as a Temperature Indicator in the Late Holocene: A Review of Results on Regional, Continental and Global Scales. Front. Earth Sci. 10, 845650. https://doi.org/10.3389/feart.2022.845650

Rasmussen, S.O., Dahl-Jensen, D., Fischer, H., Fuhrer, K., Hansen, S.B., Hansson, M., Hvidberg, C.S., Jonsell, U., Kipfstuhl, S., Ruth, U., Schwander, J., Siggaard-Andersen, M.-L., Sinnl, G., Steffensen, J.P., Svensson, A.M., Vinther, B.M., 2023. Ice-core data used for the construction of the Greenland Ice-Core Chronology 2005 and 2021 (GICC05 and GICC21). Earth Syst. Sci. Data 15, 3351–3364. https://doi.org/10.5194/essd-15-3351-2023

Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., Van Der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 Northern Hemisphere Radiocarbon Age Calibration Curve (0–55 cal kBP). Radiocarbon 62, 725–757. https://doi.org/10.1017/RDC.2020.41

Renberg, I., Wik, M., 1985. Soot Particle Counting in Recent Lake Sediments an Indirect Dating Method. Ecological Bulletins 37, 53–57.

Renssen, H., Isarin, R.F.B., Jacob, D., Podzun, R., Vandenberghe, J., 2001. Simulation of the Younger Dryas climate in Europe using a regional climate model nested in an AGCM: preliminary results. Global and Planetary Change 30, 41–57. https://doi.org/10.1016/S0921-8181(01)00076-5

Republic of Estonia Land and Spatial Development Board, 2025. False-color forestry NGR orthophoto 06.07.2017.

Rigterink, S., Krahn, K.J., Kotrys, B., Urban, B., Heiri, O., Turner, F., Pannes, A., Schwalb, A., 2024. Summer temperatures from the Middle Pleistocene site Schöningen 13, northern Germany, determined from subfossil chironomid assemblages. Boreas 53, 525–542. https://doi.org/10.1111/bor.12658

Rose, N., 2002. Fly-Ash Particles, in: Last, W.M., Smol, J.P. (Eds.), Tracking Environmental Change Using Lake Sediments, Developments in Paleoenvironmental Research. Springer Netherlands, Dordrecht, pp. 319–349. https://doi.org/10.1007/0-306-47670-3_12

Saarse, L., Veski, S., 2001. SPREAD OF BROAD-LEAVED TREES IN ESTONIA. Proceedings of the Estonian Academy of Sciences. Geology 50, 51. https://doi.org/10.3176/geol.2001.1.05

Salonen, J.S., Seppä, H., Luoto, M., Bjune, A.E., Birks, H.J.B., 2012. A North European pollen–climate calibration set: analysing the climatic responses of a biological proxy using novel regression tree methods. Quaternary Science Reviews 45, 95–110. https://doi.org/10.1016/j.quascirev.2012.05.003

Sapelko, T., Pozdnyakov, S., Kuznetsov, D., Ludikova, A., Ivanova, E., Guseva, M., Zazovskaya, E., 2019. Holocene sedimentation in the central part of Lake Ladoga. Quaternary International, Quaternary Freshwater ecosystem: a paleoclimate, paleolandscapes and biostratigraphy approach 524, 67–75. https://doi.org/10.1016/j.quaint.2019.05.028

Scheffer, M., Van Nes, E.H., 2007. Shallow lakes theory revisited: various alternative regimes driven by climate, nutrients, depth and lake size. Hydrobiologia 584, 455–466. https://doi.org/10.1007/s10750-007-0616-7

Šeirienė, V., Gastevičienė, N., Luoto, T.P., Gedminienė, L., Stančikaitė, M., 2021. The Lateglacial and early Holocene climate variability and vegetation dynamics derived from chironomid and pollen records of Lieporiai palaeolake, North Lithuania. Quaternary International, The Quaternary of Europe and Adjacent Areas: Stratigraphical Perspectives and Tools for Correlations – SEQS-2019 605–606, 55–64. https://doi.org/10.1016/j.quaint.2020.12.017

Self, A., Brooks, S., Birks, H., Nazarova, L., Porinchu, D., Odland, A., Yang, H., Jones, V., 2011. The distribution and abundance of chironomids in high-latitude Eurasian lakes with respect to temperature and continentality: development and application of new chironomid-based climate-inference models in northern Russia. https://doi.org/10.1016/j.quascirev.2011.01.022

Seppä, H., Birks, H.J.B., 2001. July mean temperature and annual precipitation trends during the Holocene in the Fennoscandian tree-line area: pollen-based climate reconstructions. The Holocene 11, 527–539. https://doi.org/10.1191/095968301680223486

Seppä, H., Bjune, A.E., Telford, R.J., Birks, H.J.B., Veski, S., 2009. Last nine-thousand years of temperature variability in Northern Europe. Climate of the Past 5, 523–535. https://doi.org/10.5194/cp-5-523-2009

Seppä, H., Hammarlund, D., Antonsson, K., 2005. Low-frequency and high-frequency changes in temperature and effective humidity during the Holocene in south-central Sweden: implications for atmospheric and oceanic forcings of climate. Clim Dyn 25, 285–297. https://doi.org/10.1007/s00382-005-0024-5

Seppä, H., Poska, A., 2004. Holocene annual mean temperature changes in Estonia and their relationship to solar insolation and atmospheric circulation patterns. Quat. res. 61, 22–31. https://doi.org/10.1016/j.yqres.2003.08.005

Sher, A., Kuzmina, S., Kiseyov, S., Lister, A., 2003. Tundra-steppe environment in Arctic Siberia and the evolution of the woolly mammoth. Presented at the 3rd International Mammoth Conference, 2003 : Program and Abstracts, Occasional Papers in Earth Sciences, 5 . Palaeontology Program, Department of Tourism and Culture, Government of Yukon, Yokon, Canada, pp. 136–142.

Shuman, B., 2012. Patterns, processes, and impacts of abrupt climate change in a warm world: the past 11,700 years. WIREs Climate Change 3, 19–43. https://doi.org/10.1002/wcc.152

Solomina, O.N., Bradley, R.S., Hodgson, D.A., Ivy-Ochs, S., Jomelli, V., Mackintosh, A.N., Nesje, A., Owen, L.A., Wanner, H., Wiles, G.C., Young, N.E., 2015. Holocene glacier fluctuations. Quaternary Science Reviews 111, 9–34. https://doi.org/10.1016/j.quascirev.2014.11.018

Stansell, N.D., Klein, E.S., Finkenbinder, M.S., Fortney, C.S., Dodd, J.P., Terasmaa, J., Nelson, D.B., 2017. A stable isotope record of Holocene precipitation dynamics in the

Baltic region from Lake Nuudsaku, Estonia. Quaternary Science Reviews 175, 73–84. https://doi.org/10.1016/j.quascirev.2017.09.013

Steiner, D., Pauling, A., Nussbaumer, S.U., Nesje, A., Luterbacher, J., Wanner, H., Zumbühl, H.J., 2008. Sensitivity of European glaciers to precipitation and temperature – two case studies. Climatic Change 90, 413–441. https://doi.org/10.1007/s10584-008-9393-1

Stocker, T.F., Qin, D., Xia, Y., Bex, V., Midgley, P.M., 2013. IPCC, 2013: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Stockmarr, J., 1971. Tables with spores used in absolute pollen analysis. Pollen et spores 615–21.

Stonevicius, E., Stankunavicius, G., Rimkus, E., 2018. Continentality and Oceanity in the Mid and High Latitudes of the Northern Hemisphere and Their Links to Atmospheric Circulation. Advances in Meteorology 1, 5746191. https://doi.org/10.1155/2018/5746191

Stralberg, D., Arseneault, D., Baltzer, J.L., Barber, Q.E., Bayne, E.M., Boulanger, Y., Brown, C.D., Cooke, H.A., Devito, K., Edwards, J., Estevo, C.A., Flynn, N., Frelich, L.E., Hogg, E.H., Johnston, M., Logan, T., Matsuoka, S.M., Moore, P., Morelli, T.L., Morissette, J.L., Nelson, E.A., Nenzén, H., Nielsen, S.E., Parisien, M., Pedlar, J.H., Price, D.T., Schmiegelow, F.K., Slattery, S.M., Sonnentag, O., Thompson, D.K., Whitman, E., 2020. Climate-change refugia in boreal North America: what, where, and for how long? Frontiers in Ecol & Environ 18, 261–270. https://doi.org/10.1002/fee.2188

Strandberg, G., Chen, J., Fyfe, R., Kjellström, E., Lindström, J., Poska, A., Zhang, Q., Gaillard, M.-J., 2023. Did the Bronze Age deforestation of Europe affect its climate? A regional climate model study using pollen-based land cover reconstructions. Climate of the Past 19, 1507–1530. https://doi.org/10.5194/cp-19-1507-2023

Szeroczynska, K., Sarmaja-Korjonen, K., 2007. Atlas of Subfossil Cladocera from Central and Northern Europe Atlas of Subfossil Cladocera from Central and Northern Europe Krystyna Szeroczynska. Library.

Team, B.A., 2008. Assessment of Climate Change for the Baltic Sea Basin. Springer Science & Business Media.

ter Braak, C.J.F., Juggins, S., 1993. Weighted averaging partial least squares regression (WA-PLS): an improved method for reconstructing environmental variables from species assemblages. Hydrobiologia 269, 485–502. https://doi.org/10.1007/BF00028046

Theuerkauf, M., Joosten, H., 2012. Younger Dryas cold stage vegetation patterns of central Europe–climate, soil and relief controls. Boreas 41, 391–407. https://doi.org/10.1111/j.1502-3885.2011.00240.x

Töchterle, P., Baldo, A., Murton, J.B., Schenk, F., Edwards, R.L., Koltai, G., Moseley, G.E., 2024. Reconstructing Younger Dryas ground temperature and snow thickness from cave deposits. Clim. Past 20, 1521–1535. https://doi.org/10.5194/cp-20-1521-2024

Tóth, M., Magyari, E.K., Buczkó, K., Braun, M., Panagiotopoulos, K., Heiri, O., 2015. Chironomid-inferred Holocene temperature changes in the South Carpathians (Romania). The Holocene. https://doi.org/10.1177/0959683614565953

Ursenbacher, S., Stötter, T., Heiri, O., 2020. Chitinous aquatic invertebrate assemblages in Quaternary lake sediments as indicators of past deepwater oxygen concentration. Quaternary Science Reviews 231, 106203. https://doi.org/10.1016/j.quascirev.2020.106203

Väliranta, M., Salonen, J.S., Heikkilä, M., Amon, L., Helmens, K., Klimaschewski, A., Kuhry, P., Kultti, S., Poska, A., Shala, S., Veski, S., Birks, H.H., 2015. Plant macrofossil evidence for an early onset of the Holocene summer thermal maximum in northernmost Europe. Nat Commun 6, 6809. https://doi.org/10.1038/ncomms7809

Van Damme, K., Kotov, A.A., 2016. The fossil record of the Cladocera (Crustacea: Branchiopoda): Evidence and hypotheses. Earth-Science Reviews 163, 162–189. https://doi.org/10.1016/j.earscirev.2016.10.009

Velle, G., Brodersen, K.P., Birks, H.J.B., Willassen, E., 2010. Midges as quantitative temperature indicator species: Lessons for palaeoecology. The Holocene 20, 989–1002. https://doi.org/10.1177/0959683610365933

Veski, S., Seppä, H., Stančikaitė, M., Zernitskaya, V., Reitalu, T., Gryguc, G., Heinsalu, A., Stivrins, N., Amon, L., Vassiljev, J., Heiri, O., 2015. Quantitative summer and winter temperature reconstructions from pollen and chironomid data between 15 and 8 ka BP in the Baltic–Belarus area. Quaternary International 19, 4–11.

Visconti, A., Manca, M., De Bernardi, R., 2008. Eutrophication-like response to climate warming: an analysis of Lago Maggiore (N. Italy) zooplankton in contrasting years. J Limnol 67, 87. https://doi.org/10.4081/jlimnol.2008.87

Vollweiler, N., Scholz, D., Mühlinghaus, C., Mangini, A., Spötl, C., 2006. A precisely dated climate record for the last 9 kyr from three high alpine stalagmites, Spannagel Cave, Austria. Geophysical Research Letters 33, 2006GL027662. https://doi.org/10.1029/2006GL027662

Walker, I.R., 2001. Midges: Chironomidae and Related Diptera, in: Smol, J.P., Birks, H.J.B., Last, W.M. (Eds.), Tracking Environmental Change Using Lake Sediments, Developments in Paleoenvironmental Research. Springer Netherlands, Dordrecht, pp. 43–66. https://doi.org/10.1007/0-306-47671-1_3

Walker, M.J.C., Berkelhammer, M., Björck, S., Cwynar, L.C., Fisher, D.A., Long, A.J., Lowe, J.J., Newnham, R.M., Rasmussen, S.O., Weiss, H., 2012. Formal subdivision of the Holocene Series/Epoch: a Discussion Paper by a Working Group of INTIMATE (Integration of ice-core, marine and terrestrial records) and the Subcommission on Quaternary Stratigraphy (International Commission on Stratigraphy). Journal of Quaternary Science 27, 649–659. https://doi.org/10.1002/jqs.2565

Wang, W., Xiang, L., Li, Y., Suo, Q., Song, X., Zhang, Y., Huang, C., Muhammad, F., Wang, T., Ren, X., Chen, S., Chen, G., Huang, X., 2024. Modern distribution of Cladocera in lakes of northern China and western Mongolia and its environmental implications. Fundamental Research. https://doi.org/10.1016/j.fmre.2024.09.004

Wanner, H., Beer, J., Bütikofer, J., Crowley, T.J., Cubasch, U., Flückiger, J., Goosse, H., Grosjean, M., Joos, F., Kaplan, J.O., Küttel, M., Müller, S.A., Prentice, I.C., Solomina, O., Stocker, T.F., Tarasov, P., Wagner, M., Widmann, M., 2008. Mid- to Late Holocene climate change: an overview. Quaternary Science Reviews 27, 1791–1828. https://doi.org/10.1016/j.quascirev.2008.06.013

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Grolemund, G., Hayes, A., Henry, L., Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Müller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the Tidyverse. Journal of Open Source Software 4, 1686. https://doi.org/10.21105/joss.01686

Wickham, H., Francois, R., Henry, L., Muller, K., 2022. Dplyr: a grammar of data manipulation. R package version 1.0.10.

Yao, F., Ma, C., Zhu, C., Li, J., Chen, G., Tang, L., Huang, M., Jia, T., Xu, J., 2017. Holocene climate change in the western part of Taihu Lake region, East China. Palaeogeography, Palaeoclimatology, Palaeoecology 485, 963–973. https://doi.org/10.1016/j.palaeo.2017.08.022

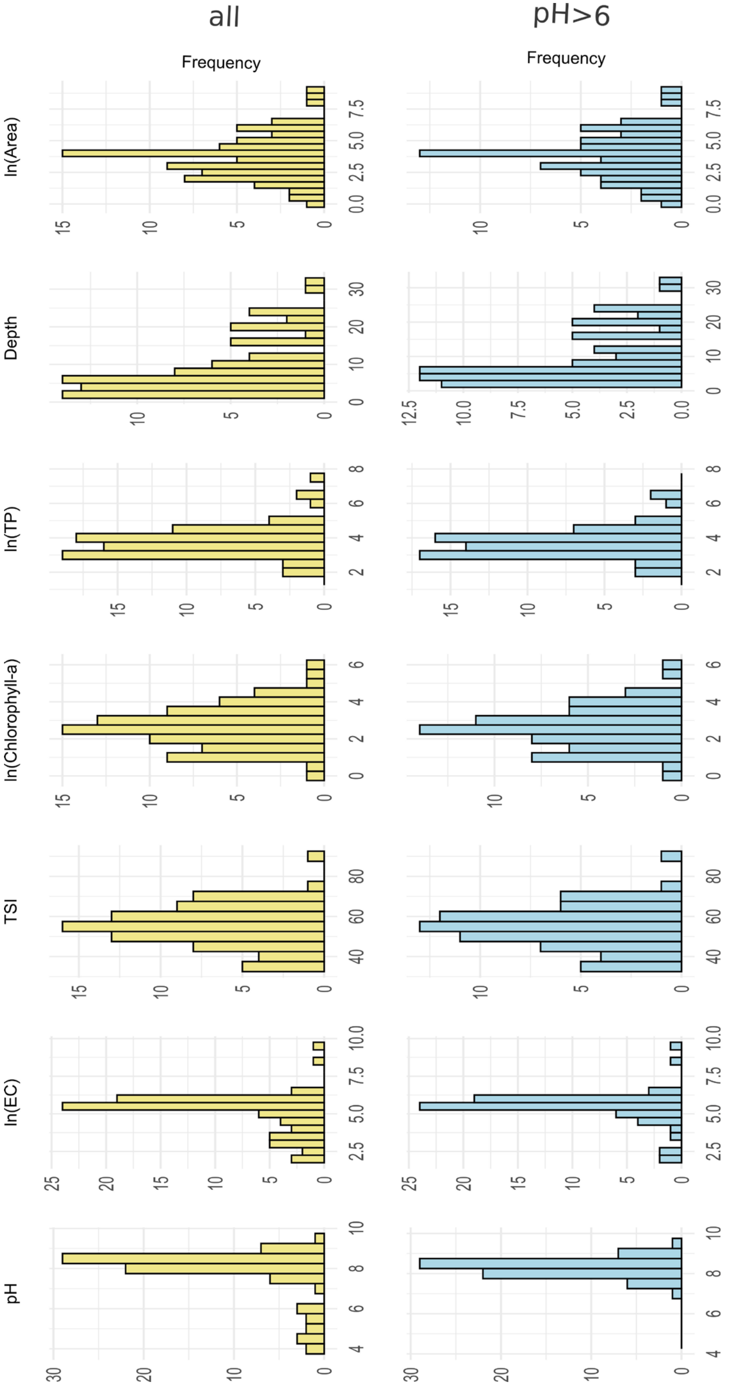
Zani, D., Lischke, H., Lehsten, V., 2023. Climate and dispersal limitation drive tree species range shifts in post-glacial Europe: results from dynamic simulations. Front. Ecol. Evol. 11, 1321104. https://doi.org/10.3389/fevo.2023.1321104

Zawiska, I., Correa-Metrio, A., Rzodkiewicz, M., Wolski, J., 2025. Cladocera assemblages indicate environmental gradients of lake productivity and morphometry in central Europe. Boreas 54, 258–272. https://doi.org/10.1111/bor.70001

Zawiska, I., Luoto, T.P., Nevalainen, L., Tylmann, W., Jensen, T.C., Obremska, M., Słowiński, M., Woszczyk, M., Schartau, A.K., Walseng, B., 2017. Climate variability and lake ecosystem responses in western Scandinavia (Norway) during the last Millennium. Palaeogeography, Palaeoclimatology, Palaeoecology 466, 231–239. https://doi.org/10.1016/j.palaeo.2016.11.034

Appendix 5

Data distribution of the surface sediment training set environmental gradients for datasets “all” and “pH>6”.



Appendix 6

The lake list of each fold used for the WA-PLS and BRT k-10 cross-validation procedure. The numbers of lakes correspond to the ones presented in Table 2.

Folds for datasets “all” and “Eubosmina”

```
folds <-list(
  fold1 = c(7,76,15,2,22,45,68,37),    # Site numbers for fold 1
  fold2 = c(23,19,4,25,46,71,9,6),     # Site numbers for fold 2
  fold3 = c(26,28,21,5,27,50,74,31), # And so on
  fold4 = c(32,52,38,11,29,51,10,34),
  fold5 = c(42,56,49,12,30,53,13,72),
  fold6 = c(44,57,60,14,35,54,24,62),
  fold7 = c(48,58,61,16,36,55,33,78),
  fold8 = c(63,59,67,17,39,64,47),
  fold9 = c(69,3,70,18,40,65,77),
  fold10 = c(73,8,43,75,20,41,66,1))
```

Folds for datasets “pH>6” and “Eubosmina (pH>6)”

```
folds_alk <-list(
  fold1 = c(1,14,16,17,32,47,9),
  fold2 = c(6,18,15,19,35,54,12),
  fold4 = c(44,33,11,23,37,56,40),
  fold5 = c(48,34,10,24,38,57,65),
  fold6 = c(49,41,8,26,39,59),
  fold7 = c(50,52,5,27,42,61),
  fold8 = c(51,53,4,28,43,62),
  fold9 = c(3,58,2,30,45,63),
  fold10 = c(7,60,64,31,46,66))
```

As Lake Sekšu and Velnezers did not have EC values that would fit the criteria in the methodology, EC “all” and “Eubosmina” had their separate folds

```
folds_EC <-list(
  fold1 = c(7,74,15,2,22,45,67,37),
  fold2 = c(23,19,4,25,46,9,6),
  fold3 = c(26,28,21,5,27,50,72,31),
  fold4 = c(32,52,38,11,29,51,10,34),
  fold5 = c(42,55,49,12,30,53,13,70),
  fold6 = c(44,56,59,14,35,54,24,61),
  fold7 = c(48,57,60,16,36,33,76),
  fold8 = c(62,58,66,17,39,63,47),
  fold9 = c(68,3,69,18,40,65,75),
  fold10 = c(71,8,43,73,20,41,64,1))
```

Appendix 7

Hyperparameters used for BRT model building. Hyperparameters were selected during the hyperparameter tuning procedure.

Model	shrinkage	Bag fraction	Interaction depth	Minimum terminal node sample size	Average best number of trees	Distribution
pH „all“	0,1	0,6	3	2	442	Laplace
pH „Eubosmina“	0,1	0,6	2	5	1008	Laplace
EC „all“	0,05	0,6	1	2	794	Tdist
EC „Eubosmina“	0,1	0,6	1	10	658	Gaussian
TP „all“	0,1	0,75	1	10	326	Tdist
TP „Eubosmina“	0,1	0,75	1	10	202	Gaussian
TP „pH>6“	0,05	0,6	1	3	392	Gaussian
TP „Eubosmina(pH>6“	0,1	0,65	3	3	216	Tdist
Chl „all“	0,1	0,65	1	2	430	Tdist
Chl „Eubosmina“	0,1	0,6	1	5	302	Tdist
Chl „pH>6“	0,05	0,75	1	2	518	Tdist
Chl „Eubosmina (pH>6)“	0,05	0,7	1	3	332	Tdist
TSI „all“	0,1	0,7	1	5	824	Tdist
TSI „Eubosmina“	0,05	0,75	1	5	904	Tdist
TSI „pH>6“	0,1	0,6	1	3	296	Tdist
TSI „Eubosmina (pH>6)“	0,05	0,6	2	2	470	Tdist
Depth „all“	0,1	0,65	1	10	116	Gaussian
Depth „Eubosmina“	0,1	0,6	1	10	252	Gaussian
Depth „pH>6“	0,05	0,65	1	3	660	Gaussian
Depth „Eubosmina (pH>6)“	0,1	0,65	1	5	556	Gaussian

Curriculum vitae

Personal data

Name: Anna Lanka
Date of birth: 22.03.1994
Place of birth: Talsi, Latvia
Citizenship: Latvian

Contact data

E-mail: anna.lanka@taltech.ee

Education

2020–2025	Tallinn University of Technology, PhD (specialty: Earth Sciences)
2017–2020	University of Latvia, Department of Biology, MSc
2015–2017	University of Latvia, Department of Physics and Mathematics, BSc (unfinished)
2012–2015	University of Latvia, Department of Biology, BSc
2009–2012	Tukuma Raiņa State gymnasium

Language competence

Latvian	Native
English	Fluent
Russian	Average/Basic

Professional employment

2020–Present	Tallinn University of Technology, Department of Geology, Early-stage researcher
2019–2020	Latvian Institute of Aquatic Ecology, Lab assistant
2018–2020	Latvian Fund of Nature, Field assistant
2015–2016	Natural History Museum of Latvia, Entomologist

Elulookirjeldus

Isikuandmed

Nimi:	Anna Lanka
Sünniaeg:	22.03.1994
Sünnikoht:	Talsi, Läti
Kodakondsus:	Läti

Kontaktandmed

E-post:	anna.lanka@taltech.ee

Hariduskäik

2020–2025	Tallinna Tehnikaülikool, doktorantuur (eriala: maateadused)
2017–2020	Läti Ülikool, bioloogia osakond, magistrikraad
2015–2017	Läti Ülikool, füüsika ja matemaatika osakond, bakalaureuseõpingud (katkestatud)
2012–2015	Läti Ülikool, bioloogia osakond, bakalaureusekraad
2009–2012	Tukuma Raiņa Riigigümnaasium

Keelteoskus

Läti keel	Emakeel
Inglise keel	Kõrgtase
Vene keel	Keskmine / Algtase

Teenistuskäik

2020–praeguseni	Tallinna Tehnikaülikool, geoloogia instituut, nooremteadur
2019–2020	Läti Veekeskkonna Instituut, laboritehnik
2018–2020	Läti Looduse Fond, välitöödetehnik
2015–2016	Läti Loodusmuuseum, entomoloog

ISSN 2585-6901 (PDF)
ISBN 978-9916-80-336-3 (PDF)