

Urbanization-driven Cladocera community shifts in the lake - a case study from Baltic region, Europe

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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,

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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 '70s 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 (apkaimēs, 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 Cladocera 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

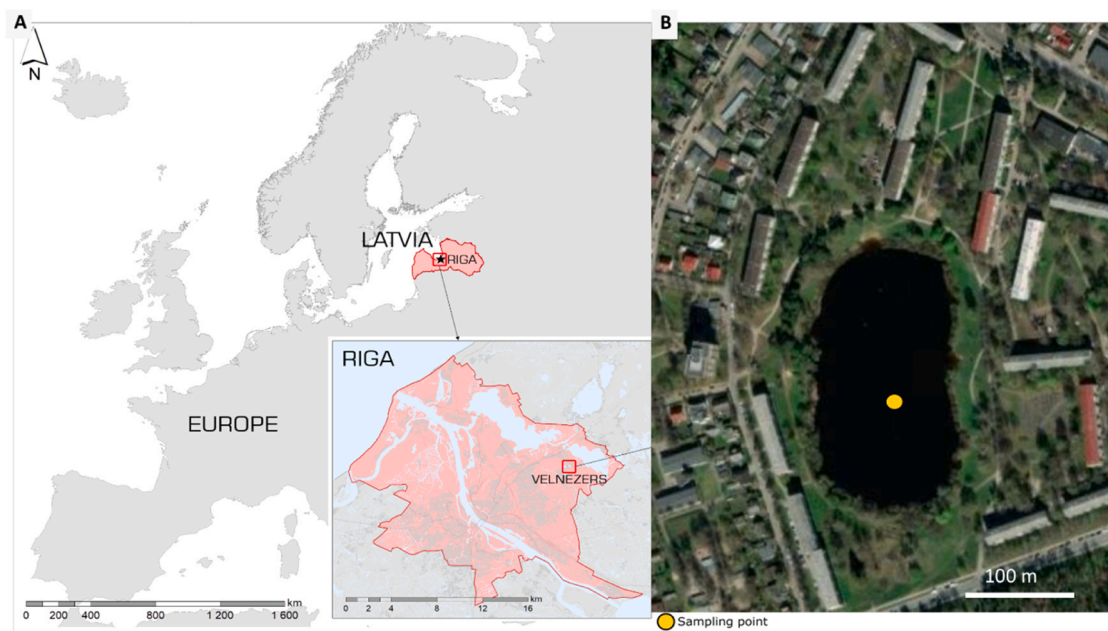


Fig. 1. (A) Sampling area – Lake Velnezers (Latvia, Northern Europe) location in Riga city and (B) sampling point indicated with a yellow dot.

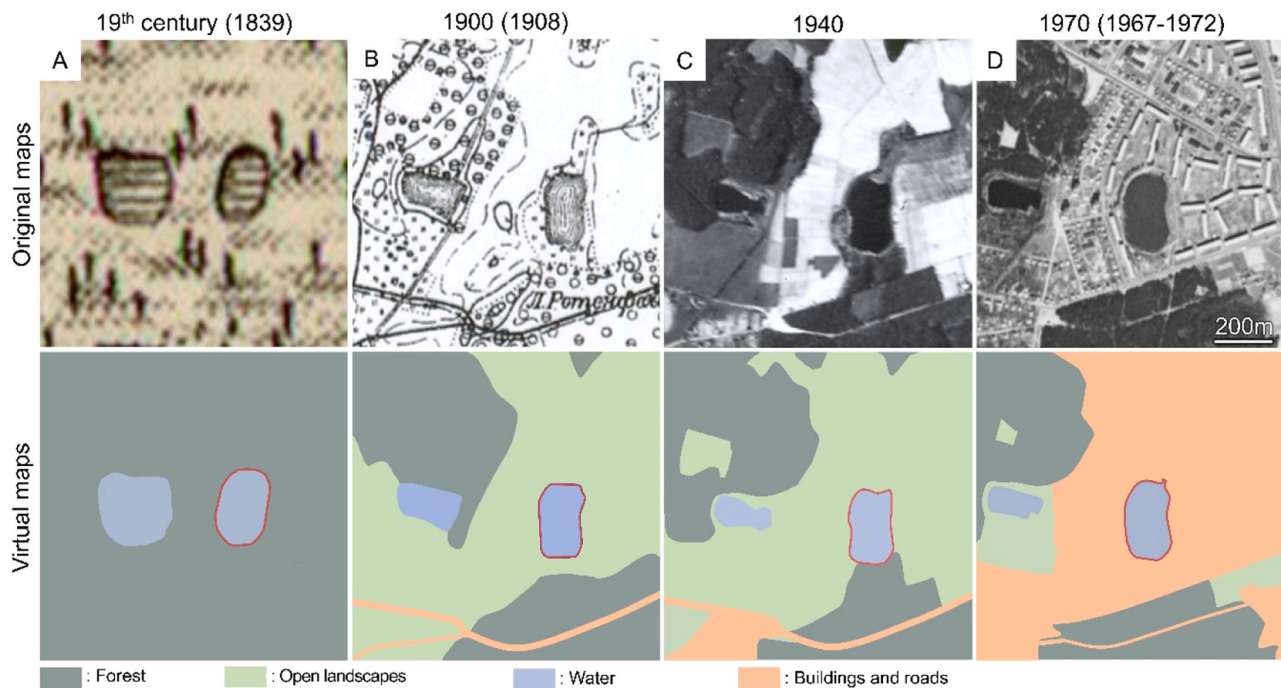


Fig. 2. Lake Velnezers landscape development based on maps and aerial photos throughout the time (from 19th to 20th century). Forest (dark green), open landscapes consisting of meadows, agricultural lands, possibly also grazed wetlands (light green), and old agricultural lands starting to be gradually 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 $\mu\text{g}/\text{l}$ (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; Ličīte, 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 $\pm 5\%$. 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 HNO_3 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 cm³ 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-Courts 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 ²¹⁰Pb 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

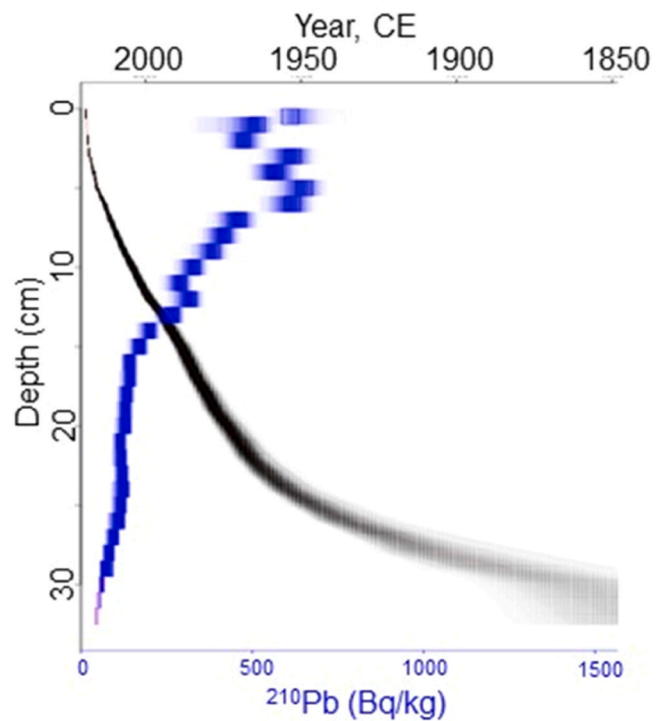


Fig. 3. Lake Velnezers chronology where: (1) blue-scale indicates the modeled ²¹⁰Pb values (based on the posterior values for the age model and the ²¹⁰Pb parameters), (2) blue boxes indicate the measured values, (3) grey-scale is the age-depth model at 95 % probability range.

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 ²¹⁰Pb 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.

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

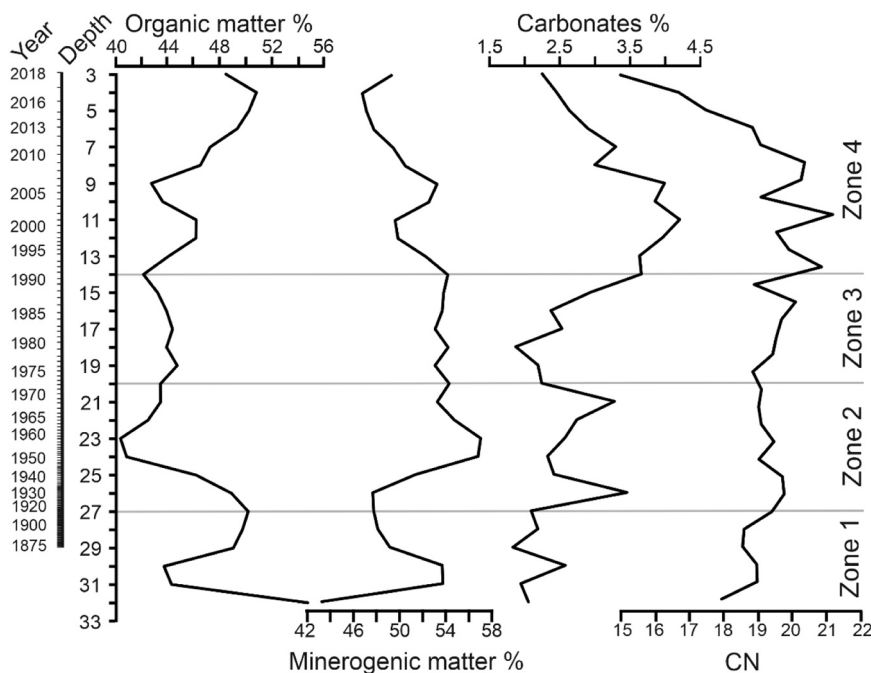


Fig. 4. Loss on Ignition (LOI) results expressed in percentages and carbon/nitrogen (CN) expressed as an atomic ratio in the sediment profile of Lake Velnezers.

(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

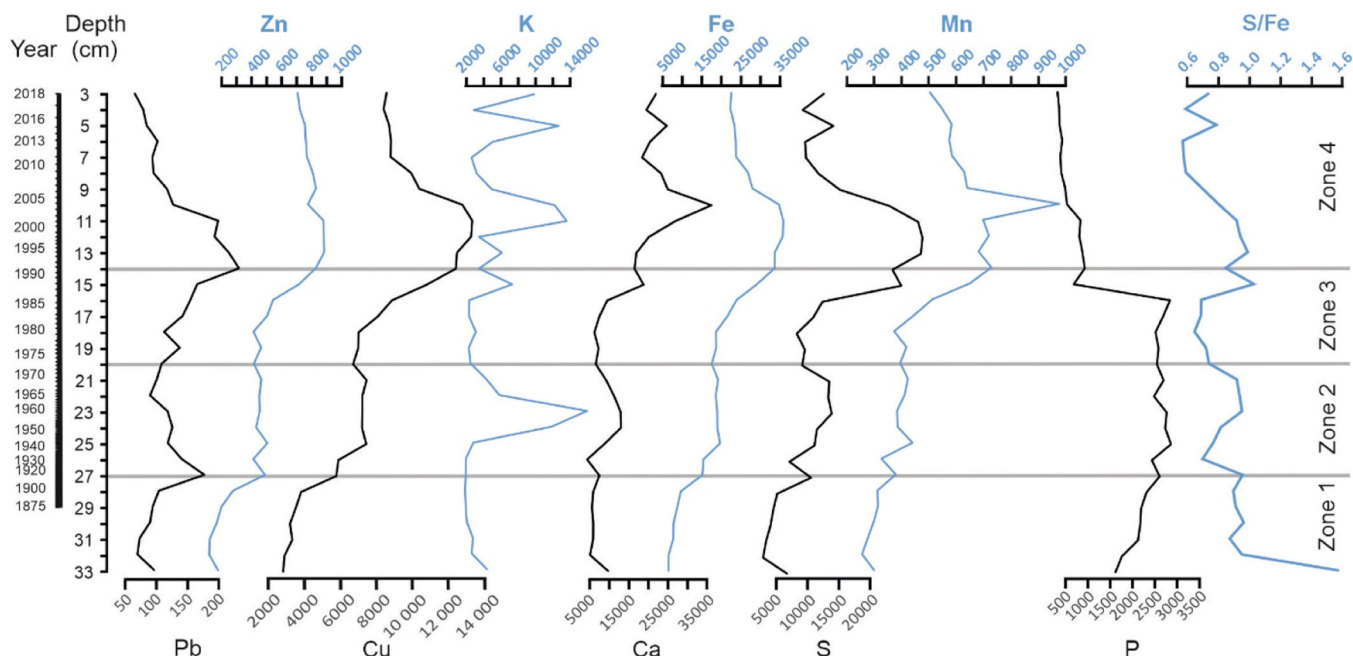


Fig. 5. Vertical distribution of major elements (mg/kg) in Lake Velnezers sediment core.

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*, *Eurycerus*, *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 acanthoceroides*, *L. leydigi*, *Phreatolona 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 *Ilyocryptus* 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

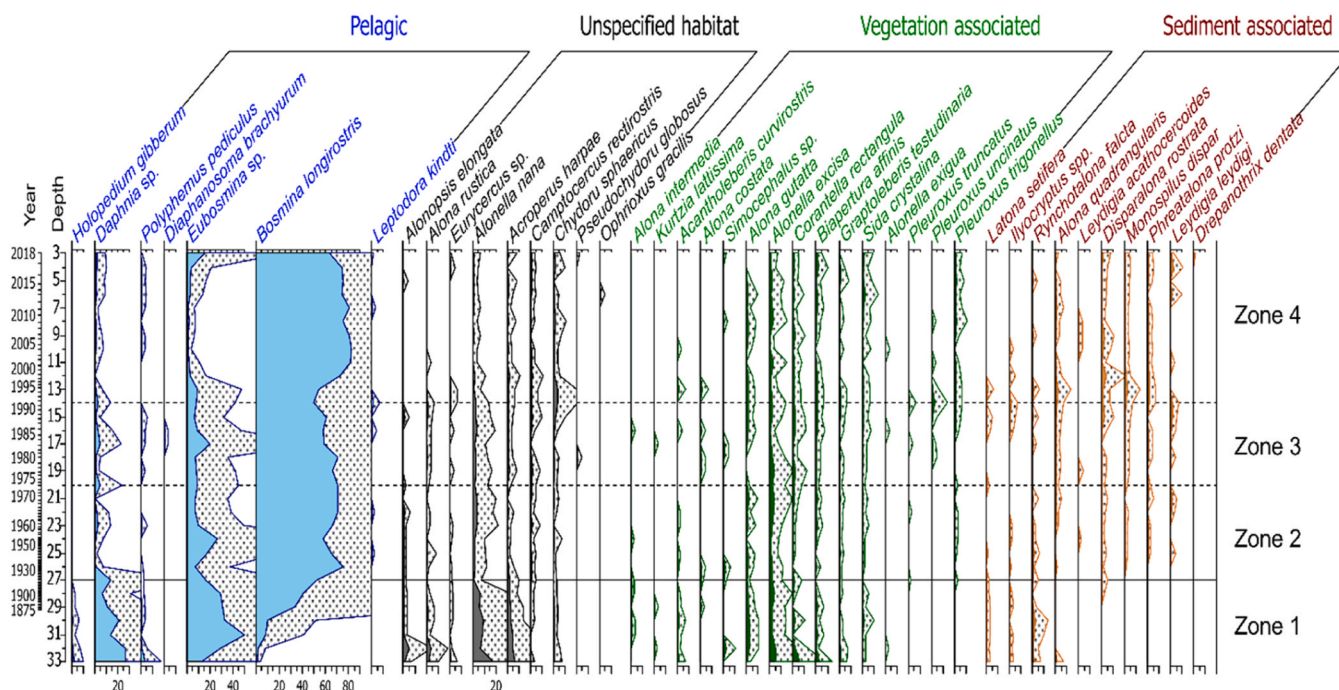


Fig. 6. Cladoceran assemblages based on habitat preference throughout the sediment core of Lake Velnezers. The diagram shows the relative abundance of the taxa.

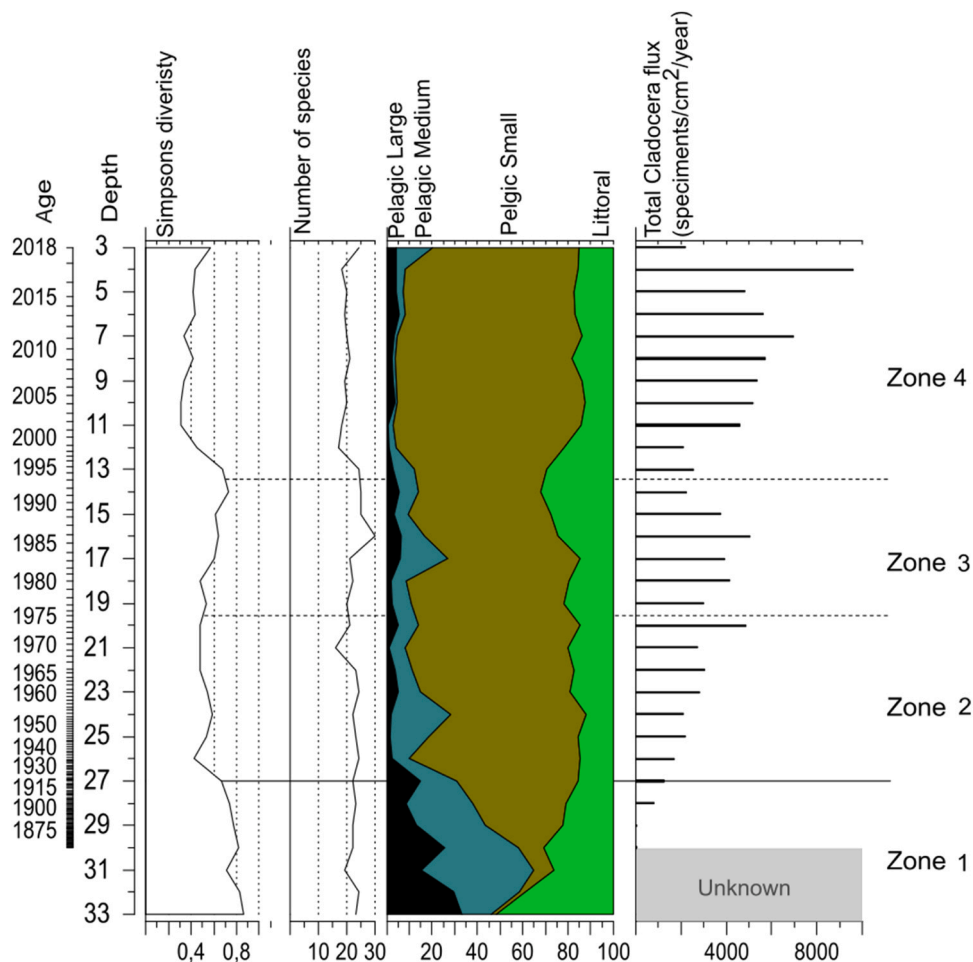


Fig. 7. Summary of parameters describing subfossil Cladocera communities throughout the sediment core of Lake Velnezers. The colorful diagram depicted the relative abundance of Large pelagic (Black), Medium pelagic (Blue), Small pelagic (Brown), and Littoral (Green) species. Total Cladocera flux shows 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; Āeirāns, 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 oligotrophy (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-Goldyn 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 Bertilsson 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 Kļaviņš 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 of 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. **Saim 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.

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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.

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