

Habitat transformations during abrupt climate changes at the Late Glacial/Holocene transition, as revealed by cladocerans

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We describe a high-resolution analysis of subfossil Cladocera conducted at the Ługi site in Poland, a peatland ecosystem that developed within a former lake in the Warta River Valley. Study focused on core sections corresponding to periods of rapid climatic change during the Late Glacial/Holocene transition, enabling detailed observation of environmental transformations. Palynological analysis facilitated the determination of boundaries between cold and warm periods. The Cladocera analysis revealed that, during the end of Oldest Dryas, the lake was shallow with conditions unfavourable for Cladocera development. At the onset of the Bølling period, warming led to increased species diversity and a rise in water levels within the lake. Following this warming and associated ecological changes, the Bølling-Allerød period was characterized by continued progressive warming, that was interrupted by the Older Dryas cooling event, marked by a sharp decline in Cladocera species. At the end of the Allerød, there was a decline in lake water levels, followed by the onset of the Younger Dryas, which brought a notable cooling trend. The Younger Dryas/Holocene transition was not captured due to a hiatus in sediment deposition. Data from the sediment section corresponding to the Holocene (Boreal period) revealed improved habitat conditions and a warming of the waters. These analyses and interpretations are aimed at comparing records of rapid climatic changes as recorded by Cladocera remains, and demonstrating differences in their course in basins that differ from each other as regards habitat features.

Key words: subfossil Cladocera, high resolution, Late Vistulian, Warta River Valley, central Poland.

INTRODUCTION

As lake ecosystems adapt to changes in climatic conditions, they undergo alterations in their physical, chemical and biological characteristics (Adrian et al., 2009). These climatic shifts impact lake levels and the duration of water retention, which in turn lead to alterations in littoral habitats, sediment distribution, water chemistry and nutrient availability (Battarbee, 2000; De Senerpont Domis et al., 2013). As a result, the aquatic biota community, including fish, invertebrate and plant assemblages,

undergo significant changes. Species compositions may shift as certain organisms adapt to new conditions and others decline or migrate. These changes can also lead to the introduction of invasive species, disruption of food webs, and alterations in reproductive cycles, ultimately impacting biodiversity and ecosystem stability (EPA, 2008; Woodward et al., 2010).

Aquatic biotas respond to climate change in various ways, which can lead to altered growth rates, shifts in species composition, and changes in abundance. The response, however, is both species-specific and influenced by their trophic position (Sweetman et al., 2008; Adrian et al., 2009). For instance, changes in abundance often differ between species (Adrian et al., 2009), with some plankton species responding to warming by changing their populations, while others remain stable. This suggests that these species may be more resilient to climate change or influenced by other ecological factors affecting their abundance and distribution. A notable shift was observed in di-

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atom communities, transitioning from benthic (bottom-dwelling) to planktonic (free-floating) species. Similar changes have been seen in invertebrate communities, such as chironomids, which increased in abundance and diversity in response to warming (Smol et al., 2005). Rising temperatures accelerate phytoplankton growth and promote the development of cyanobacteria, giving them a competitive edge over other phytoplankton groups. Temperature shifts and physical mixing further enhance the competitive advantage of smaller diatom cells, such as those of the genus *Cyclotella* (Winder and Sommer, 2012). Additionally, as the climate warms, zooplankton species preferring colder, oligotrophic waters are being replaced by those adapted to warmer, nutrient-rich environments. Zooplankton also adapt to these changing conditions by adjusting their body size (Rizo et al., 2019).

Reorganizations of phyto- and zooplankton communities can have cascading ecosystem effects influencing their functions. Studying the responses of phytoplankton and zooplankton to environmental changes driven by past climate shifts provides valuable insights into the adaptive mechanisms of these organisms. Understanding these reactions not only aids in reconstructing historical climate changes but also enhances our ability to predict the future impacts of global warming on modern aquatic ecosystems. The organisms most studied in the context of past environmental changes include diatoms, chironomids and cladocerans, and their responses seem to vary significantly depending on different factors.

In this study we concentrate on analysis of subfossil Cladocera remains, as these respond rapidly to climatic events, making them valuable indicators of past and present environmental changes and allowing us to understand the timing and magnitude of rapid climate events. Moreover, as primary consumers, they play an important role linking primary producers to higher trophic levels; thus, changes in Cladocera populations can have cascading effects on the entire freshwater ecosystem.

In the past, the latest marked climate shift occurred during the transition from the Pleistocene to the Holocene, ~11,700 years ago. As the transition into the Holocene began, temperatures started to rise, leading to rapid warming and the subsequent melting of glaciers, with a general increase in summer temperatures of 5–6°C in Europe over a few centuries (Heiri et al., 2014). This climate shift from the Late Glacial to the Holocene was not gradual; rather, it was marked by several rapid climate phases occurring on millennial to centennial scales, such as the Allerød Interstadial and Younger Dryas Stadial. During these phases, environmental upheavals occurred, leading to significant reorganisation of both terrestrial and aquatic biota. However, the intensity and impact of these phases varied both across different regions and between the phases themselves. The fastest and most pronounced biotic shifts are usually related to the Oldest Dryas Stadial/Bølling Interstadial transition (~14,700 years BP; Brooks and Heiri, 2013) and the Younger Dryas/Holocene transition (~11,700 years BP; Engels et al., 2024), that are regarded as a palaeoanalogues of current climate changes (Stivrrins et al., 2016).

In this study, we focused on four distinct sections of the sedimentary profile obtained from the Ługi peatland in central Poland, specifically at depths of 327–310 cm (Oldest Dryas/Bølling), 300–270 cm (Bølling/Older Dryas/Allerød), 245–230 cm (Allerød/Younger Dryas), and 210–160 cm (Younger Dryas–Holocene). These sections were carefully selected on the assumption that they capture periods of rapid climatic and environmental change.

Previous multi-proxy studies conducted at the Ługi peatland – including analyses of Cladocera and pollen – have provided a valuable scientific foundation for this research (Pawłowski, 2017; Mielczarek, 2018; Forsyia et al., 2023). Building on this background, our investigation focused primarily on subfossil Cladocera remains, supplemented by palynological analyses. While the latter served chiefly for stratigraphic control, the central objective was to explore how Cladocera assemblages in central Poland responded to abrupt climate shifts during the transition from the Late Glacial to the Holocene. Our research centred on analysing subfossil cladoceran remains, complemented by palynological analyses. While the latter were primarily employed for stratigraphic purposes, the primary aim of the study was to deepen our understanding of how cladoceran assemblages in central Poland responded to rapid climate changes during the cold-warm phases of the Late Glacial to Holocene transition. Additionally, Cladocera assemblages from two sediment cores (Ł-1 and Ł-2) are compared to identify both similarities and differences in palaeoenvironmental responses. This comparative and resolution-sensitive approach may contribute to broader insights in future palaeolimnological research.

MATERIALS AND METHODS

STUDY SITE

The Ługi peatland is located in the Warta River Valley system in the north of the Sieradz Basin, central Poland (Fig. 1). The lake basin formed as a result of the cutting-off of a section of the Warta Valley at the end of the Last (Vistulian) Glaciation due to increased erosion after the Poznań Phase of the Last Glacial Maximum. The Ługi wetland consists of two parts, but only in the western one were lacustrine accumulations found (Forsyia, 2012). The western part of the wetland covers ~28 ha, and the total thickness of biogenic deposits reaches 3.3 m (Ł-2; Rudna and Forsyia, 2023).

CORING AND SUBSAMPLING

The biogenic deposits of the Ługi peatland were initially studied as part of geological mapping efforts (Klatkova and Zoloba, 1992). Subsequent lithological investigations via soundings identified peat and gyttja deposits exceeding 2.5 metres in thickness at its centre. The first Ługi core (Ł-1) was collected, and samples were analysed for dating and preliminary palaeoecological assessment (Forsyia, 2012). Detailed analyses of the sequence from Ł-1, including pollen, Cladocera, Chironomidae, and geochemical studies, revealed that biogenic accumulation began during the Oldest Dryas (Forsyia et al., 2023). This sequence provided insights into environmental changes during the Late Glacial and Early Holocene.

In this study, we focused on the second core (Ł-2), which was collected after further reconnaissance in the central part of the wetland, ~15 metres north-west of the Ł-1 profile (Fig. 2). The Ł-2 core features a sedimentary profile about 335 cm thick with a slightly different stratigraphic sequence compared to the core Ł-1. The lithology of the Ł-2 core predominantly consists of various types of gyttja, with sands confined to the basal section of the profile. From 350–334 cm, the deposit comprises sand of various grain sizes and organic matter, transitioning to sand mixed with organic mud between 334–327 cm. Above this layer, the profile is dominated by gyttja types in the following se-

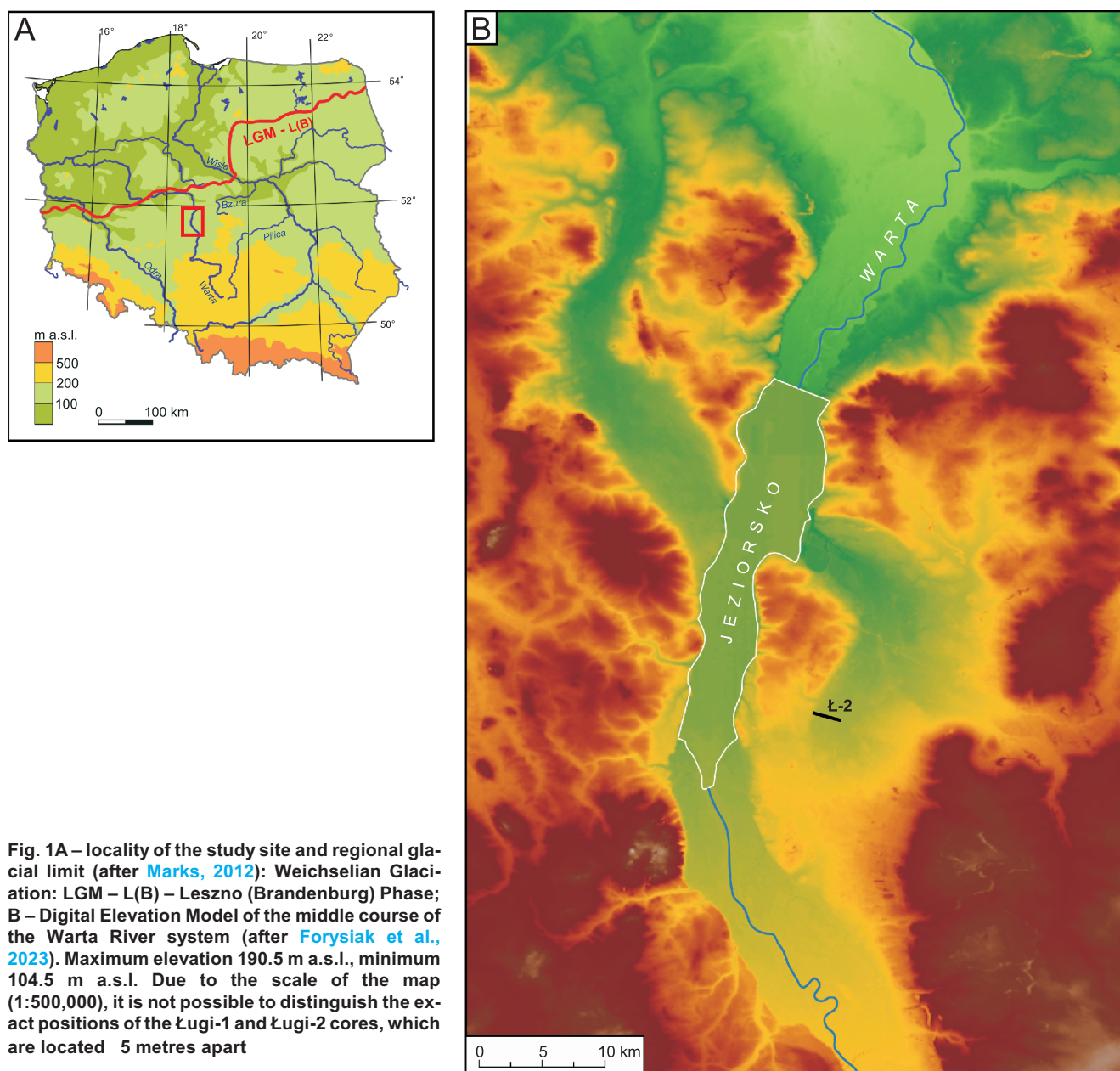


Fig. 1A – locality of the study site and regional glacial limit (after Marks, 2012): Weichselian Glaciation: LGM – L(B) – Leszno (Brandenburg) Phase; B – Digital Elevation Model of the middle course of the Warta River system (after Forysiak et al., 2023). Maximum elevation 190.5 m a.s.l., minimum 104.5 m a.s.l. Due to the scale of the map (1:500,000), it is not possible to distinguish the exact positions of the Ługi-1 and Ługi-2 cores, which are located 5 metres apart

quence: coarse-detrital gyttja with sandy admixtures from 327–323 cm, detrital-calcareous gyttja from 323–312 cm, calcareous gyttja from 312–255 cm, calcareous-detrital gyttja from 255–178, and reed peat from 178 cm upwards.

PALYNOLOGICAL ANALYSIS

Pollen samples, each 1 cm³ in volume, were taken at 1 cm resolution for analysis and prepared following the standard chemical procedure described by Berglund and Ralska-Jasiewiczowa (1986). As a marker to determine the concentration of palynomorphs in the sediment, 1 tablet of *Lycopodium* (Stockmarr, 1971) was added. The pollen was analysed using a microscope at 400× and 1000× magnification and recognized based on the available literature (Moore et al., 1991; Beug, 2004). The calculation sum consisted of pollen grains of trees and shrubs (arboreal pollen AP) and terrestrial herbaceous

plants (non-arboreal pollen NAP). Pollen and spores of aquatic and local telmatic plants were excluded from the calculation sum. The results are shown as a simplified percentage diagram. Palynological analysis was instrumental in identifying zones associated with the climatic phases, including the Oldest Dryas/Bølling, Bølling/Older Dryas/Allerød, Allerød/Younger Dryas, and the Younger Dryas-Holocene boundary.

CLADOCERA ANALYSIS

The analysis of subfossil Cladocera was conducted on core sections representing warm and cold phases during the transition from the Late Glacial to the present interglacial (Holocene). The research involved analysis of four sections of core Ł-2 (327–310 cm: Oldest Dryas/Bølling; 300–270 cm: Bølling/Older Dryas/Allerød; 245–230 cm: Allerød/Younger Dryas; 210–160 cm: Younger Dryas-Holocene boundary), which, according to

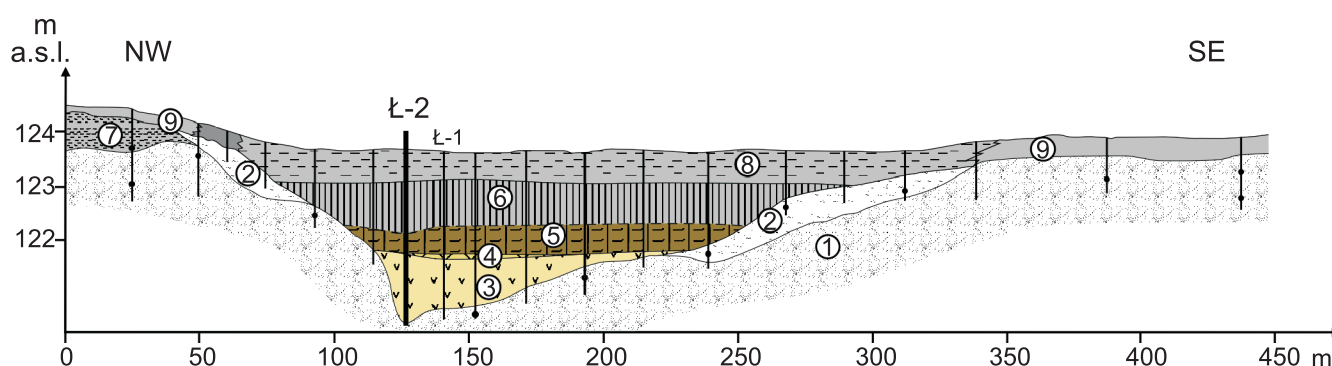


Fig. 2. Geological cross-section of the Ługi peatland, indicating the location of the Ł-1 and Ł-2 profiles

The section includes distinct layers of different lithologies, as follows: 1 – sand of various grain sizes, 2 – sand with biogenic matter, 3 – detrital-calcareous gyttja, 4 – detrital gyttja, 5 – calcareous-detrital gyttja, 6 – reed peat, 7 – aeolian sand, 8 – sedge peat with muck, 9 – soil

pollen analysis results, align with key climatic shifts between cold and warm phases during the transition from the Late Glacial to the Holocene. The sampling resolution mainly ranged from 0.5 to 1 cm. However, in layers where the material for analysis was insufficient, it was necessary to reduce the resolution to 24 cm. Samples were prepared according to the standard methodology by Frey (1986), which involves boiling 1 cm³ of fresh sediment in 10% KOH. The residue was rinsed through a 38 µm sieve, transferred to test tubes, and filled up with distilled water to 10 ml. The final solution was stained with safranin and a 100 µL volume slide was prepared. For each sample, one to five slides were analysed, and at least 100 individuals were counted (Kurek et al., 2010). All Cladocera remains were counted: headshields, shells, postabdomens, postabdominal claws, and ephippia, using a biological microscope with magnifications of 100×, 200×, and 400×. Species identification was carried out following Szeroczyńska and Sarmaja-Korjonen (2007), Sinev (2020) and Van Damme and Dumont (2008). The results of subfossil Cladocera analysis for four core sections are shown in a percentage diagram, including the ratio of planktonic to littoral taxa. The diagram was plotted using the C2 software (Juggins, 2007). The variability in total abundance, species composition, and individual frequency enabled the identification of distinct periods with different environmental conditions within the sections analysed.

The Cladocera data were further analysed using detrended correspondence analysis (DCA; Hill and Gauch, 1980) to summarize environmental changes. Rare species contributing less than 5% were excluded. The analysis was performed in the R statistical software environment (R Core Team, 2020) using the vegan package (Oksanen et al., 2015).

RESULTS

POLLEN RECORD

The results of the palynological analysis are briefly summarised in Table 1 and illustrated in a simplified diagram in Figure 3. The boundaries between the subunits identified reflect the transitions between cold and warm phases during the Late Gla-

cial to Holocene transition, including the Oldest Dryas/Bølling, Bølling/Older Dryas/Allerød, Allerød/Younger Dryas phases, and Younger Dryas-Holocene boundary.

SUBFOSSIL CLADOCERA ASSEMBLAGES

The results of the subfossil Cladocera analysis are visualized in Figure 4. A total of 23 species were identified, with Cladocera belonging to four families – Daphniidae, Bosminidae, Chydoridae and Sididae. Chydorids dominated the cladoceran assemblages throughout the sedimentary sequence, with littoral Cladocera predominantly represented by taxa such as *Chydorus sphaericus* and *Coronatella rectangula*. Across the four sections where Cladocera fauna was analysed, their total abundance ranged from 100 individuals per cubic centimetre to 6750 ind./cm³.

SECTION I

(310–327 cm; OLDEST DRYAS-BØLLING TRANSITION)

The total abundance of Cladocera ranged from 100 ind./cm³ at ~327 cm depth to 900 ind./cm³ at ~313 cm depth. In this section of the core, very few taxa appeared. However, two distinct periods with different Cladocera assemblages can be distinguished. The Oldest Dryas to the Bølling phase (section I), is characterized by a gradual increase in the total abundance of Cladocera.

In the lower portion of the section, corresponding to the Oldest Dryas, the assemblage is dominated by the littoral species *C. rectangula* and the pioneer species *Chydorus sphaericus*. Initially, *C. rectangula* is the sole species, but its proportion significantly declines as *Ch. sphaericus* becomes more dominant. The upper part of section I (Bølling beginning) is still characterized by the domination of *Ch. sphaericus* and *C. rectangula* but planktonic species from the families Bosminidae and Daphniidae begin to appear. The first planktonic species to emerge is *Bosmina* (E.) *coregoni*, followed by *Daphnia longispina* and *Bosmina* (E.) *longispina*. At a depth of ~315 cm, *B. (E.) longispina* and *B. (E.) coregoni* co-occur, after which *B. (E.) coregoni* disappears from the assemblage. After its initial disappearance, *B. (E.) longispina* returns periodically, although only in small

Table 1

Pollen chronozones (with brief descriptions of the vegetation cover) in relation to the Cladocera section

Cladocera core section	Chronozones	Vegetation	Environmental conditions
Sec. I 310–327 cm	327 cm Oldest Dryas 322 cm	An open, treeless landscape was dominated by herbaceous and shrubby, light-demanding plant communities, with: <i>Helianthemum</i> , <i>Dryas octopetala</i> , <i>Saxifraga</i> species, and <i>Gypsophila</i> species. The higher vegetation layer was mainly composed of sea buckthorn shrubs (<i>Hippophae rhamnoides</i>), with juniper (<i>Juniperus</i>) also present. Moist habitats were occupied by shrub communities featuring <i>Betula nana</i> and <i>Salix</i> . Widespread sedge meadows (Cyperaceae) developed	Cold
	Bølling 285 cm	The vegetation cover has changed with the appearance of sparse pioneer trees of <i>Betula</i> and <i>Pinus</i> . The proportion of shrubby vegetation, including juniper and buckthorn, has declined, while the open landscape with light-demanding herbaceous communities remained dominant	Improving conditions (warming)
Sec. II 270–300 cm	Older Dryas 277 cm	There have been slight changes of the vegetation. The proportion of pine has decreased, the presence of juniper bushes has increased again, while buckthorn has also reappeared.	Deterioration of conditions (cooling)
	Allerød 235 cm	The area dominated by herbaceous plant communities has decreased (decline of NAP). The juniper shrubland has diminished, replaced by the developing open birch-pine woodlands. Decline in the proportion of plant communities composed of <i>Betula nana</i> , <i>Salix</i> , and Cyperaceae, which are typically associated with wetland habitats.	Improving conditions (warming)
Sec. III 230–245 cm	Younger Dryas 175 cm	The proportion of pine decreased, whilst the presence of juniper bushes increased again. Herbaceous light-demanding species reappear. Open landscape with abundant juniper shrubs and shade-intolerant herbaceous vegetation communities (e.g., <i>Helianthemum</i> , <i>Saxifraga</i> sp.). Large proportion of mire, with notable <i>Betula nana</i> , <i>Sphagnum</i> and Cyperaceae.	Deterioration of conditions (cooling)
	Holocene	Significant change in the vegetation cover, with the appearance of mesophilous trees and the development of forest communities.	Improving conditions (warming)

numbers. Moreover, this part of the section is marked by a gradual increase in the share of *Acroperus harpae*, which reached 37.5% at a depth of 312 cm, where it co-occurred exclusively with *Ch. sphaericus* (62.5%).

SECTION II

(270–300 cm; BØLLING/OLDER DRYAS/ALLERØD TRANSITION)

In this core section, fifteen Cladocera species were identified, belonging to three families: Daphniidae, Bosminidae and Chydoridae. The total abundance of Cladocera ranged from 350 ind./cm³ at 289 cm depth to 3400 ind./cm³ at 282 cm depth with an increasing trend towards the upper portion of this core section.

In the lower part of core section II, corresponding to the end of the Bølling period, the total abundance of Cladocera ranged from 350 to 1450 ind./cm³, with littoral species dominating the assemblage. *Ch. sphaericus* was the most abundant species in

the bottom layer, accounting for up to 83% of the assemblage at a depth of 300 cm. This dominance was later replaced by *C. rectangularis*, which peaked at 81% at a depth of 293 cm.

Cladoceran assemblages in the middle part of the section remained dominated by *C. rectangularis* with its share ranging from 62 to 94%. At that time, planktonic species also reappeared (a depth of 286 cm), collectively accounting for just over 6% of the population, including species such as the *D. longispina* group and *B. (E.) coregoni*. The presence of *Alona affinis* and *A. harpae* declined, with these species being recorded only occasionally, while the abundance of *Alona quadrangularis* increased, with this species appearing regularly in this section of the sedimentary profile.

In the upper part of section II, corresponding to the onset of the Allerød period, a significant increase in Cladocera species diversity was recorded. The initial phase of this period was marked by a decrease in total Cladocera abundance to 395 ind./cm³ at a depth of 278 cm, accompanied by a reduction in

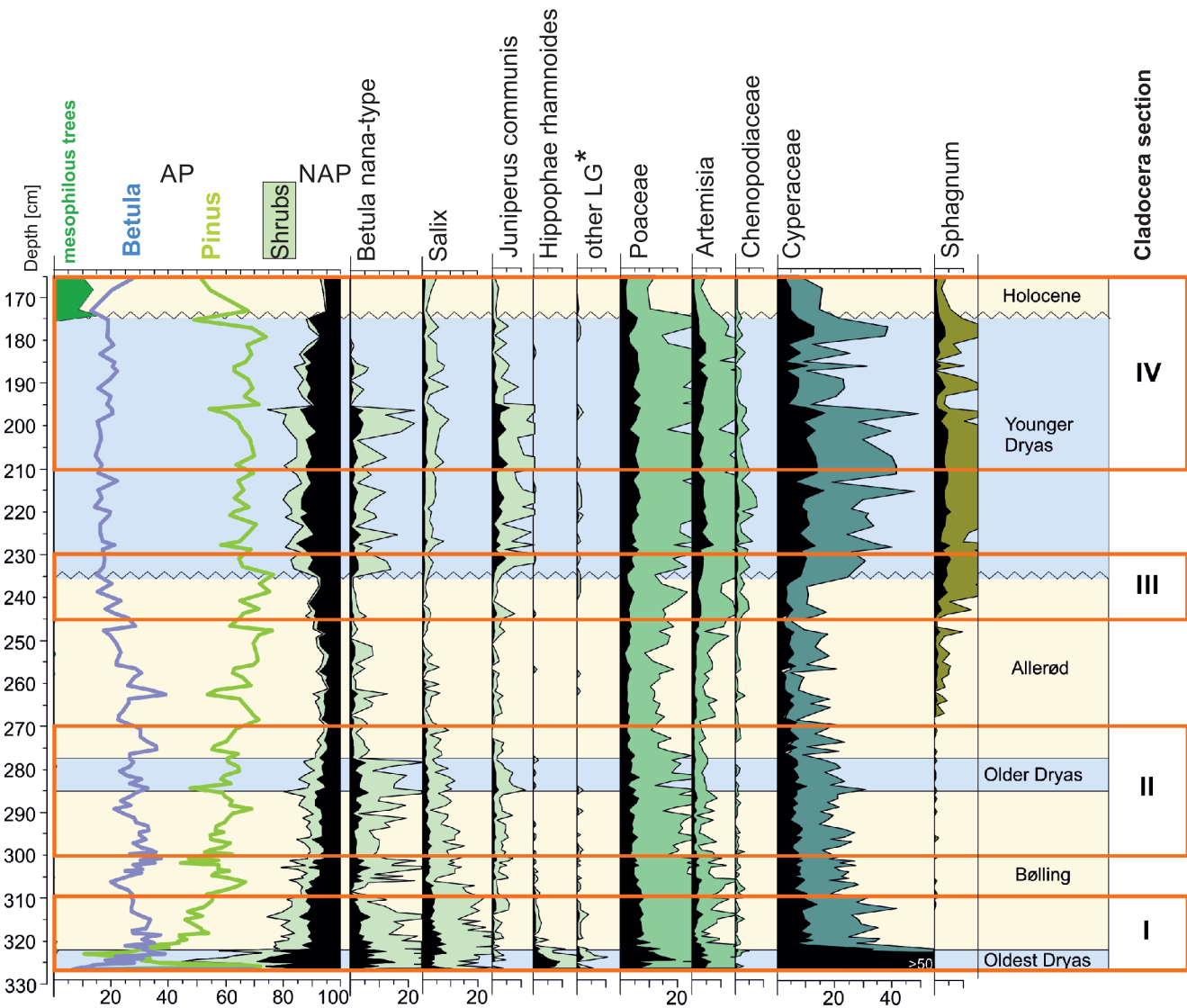


Fig. 3. Percentage diagram of selected pollen taxa from core Ł-2 (Ługi peatland)

Wavy lines denote stratigraphic uncertainties at the boundary between the Allerød and Younger Dryas, and between the Younger Dryas and Holocene; * – other LG- curve including other LG-specific plants: *Helianthemum*, *Dryas octopetala*, *Saxifraga* sp., *Gypsophila repens*-type, *Selaginella selaginoides*, *Ephedra* sp., *Bupleurum*, *Artemisia*, *Chenopodiaceae*

the proportion of *C. rectangularis* to 3–8%. At a depth of 279 cm, *Ch. sphaericus* accounted for 48% of the assemblage, while *A. quadrangularis* comprised 22%. Moreover, *A. harpae*, *A. affinis*, and *Pleuroxus uncinatus* were also present. From a depth of ~275 cm, total Cladocera abundance increased, reaching 2150 ind./cm³. At a depth of 273 cm, the planktonic species *B. (E.) coregoni*, *B. (E.) longispina*, and *Bosmina longirostris* were recorded, with relative abundances ranging from 5 to 29%. The littoral species *Alonella excisa*, *Alonella exigua* and *Camptocercus rectirostris* were also identified from this part of the core.

thirteen species of Cladocera were recorded in the lower part of section III. Littoral species dominated, with their share ranging from 92 to 100%. The most abundant species were *Ch. sphaericus*, which accounted for up to 56% at a depth of 238 cm, followed by *C. rectangularis*, *A. affinis* and *Pleuroxus trigonellus*.

During the period corresponding to the upper part of section III, total Cladocera abundance experienced a sharp decline to 260 ind./cm³ (a depth of 233 cm). Littoral species continued to dominate, accounting for over 90% of the assemblage, with *Ch. sphaericus* being the most prevalent. Key changes in the Cladocera assemblage included the disappearance of *A. affinis* and a gradual increase in *A. harpae*.

SECTION III

(230–245 cm; ALLERØD/YOUNGER DRYAS TRANSITION)

Eighteen species of Cladocera were identified from three families: Daphniidae, Bosminidae and Chydoridae. The total abundance of Cladocera ranged from 260 ind./cm³ at a depth of 233 cm to 2400 ind./cm³ at a depth of 235 cm. Between six and

SECTION IV

(160–210 cm; YOUNGER DRYAS-HOLOCENE BOUNDARY)

From this section, twenty species of Cladocera were identified, belonging to four families: Daphniidae, Bosminidae, Chydoridae and Sididae. The total abundance of Cladocera

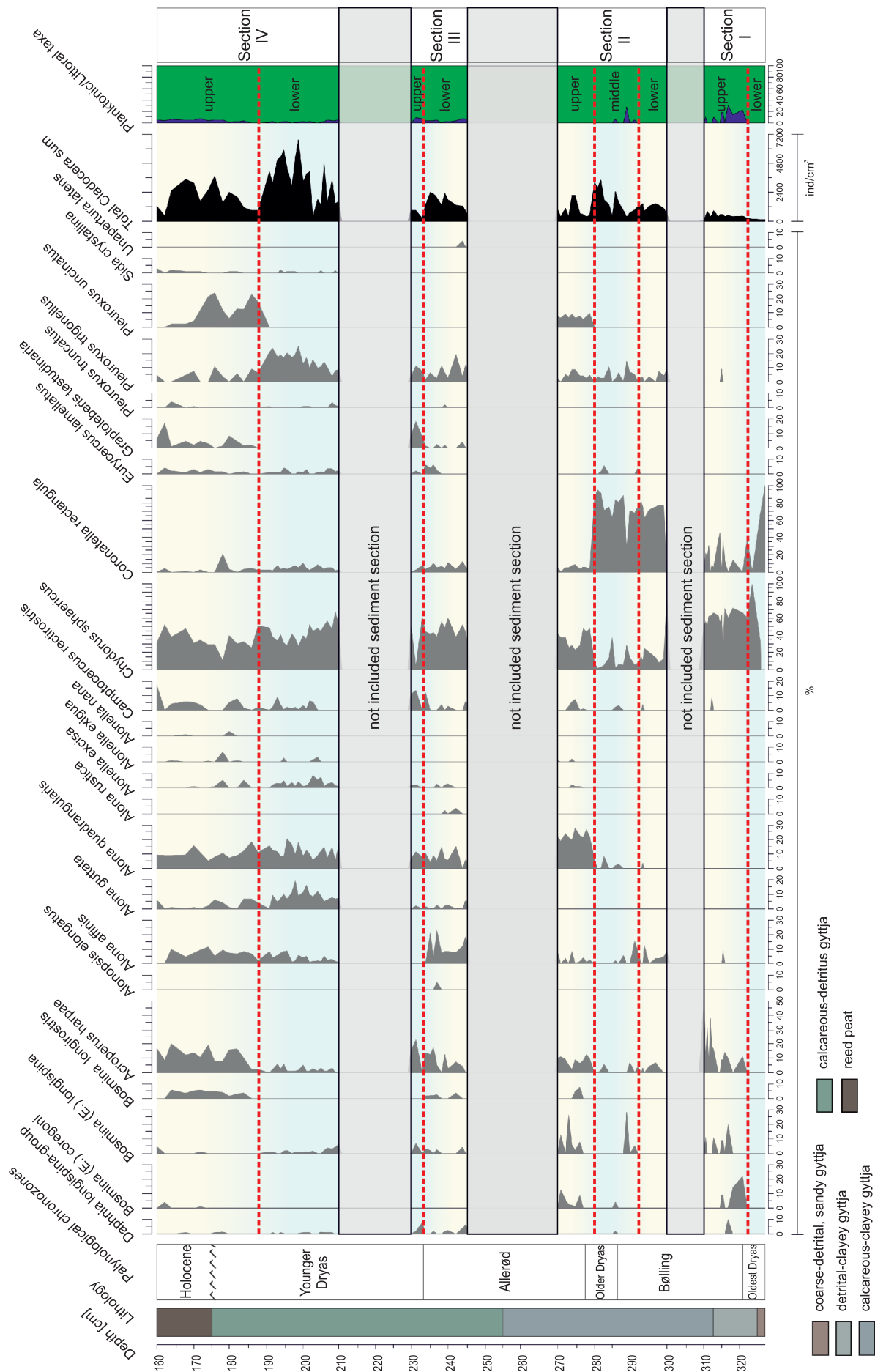


Fig. 4. Diagram of percentage composition and the total sum of Cladocera specimens analysed from the core L-2

ranged from 355 ind./cm³ at a depth of 203 cm to 6750 ind./cm³ at a depth of 199 cm. In the core layers corresponding to the Younger Dryas period (lower part of section IV), the share of planktonic species reached a maximum of 6% at a depth of 210 cm. Littoral species still dominated, accounting for between 94% and occasionally up to 100% of the total abundance. The number of species ranged between 8 and 14. Among these, *Ch. sphaericus* was the most abundant, reaching 67% at a depth of 209 cm and 27% at a depth of 199 cm, followed by *P. trigonellus* (up to ~25%), *P. uncinatus* (up to ~23%) and *A. quadrangularis* (up to ~20%).

According to the results of the palynological analysis, the Younger Dryas/Preboreal transition could not be captured due to a sedimentary hiatus. The upper part of section IV corresponds to the Boreal period. In this part of section IV, the Cladocera assemblage remained dominated by littoral species, comprising from 92 to 100%, with the number of species varying between 7 and 20. The total abundance of Cladocera varied from 460 to 3700 ind./cm³. The period corresponding to this part of the core is marked by a decline in *Ch. sphaericus* proportions to ~10% (at 178 cm), followed by an increase in several other taxa, including *A. harpae* (reaching ~19% at 174 cm), *A. quadrangularis* (up to ~16% at 170 cm), *P. uncinatus* (up to ~24%), and *C. rectangula* (up to ~21%).

In the ordination of samples, the lengths of DCA Axes 1 and 2 measured 2.4 and 1.99 standard deviations (SD), respectively. Together, these two axes explained 67% of the total variation in the dataset, with Axis 1 accounting for 46% and Axis 2 contributing 21% (Fig. 5). The DCA plot for taxa (Fig. 5A) indicated that *C. rectangula* had the highest positive score on Axis 1, while *P. uncinatus*, *Graptoleberis testudinaria* and *B. longirostris* had the lowest (negative) score. On Axis 2, *B. (E.) coregoni*, *A. harpae*, *B. (E.) longispina*, and *G. testudinaria* showed the highest scores, whereas *A. exigua*, *A. excisa* and *Alona guttata* had the lowest (negative) scores. The DCA results for the samples (Fig. 5B) revealed a clear differentiation between the core sections analysed, highlighting distinct shifts in Cladocera communities between the sections studied. The DCA results indicate a significant differentiation among the samples, with the end of Younger Dryas and Allerød appearing to be the most closely related. The most significant shift was observed during the Oldest Dryas-Bølling transition and the Bølling/Older Dryas/Allerød transitions (Fig. 5C).

DISCUSSION

The Cladocera record from the Ługi palaeolake illustrates how climate indirectly influenced the assemblages. The dynamics of Cladocera during the Late Glacial/Holocene transition, as revealed by DCA results, were primarily driven by two key factors. The highest positive values on DCA Axis 1 are associated with *C. rectangula*, a littoral species commonly found among macrophytes and capable of tolerating a wide range of temperatures and trophic conditions (Błędzki and Rybak, 2016). However, this taxon typically thrives in calcium-rich waters, suggesting that DCA Axis 1 (Fig. 5A) likely reflects calcium concentrations in the water column and habitat availability. Higher values on this axis indicate elevated Ca levels and a more limited macrophyte structure, likely due to the small size of the lake. DCA Axis 2 is primarily positively associated with *B. (E.) coregoni*, *B. (E.) longispina*, *A. harpae*, and *G. testudinaria*, while it shows a negative relationship with *A. exigua*, *A. excisa* and *A. guttata* (Fig. 5A). Axis 2 appears to be linked to water pH

and transparency, likely as an indirect consequence of temperature fluctuations, hydrological changes, and terrestrialization. More negative values correspond to lower pH levels and reduced water transparency, reflecting increased organic matter accumulation and shifts in aquatic ecosystem dynamics (Fig. 5B, C).

The extent of change within the Cladocera assemblages as response to the above factors was closely tied to the intensity of environmental fluctuations, with more pronounced changes leading to greater alterations in species composition and abundance. This highlights the adaptability of cladocerans as well as their vulnerability to rapid environmental shifts.

ENVIRONMENTAL CHANGES IN RESPONSE TO RAPID CLIMATE SHIFTS DURING THE LATE GLACIAL/HOLOCENE TRANSITION FROM SUBFOSSIL CLADOCERA PERSPECTIVE

OLDEST DRYAS/BØLLING TRANSITION (SECTION I)

At the end of the Oldest Dryas period, Cladocera species indicative of high nutrient content, such as *Ch. sphaericus* and *C. rectangula* (Szeroczyńska, 1985), were dominant. However, *Ch. sphaericus* is a eurytopic species, highly resilient, and often dominant in challenging conditions, while *C. rectangula* can adapt to both oligotrophic and eutrophic waters, typically associated with macrophytes (Błędzki and Rybak, 2016). The low abundance of these species and lack of other taxa, therefore, suggests rather limited nutrient availability and unfavourable conditions for Cladocera fauna development. DCA analysis (Fig. 5C) revealed that this period was characterized by higher pH levels, likely slightly alkaline, as supported by chironomid analysis (Forysiak et al., 2023). We infer that, during this period, the Ługi Lake was a shallow waterbody perhaps with some macrophyte presence, but its surface area was limited, restricting habitat availability. A limited number of species and their low abundance may have resulted from harsh environmental conditions, driven by prolonged ice cover and limited food availability. As the Bølling period approached, warming led to improved edaphic conditions, as shown by pollen data, which in turn facilitated the appearance of additional Cladocera species. However, despite the overall warming, conditions remained relatively cold. The presence of *A. harpae*, an "arctic species" alongside *Ch. sphaericus* indicates persistent cold conditions, while the low species diversity suggests that the environment was still unfavourable. This may have been due to the supply to the palaeolake of cold groundwater. This is further supported by the presence of *D. longispina*, a species characteristic of cold waters (Szeroczyńska and Zawisza, 2011). These unfavourable conditions are also reflected in the overall low trophic state of the ecosystem, as suggested by the presence of taxa favouring low nutrient contents, such as *B. (E.) longispina* (Zawiska, 2021) and *B. (E.) coregoni* (Miotk-Szpiganowicz and Niska, 2008).

At the beginning of the Bølling period, the first planktonic taxa – *B. (E.) coregoni* and *B. (E.) longispina* – appeared, indicating an increase in water depth, likely driven by rising moisture availability (Naughton et al., 2023). Moreover, their presence may also suggest a prolonged open-water season, potentially due to a shorter ice-cover duration. However, the environmental conditions during the onset of the Bølling period appear to have been unstable, particularly in terms of temperature and water levels, leading to abrupt disruptions in Cladocera assemblage. Shortly after the environmental conditions improved, the

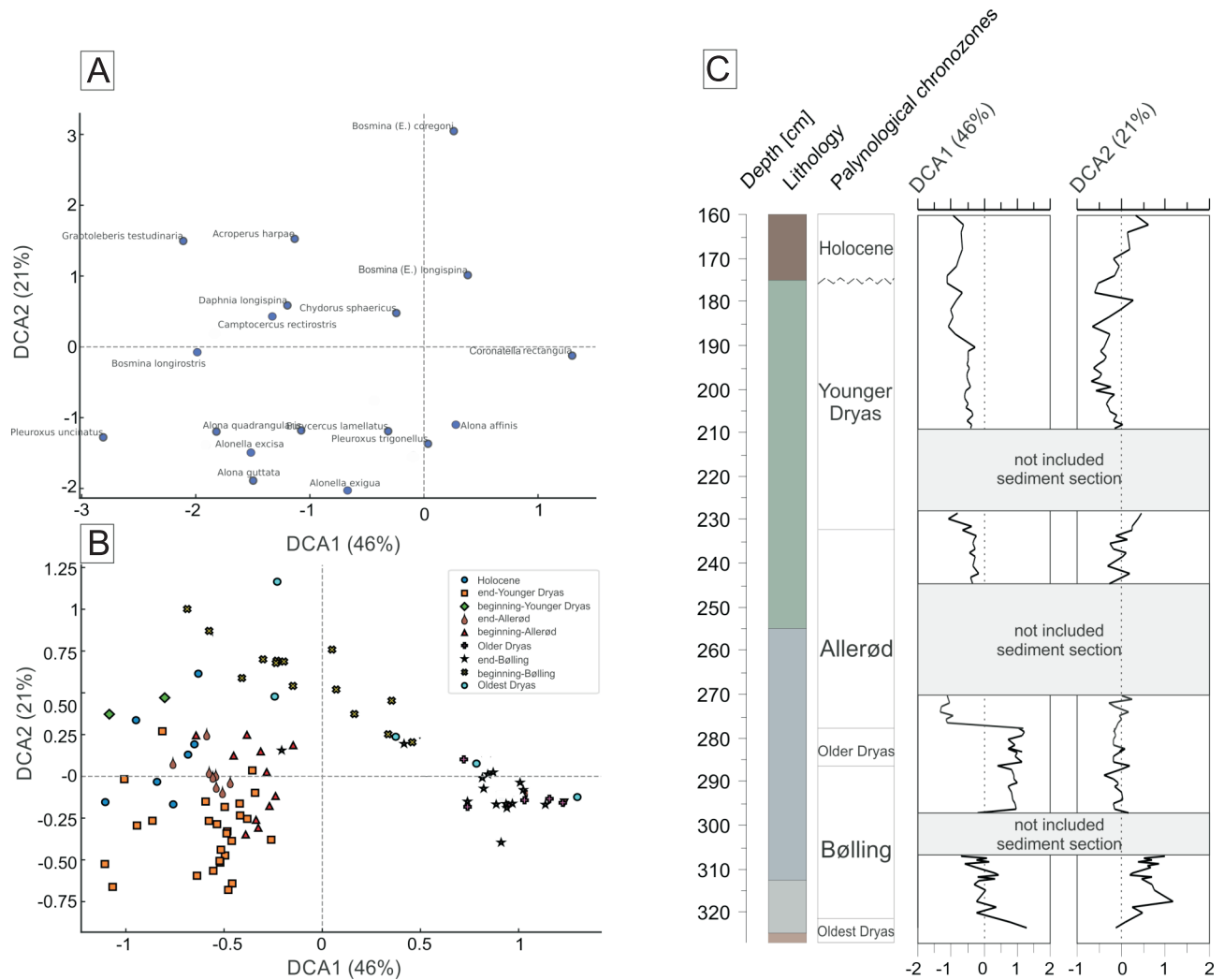


Fig. 5. Detrended correspondence analysis (DCA) of cladoceran assemblages from sedimentary section Ł-2

A – ordination of cladoceran species, illustrating their distribution along DCA axes; **B** – ordination of sediment samples, showing compositional differences among palynological chronozones; **C** – variation in sample scores along depth for DCA Axis 1 and Axis 2, highlighting shifts in assemblage composition over time

water body reverted to an earlier state observed at the beginning of the section studied, where *Ch. sphaericus* and *C. rectangula* once again dominated.

An initial warming phase was followed by a period of cooling, as shown by the Cladocera record, which shows the reappearance of *B. (E.) longispina* and *A. harpae*. Shortly thereafter, *B. (E.) longispina* disappears, while the proportion of *A. harpae* declines, coinciding with the emergence of *C. rectirostris*, a species favouring warmer and clearer waters (Szeroczyńska and Zawisza, 2011).

BØLLING/OLDER DRYAS/ALLERØD TRANSITIONS (SECTION II)

During the Bølling/Older Dryas/Allerød interval, the thermophilic species *P. trigonellus* was present throughout the entire section, indicating higher water temperatures compared to the early Bølling period. However, the co-occurrence of *P. trigonellus* with *A. affinis* and *A. harpae* – species from the “arctic species” group (Whiteside, 1970) – suggests rather a moderately cool climate. Similarly to the Oldest Dryas/Bølling transi-

tion (section I), there was a noticeable dominance of species appearing rather in shallow waters, such as *Ch. sphaericus* and *C. rectangula*.

Initially, *Ch. sphaericus* dominated, but as the boundary between the Bølling and Older Dryas approached, it was quickly replaced by *C. rectangula*. This shift in dominance may have been linked to changes in water chemistry, as reflected by DCA1 and DCA2. *C. rectangula* thrives in calcium-rich environments, and a decline in calcium levels could have contributed to the decrease in its population (Shapiera et al., 2011). This interpretation is further supported by the increased CaCO_3 content in the deposits from the Ł-1 core, as reported by Forsyia et al. (2023) during the Bølling-Allerød interstadial. This increase in Ca content has been attributed to changes in water supply, driven by a higher influx of groundwater. Such conditions created a favourable environment for the development of *C. rectangula*, which competed with *Ch. sphaericus*.

The shallow-water nature of the waterbody is further corroborated by the absence of planktonic species up to a core depth of 291 cm. At this depth, *B. (E.) longispina* reappears, suggesting a rise in water levels, likely due to reduced evaporation as-

sociated with cooler conditions. This period coincided with a decline in total Cladocera abundance (~ 350 ind./cm³), associated with the onset of short-term cooling linked to the Older Dryas. Evidence of this temperature drop is reflected in pollen records as an increased presence of juniper shrubs. The response of Cladocera has been recorded slightly earlier than that of vegetation, due to their high sensitivity and rapid adaptability to environmental changes. After a brief cooling period related to the Older Dryas, environmental conditions gradually improved, as indicated by the Cladocera record. This warming trend is reflected in the emergence of *A. quadrangularis* and *C. rectirostris*, species that favour higher water temperatures (Szeroczyńska, 1985; Szeroczyńska and Zawisza, 2007). Concurrently, the total abundance of Cladocera increased (the middle part of section II), suggesting enhanced ecosystem productivity. Additionally, the improved thermal regime promoted the growth of aquatic vegetation, creating favourable habitats for *Eurycercus lamellatus*, which thrives in plant-rich environments (Zawisza and Cedro, 2012).

Further improvement in edaphic conditions was associated with the onset of the Allerød period (upper part of section II). The appearance of thermophilic species such as *A. quadrangularis* and *P. uncinatus*, clearly indicates higher water temperatures and, consequently, a warming climate (Szeroczyńska and Zawisza, 2007). The dominance of *Ch. sphaericus*, coupled with a significant increase in the share of *A. quadrangularis*, suggests a rise in trophic levels within the water body (Błędzki and Rybak, 2016; Zawisza, 2021). The decline in *C. rectangula*, a species sensitive to acidification (Sandøy and Nilssen, 1986), may indicate a decrease in water alkalinity. Additionally, the presence of *A. excisa* and *A. exigua*, which prefer lower pH conditions, further supports this interpretation (Szeroczyńska and Zawisza, 2007). The occurrence of planktonic species suggests the development of a pelagic zone and a slight deepening of the water body. The significant presence of *A. quadrangularis* and *A. harpae* indicates well-developed submerged vegetation (Szeroczyńska and Zawisza, 2007), reflecting relatively stable conditions in the littoral zone of the lake.

ALLERØD/YOUNGER DRYAS TRANSITION (SECTION III)

The Allerød/Younger Dryas transition was a period of abrupt climate change that caused significant shifts in both terrestrial and aquatic ecosystems. In the Ługi record, progressive cooling was indicated by a decline in the proportions of *Pinus*, *Betula nana*, *Salix*, and *Cyperaceae*, along with a rising prevalence of juniper bushes.

The Cladocera record suggests that the late Allerød period was characterized by low water levels at the Ługi site, as shown by the dominance of littoral species and a minimal presence of planktonic species. This indicates that habitat conditions were likely shallow, with limited open water zones, favouring species adapted to littoral and benthic environments. The presence of species typically found in both oligo-mesotrophic and eutrophic waters, along with higher total Cladocera abundance indicates that the water body was likely mesotrophic during that period. Higher lake productivity is also seen from geochemical indices and an increased organic matter content, as observed in a previously analysed core from Ługi (Forysiak et al., 2023).

The presence of thermophilic species of the genus *Pleuroxus* coupled with the cold-tolerant *Eurycercus* spp. (Niska and Mirosław-Grabowska, 2015), suggests a moderately warm climate. The warm climate may also have favoured the occurrence of *A. guttata*, and *A. quadrangularis* (Harmsworth, 1968;

Szeroczyńska and Zawisza, 2007). The presence of the latter species may also be related to the increased availability of resources, particularly food (Szeroczyńska, 1985; Zawisza, 2021).

At the transition to the Younger Dryas (section III, upper part), there was a slight increase in the proportion of planktonic species such as *D. longispina*-group and *B. (E.) longispina*. This shift likely indicates an expansion of the open water zone, possibly driven by a rise in water levels. A similar scenario of increased water levels has been observed at other sites, likely driven by reduced evaporation (Starkel et al., 1998; Galka et al., 2015).

The evidence of cooling is reflected by a decrease in the proportions of *P. trigonellus* and *A. quadrangularis* (Szeroczyńska and Zawisza, 2007; Rybak and Błędzki, 2010), accompanied by a concurrent increase in *A. harpae* (Whiteside, 1970; Szeroczyńska and Zawisza, 2011), suggesting a shift in ecological conditions favouring species better adapted to cooler environments.

At the beginning of the Younger Dryas, an increase in the proportion of species associated with aquatic vegetation, such as *G. testudinaria* and *C. rectirostris* (Fryer, 1968; Rybak and Błędzki, 2010; Zawisza and Cedro, 2012), becomes evident. The growing density of aquatic vegetation within the ecosystem may have created more diverse and stable microhabitats, promoting colonisation by these species. Moreover, the expansion of vegetation could have positively influenced water quality, for instance, by enhancing oxygenation, which in turn may have facilitated the appearance of *B. (E.) longispina*. At the onset of the Younger Dryas, a slight decrease in trophic levels may have occurred, indicated by a reduced presence of *C. rectangula* (Rybak and Błędzki, 2010) and a lower total Cladocera sum. However, this decline in trophic state was likely minor, as species characteristic of oligotrophic to eutrophic waters remained present.

YOUNGER DRYAS-HOLOCENE BOUNDARY (SECTION IV)

Palynological data indicate the presence of a stratigraphic gap in the upper part of section IV. The sedimentary profile Ł-2 contains a hiatus. The samples classified as Holocene correspond rather to the Boreal period, with the Pre-Boreal period probably absent.

The late Younger Dryas was characterized by a low overall sum of Cladocera. The number of species was slightly higher than at the beginning of the Younger Dryas (upper part of section III) suggesting more favourable conditions. The proportion of planktonic species – *D. longispina* group and *B. (E.) longispina* – remained low, suggesting a lack of significant fluctuations in water levels. There were higher shares of *A. excisa* and *A. guttata*, along with the appearance of *A. exigua*. All three species are resistant to low pH (Zawisza, 2021), which, combined with DCA results, suggests a subtle decrease in water pH, likely connected with the development of peatlands along the lake shore.

Just before the Holocene boundary, there is a notable increase in *B. (E.) longirostris*, along with a gradual rise in *A. harpae* and *A. affinis*. Additionally, *P. uncinatus* appears for the first time, signalling a warming trend. The Boreal period in this profile is characterized by an increase in the total Cladocera sum, indicating improved living conditions for a greater number of cladocerans. This growth likely resulted from an increased availability of resources such as food and habitats. The emergence of *C. rectirostris*, the increasing presence of *G. testu-*

dinaria, and the reappearance of the thermophilic species *Sida crystallina* (Rybak and Błędzki, 2010) further suggest a significant rise in water temperature (Szeroczyńska and Zawisza, 2007). The structure of Cladocera assemblages also indicates the expansion of vegetation, facilitating the development of macrophyte-associated taxa, including *C. rectirostris* (Rybak and Błędzki, 2010).

INTRA-SITE COMPARISON OF CLADOCERA ASSEMBLAGES IN THE ŁUGI PEATLAND: CORE ANALYSIS PERSPECTIVES

A previous analysis of Cladocera from the Ługi site was conducted on core Ł-1, with a resolution ranging from 10 cm (Pawłowski, 2017) to 5 cm (Forysiak et al., 2023). The analysis of subfossil Cladocera remains in cores Ł-1 and Ł-2 revealed minor differences in species composition and the dynamics of taxa in response to environmental changes. These differences primarily stem from variations in analytical resolution, as well as from local depositional and hydrological conditions. Nonetheless, they do not significantly affect the interpretation of environmental and climatic conditions.

Higher-resolution analysis in Ł-2 allowed for the identification of more taxa, including *Unapertura latens*, *Alonopsis elongatus*, *Alona rustica* and *A. quadrangularis*, which were not identified in Ł-1. Planktonic species also appeared earlier and persisted longer in Ł-2, particularly during the Bølling and Younger Dryas, while they remained scarce in Ł-1. These differences likely reflect local variations in macrophyte structure and hydrological conditions in different parts of the waterbody.

Disparities in Cladocera population dynamics suggest that environmental changes were not uniform across the site.

In Ł-2, the the Oldest Dryas-Bølling transition was marked by unstable conditions, while in Ł-1, these changes were less clearly reflected in the Cladocera record.

Notable differences in sediment composition between the two cores during the Oldest Dryas sections reflect variations in depositional conditions. In core Ł-2, finer, carbonate-rich sediments formed under higher water levels with low energy, which is reflected in the Cladocera record. The absence of planktonic taxa in this core corresponds to the deposition of coarser particles, whereas the presence of finer sediments aligns with Cladocera evidence indicating a deepening of the water. In contrast, core Ł-1 did not exhibit these patterns, with a persistent lack of planktonic taxa suggesting distinct hydrological conditions in areas lacking planktonic taxa.

The response of Cladocera to the transition to Allerød/Younger Dryas also varied. Previous lower-resolution studies (Ł-1) suggested that this period was characterized by an increase in littoral and eutrophic species, including *B. longirostris*, pointing to higher trophic levels. However, higher-resolution data from Ł-2 showed a decline in both species abundance and frequency at the onset of the Younger Dryas, contrasting with the more gradual changes observed in Ł-1. Additionally, *G. testudinaria* was significantly more abundant in Ł-2 throughout the Younger Dryas, whereas it appeared in Ł-1 only just before the transition (Pawłowski, 2017; Forysiak et al., 2023).

High-resolution analyses revealed temporary disappearance of *A. affinis*, in contrast to its continuous presence in the Ł-1 core. This suggests localized variations in environmental conditions during this period. Previous studies (core Ł-1) indicate that the late Younger Dryas was marked by the absence of plankton species, a decline in Cladocera populations, and deteriorating conditions for their development.

The results from the Ł-2 core suggest that the end of the Younger Dryas provided relatively favourable conditions for Cladocera development, as shown by the presence of both planktonic and previously unrecorded species. Additional differences include the presence of the stenothermal species *S. crystallina* in Ł-2 during the Younger Dryas, a species absent in Ł-1. Meanwhile, *A. excisa* persisted throughout this period in Ł-2 but disappeared in Ł-1 before the transition to the Holocene.

The continued presence of *A. quadrangularis* in Ł-2, despite its absence in Ł-1, further emphasizes differences in ecological conditions between the two cores.

The observed discrepancies likely result from a combination of analytical resolution, site-specific environmental conditions, and sedimentological differences. A broader comparison with other peatland sites in the Łódź region (e.g., Żabieniec, Pawłowa, Korzeń) confirms that local hydrological and geomorphological conditions played a key role in shaping Cladocera assemblages, despite similar regional climatic trends during the Late Glacial and Early Holocene (Rudna and Forysiak, 2023).

REACTION OF AQUATIC BIOTA TO CLIMATE-INDUCED ENVIRONMENTAL CHANGES DURING THE LATE GLACIAL/HOLOCENE TRANSITION IN POLAND

Many aquatic organisms, including diatoms, chironomids, and ostracods, are well known for their sensitivity to abrupt climatic shifts associated with the Late Glacial/Holocene transition. Similarly to cladocerans, they responded to variations in temperature, precipitation, and nutrient availability.

Cold phases of the Late Glacial were generally marked by low species diversity and abundance in aquatic communities, although the intensity of ecological response varied depending on the magnitude of cooling. These periods, as observed in the Cladocera record, were dominated by cold-tolerant taxa. For example, *Corynocera ambigua* dominated chironomid assemblages in the Ługi site at the end of the Oldest Dryas (Forysiak et al., 2023), suggesting oligo- to mesotrophic conditions, a pattern also recorded at other central Polish sites (Pióciennik et al., 2020).

Interestingly, chironomid records often show higher total abundance during the Oldest Dryas than in the Holocene, pointing to possible additional environmental constraints not captured in the Cladocera data. Additional evidence of harsh conditions is provided by the Niechorze basin (northern Poland), where diatom assemblages were dominated by littoral *Fragilaria*, and *Ch. sphaericus* was the only cladoceran recorded – both suggesting extremely oligotrophic environments (Marciniak, 1981; Szeroczyńska, 1985). These differences may be attributed to regional variation, including proximity to the ice-sheet margin (Mirosław-Grabowska and Zawisza, 2018). Brief cold events like the Older Dryas are rarely captured in sedimentary records but, when present, are typically dominated by cold-adapted Cladocera such as *Ch. sphaericus*, *A. harpae* and *A. affinis* (Szeroczyńska, 1985). In the Ł-2 core, assemblages remain species-poor, in line with most regional data (Rudna et al., 2023).

The Younger Dryas is again characterized by low cladoceran diversity, with cold-tolerant taxa prevailing under unstable environmental conditions (Szeroczyńska, 1985; Antczak-Orlewska et al., 2023; Rudna et al., 2023). Importantly, this period is recognized for its internal climatic variability — it began with an intense cold phase and ended with a gradual transition toward milder conditions (Pióciennik et al., 2020; Rudna et al., 2023). Survival strategies such as ephippia production were common

among cladocerans, enabling persistence through harsh conditions (Szeroczyńska and Zawisza, 2011). Chironomid and ostracod assemblages reflect similar ecological pressures, with dominance of cold-adapted species such as *Microtendipes pedellus*-type, *Micropsectra*, *Tanytarsus lugens*-type, *Candona candida* and *Fabaeformiscandona protzi* (Kulesza et al., 2008; de Mendoza et al., 2024). Diatom data further support this interpretation, showing increased abundance of small taxa such as *Staurosira* and *Staurosirella*, typical of cold, oligotrophic conditions (Gałka et al., 2015). During the Bølling, Allerød, and early Holocene, shifts toward more thermophilic species are evident. While the Bølling is seldom addressed, the Allerød and Early Holocene have been widely analysed. The Allerød interstadial shows a biphasic character, with a cooler early phase and a warmer late phase, reflected in both cladoceran and chironomid assemblages (Antczak-Orlewska et al., 2023). Warmer intervals are associated with an increase in temperate taxa such as *Polypedium* spp. and *Chironomus plumosus*-type (Kulesza et al., 2008). However, diatom records from the late Allerød suggest that increased temperatures did not always correspond with elevated primary productivity. Assemblages remained dominated by small benthic taxa, indicating that factors such as nutrient limitation or shifts in algal communities may have constrained productivity despite warming (Müller et al., 2021).

During the Younger Dryas, cladoceran, chironomid, and ostracod records indicate a pronounced response to the the Younger Dryas-Holocene boundary that represents a major ecological transition (Pióciennik et al., 2020; Müller et al., 2021; Rudna et al., 2023). Cladoceran data typically show a sharp increase in species richness and abundance, along with the appearance of stenothermic taxa. Wind-induced turbulence and changes in water column stability may also explain some of the biotic shifts observed in both cladoceran and diatom assemblages (Słowiński et al., 2017).

CONCLUSIONS

The study of Cladocera assemblages from the Oldest Dryas to the Holocene illustrates how fluctuations in climate, particularly during key transitional periods, played a crucial role in shaping biodiversity and abundance, driven by changes in water depth, chemistry, temperature and nutrient availability.

- The Oldest Dryas/Bølling transition: the Oldest Dryas period was cold and nutrient-poor, limiting species diversity. As the Bølling period approached, water depth increased slightly, but conditions remained cold, with species such as *A. harpae* indicating persistent cold water and low nutrient levels.

- During the Bølling/Older Dryas/Allerød transitions, warming was indicated by *P. trigonellus*, though coexisting cold-adapted species suggested a moderately cool climate. A shift from *Ch. sphaericus* to *C. rectangula* reflected changing water chemistry while, after short-term cooling, Cladocera abundance and aquatic vegetation increased. The onset of the Allerød period led to improved edaphic conditions, higher water temperatures, increased trophic levels, and changes in species composition, indicating a warming climate, decreased water alkalinity, and the development of a pelagic zone with well-established submerged vegetation.

- The Allerød/Younger Dryas transition: the late Allerød was characterized by low water levels, favouring littoral species. As the Younger Dryas began, cooling was indicated by a shift towards planktonic species and cold-tolerant species. Increased vegetation provided stable habitats.

- The Younger Dryas-Holocene boundary: the late Younger Dryas had low Cladocera abundance, but conditions improved towards its end with rising temperatures and more diverse vegetation. Thermophilic species reappeared, signalling warmer water and better living conditions for Cladocera.

Cladocera analysis from the Ługi site revealed some differences between cores Ł-1 and Ł-2, influenced by analytical resolution and local hydrological conditions. The higher-resolution data from Ł-2 identified more taxa, showed earlier planktonic species appearances, and indicated stronger environmental shifts, particularly during the Younger Dryas. These findings highlight the localized nature of environmental changes and emphasize the importance of high-resolution analysis in capturing species dynamics more accurately.

The response of biota to climate changes is diverse and depends on many factors, such as nutrient availability, ecosystem structure changes and regional environmental conditions. This is why we do not always observe the expected signals in response to warming or cooling events. For example, despite the rise in temperatures during the late Allerød, as noted in diatom studies, there was no increase in productivity (Müller et al., 2021). This could have been due to limited nutrient availability or a shift in the algal community, where other groups of algae not analysed in the study may have become dominant. Therefore, understanding the reactions of organisms to environmental changes is crucial for better comprehending the complexity of their responses to climate change and predicting future ecological processes.

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