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Cladoceran remains as a tool for reconstruction of past environmental conditions during the Late Pleistocene-Holocene in Central Karelia (NW Russia). Part II. Qualitative approach including species co-occurrence analysis

Остатки ветвистоусых ракообразных как средство для реконструкции условий среды в позднем плейстоцене-голоцене в Центральной Карелии (Северо-Запад России). Часть II. Качественный подход, в том числе анализ совместной встречаемости

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КЛЮЧЕВЫЕ СЛОВА: палеолимнология, тафоценоз, субфоссильный, Cladocera, Карелия, озеро Торосярви, донные отложения.

ABSTRACT. This paper is the second in a series devoted to the study of cladoceran taphocenoses in the bottom sediment core from Lake Torosjarvi (Central Karelia, NW Russia). The quantitative data on species abundances in each layer of the core were analysed using CONISS cluster analysis (see Part I). Here, a cladoceran species association analysis based on binary data (presence/absence) was performed, which has not previously been applied to analyse palaeodata. Two major and three small (each represented by a couple of species) clusters of mutually associated species were identified via the species association analysis. The major clusters correspond to cold-water and warm-water conditions respectively, as well as to two major periods in the lake history: an early period characterised by cold water and oligotrophic conditions, and a second period characterised by a relative warming and stronger development of higher aquatic vegetation. The conditional boundary between the periods was estimated using qualitative data clustering as ca. 10.6 ka cal. yr BP, which roughly corresponds to the separation of Lake Torosjarvi from a larger water body — Lake Segozero, which belonged to the palaeobasin of the Onega Glacial Lake. The pairs of associated species are corresponded to the zones obtained by dividing the core into smaller periods based on CONISS clustering, as outlined previously (see Part I). Division of the sediment core by the species abundances may yield a more detailed result in the revealing of a community change, and the change in environmental conditions by zones may be more gradually reconstructed. Simultaneously, the division of the core by species occurrence reflects more general changes in the lake environment.

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РЕЗЮМЕ. Данная работа является второй в серии, посвященной изучению тафоценозов ветвистоусых ракообразных в колонке донных отложений из озера Торосярви (Центральная Карелия, СЗ России). Ранее, количественные данные по видовому обилию в каждом слое колонки донных отложений были проанализированы с помощью кластерного анализа CONISS (см. Часть I). Здесь был проведен анализ видовых ассоциаций ветвистоусых ракообразных на основе бинарных данных (присутствие/отсутствие). Этот метод ранее не применялся для анализа палеоданных. В результате анализа ассоциированности видов были выявлены два крупных и три малых (каждый представлен парой видов) кластера взаимно ассоциированных видов. Крупные кластеры соответствуют холодноводным и тепловодным условиям среды. Также они представляют основные периоды в истории озера: ранний период, характеризующийся холодноводными и олиготрофными условиями, и поздний период, характеризующийся относительным потеплением и более активным развитием высшей водной растительности. Условная граница между периодами была установлена с помощью кластеризации качественных данных на рубеже 10,6 тыс. кал. л.н., что примерно совпадает по времени с отделением озера Торосярви от более крупного водоема озера Сегозеро, входившего в палеобассейн — Онежское ледниковое озеро. Пары ассоциированных видов соответствуют зонам, полученным путем разделения колонки донных отложений на более мелкие периоды на основе кластеризации CONISS, сделанной ранее (см. Часть I). Подразделение колонки по численности видов может более подробно выявить изменения сообщества, а изменение экологических условий по зонам колонки может быть реконструировано более постепенно. В то же время, разделение колонки по встречаемости видов отражает более общие изменения условий среды в озере.

Introduction

In the first communication (Part I, Ibragimova *et al*. [2025]) we have represented a general information regarding the structure of the cladoceran taphocenosis in the bottom sediments of Lake Torosjarvi (Central Karelia, 63.48°N, 33.23°E) and its changes throughout the Late Pleistocene-whole Holocene based on quantitative abundance data. Additionally, we have provided a detailed account of the material, methodology of coring, collecting of samples, and results of quantitative data analysis of the cladoceran remains in each layer. A total of 42 cladoceran taxa were identified, belonging to 31 genera and seven families. The sediment core was subdivided into five faunal zones based on the CONISS clustering of quantitative data on the cladoceran taphocenosis [Ibragimova *et al*., 2025]. It can be concluded that the dominant complex in the cladoceran taphocenosis of Lake Torosjarvi has undergone two major changes since its formation. These shifts in the subfossil cladoceran community were aligned with variations in the sediment accumulation rate.

The cladoceran taphocenosis of lower layers of Lake Torosjarvi, as in numerous other glacial lakes [Goulden, 1969], was characterised initially by a limited range of cold-water species that are tolerant of adverse environmental conditions and a low organic matter content. In the top layers, changes in the composition of cladoceran communities indicate a softening of climatic conditions due to weakening of the glacial cover effect. During this period (after 11.7 ka cal. yr BP), Lake Torosjarvi was separated from the larger Lake Segozero, marking a change in sedimentation patterns and an increase in organic matter. At the same time, an increase in the proportion of phytophilous species indicates the development of a littoral zone inhabited by macrophytes. In the top layers of the core, covering Subboreal and Subatlantic periods, the proportion of northern species increase while the proportion of warm-water species decrease, that indicate cooling of the climate. The increase in the proportion of pelagic species indicates an increase of the open-water part of the lake. Lake Torosjarvi was characterised as a cold-water, oligotrophic, and relatively deep lake, and such conclusion was supported by the results of diatom analysis based on previous studies of the lake [Shelekhova, Tikhonova, 2022].

In the second part of the study, the cladoceran taphocenosis of Lake Torosjarvi in the Holocene was subjected to a next stage of the statistical analysis. Based on the data on species presence/absence in each layer of the sediment core, positively associated species were identified and analysed using the discrete hypergeometric distribution. This methodology enables identification of the species mutual associations which are affected by certain environmental factors. This method was previously applied to recent benthic [Kurina *et al*., 2019, 2022] and planktonic [Kotov *et al*., 2022; Andreeva *et al*., 2023] freshwater invertebrate communities in spatially distant modern biotopes. Previous studies [Golovatyuk *et al.* 2025] also have enabled us to conclude that the spatial distribution of associated species is determined by the influence of

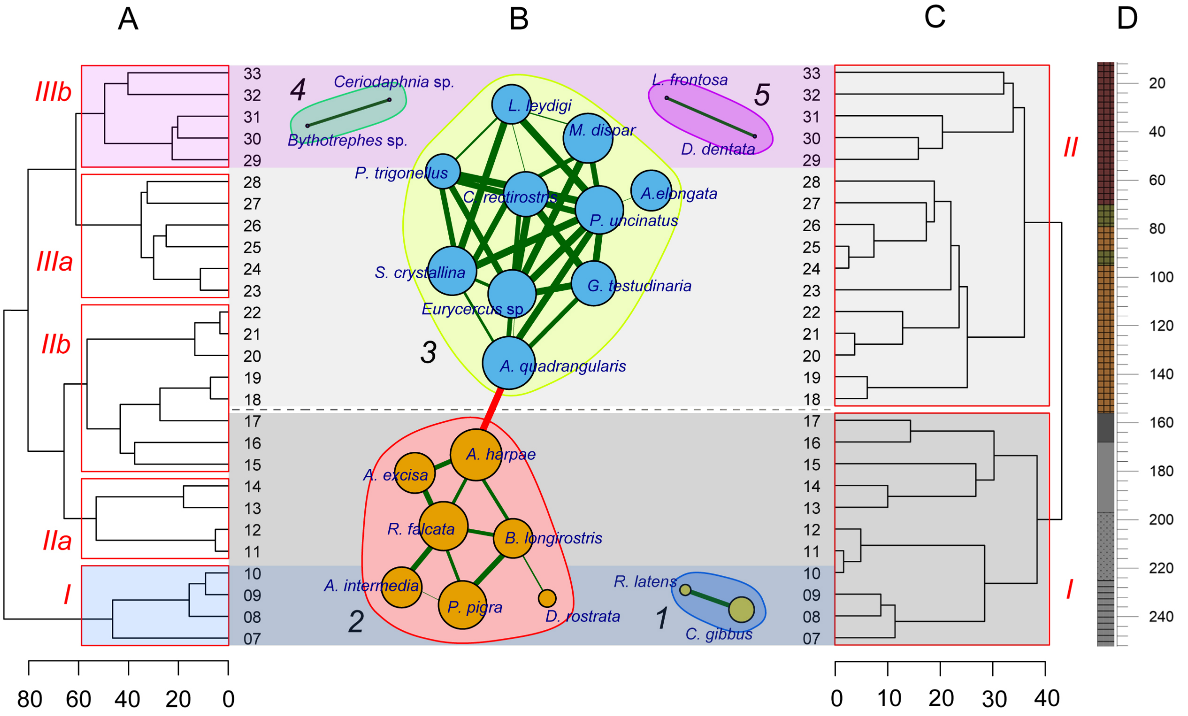

Fig. 1. Cluster diagrams. A — CONISS clustering by abundance; B — graph of positively associated species (1–5 clusters). The size of the node marker is logarithmically proportional to the species occurrence in the core, and the thickness of the edge is linearly proportional to the strength of the association between species. The red edge indicates a single inter-cluster connection; C — CONISS clustering by occurrence; D — lithostratigraphic layers of the core (grey — different types of clays, brown — silts) and depth of samples in the core (cm).

Рис. 1. Кластерные диаграммы. A — кластеризация CONISS по численности; B — граф положительно ассоциированных видов (кластеры 1–5). Размер маркера узла логарифмически пропорционален встречаемости вида в керне, а толщина линии линейно пропорциональна силе связи между видами. Красная линия указывает на единственную межкластерную связь;. C — кластеризация CONISS по встречаемости; D — литостратиграфические слои колонки (серым — различные виды глин, коричневым — илов) и глубина проб в колонке (см).

environmental factors that limit their extensive distribution, as well as by consortial relationships between species within the association.

The present study is the pioneering examination of the species associations in taphocenoses, which entails an analysis of temporal rather than spatial dimensions. The aim of this study is to investigate changes in environmental conditions by analysing qualitative data on the occurrence of Cladocera remains, and to compare the results of qualitative and quantitative analysis.

Material and Methods

Analysis of the species association by occurrence in the samples was performed using a discrete hypergeometric distribution with a 95% upper confidence interval, see details in Seleznev *et al*. [2024]. This distribution is used to simulate the probability of a joint occurrence of a species pair in a given binary matrix of the species presence/absence in samples. If the observed value of co-occurrence of two species (number of samples where two species co-occur) is higher than the 95th percentile of the hypergeometric distribution, the species are considered to be positively associated, and their co-occurrence is accepted as not random, e.g. influenced by some environmental (or historical) factors. To visualise the associated pairs, an undirected graph was constructed, wherein each node represents a species from the list of associated species and the edges represent the associations between them. The grouping of the graph nodes was performed using the method of multi-level optimization of modularity [Blondel *et al*., 2008] in the “igraph” package [Csardi, Nepusz, 2006].

The clustering of samples by the binary data on species occurrence in the sediment core was performed using the CONISS method with clusters constrained by sample order [Juggins, 2023]. The binary metric of distance was employed as a measure of the samples’ dissimilarity. The number of identified clusters was determined by comparison with the broken stick model [Legendre, Legendre, 2012]. The dependence of species occurrence from the identified clusters was determined using a permutation analysis of variance with 10.000 permutations per species, using the “permuco” package [Frossard, Renaud, 2019]. Post-hoc analysis was performed using the Tukey HSD test. All calculations were performed using the statistical analysis environment R 4.4 [R Core Team, 2024].

The initial data are represented in Supplement Table 1 in Part I [Ibragimova *et al*., 2025].

Results

The analysis of species association using the binary species-sample matrix revealed 41 positively associated species pairs and seven negatively associated species pairs. The positively associated species were grouped into five clusters (Fig. 1), with an overall modularity of 0.43.

Five clusters were identified, including two major clusters (2 and 3), comprising remains of 17 species

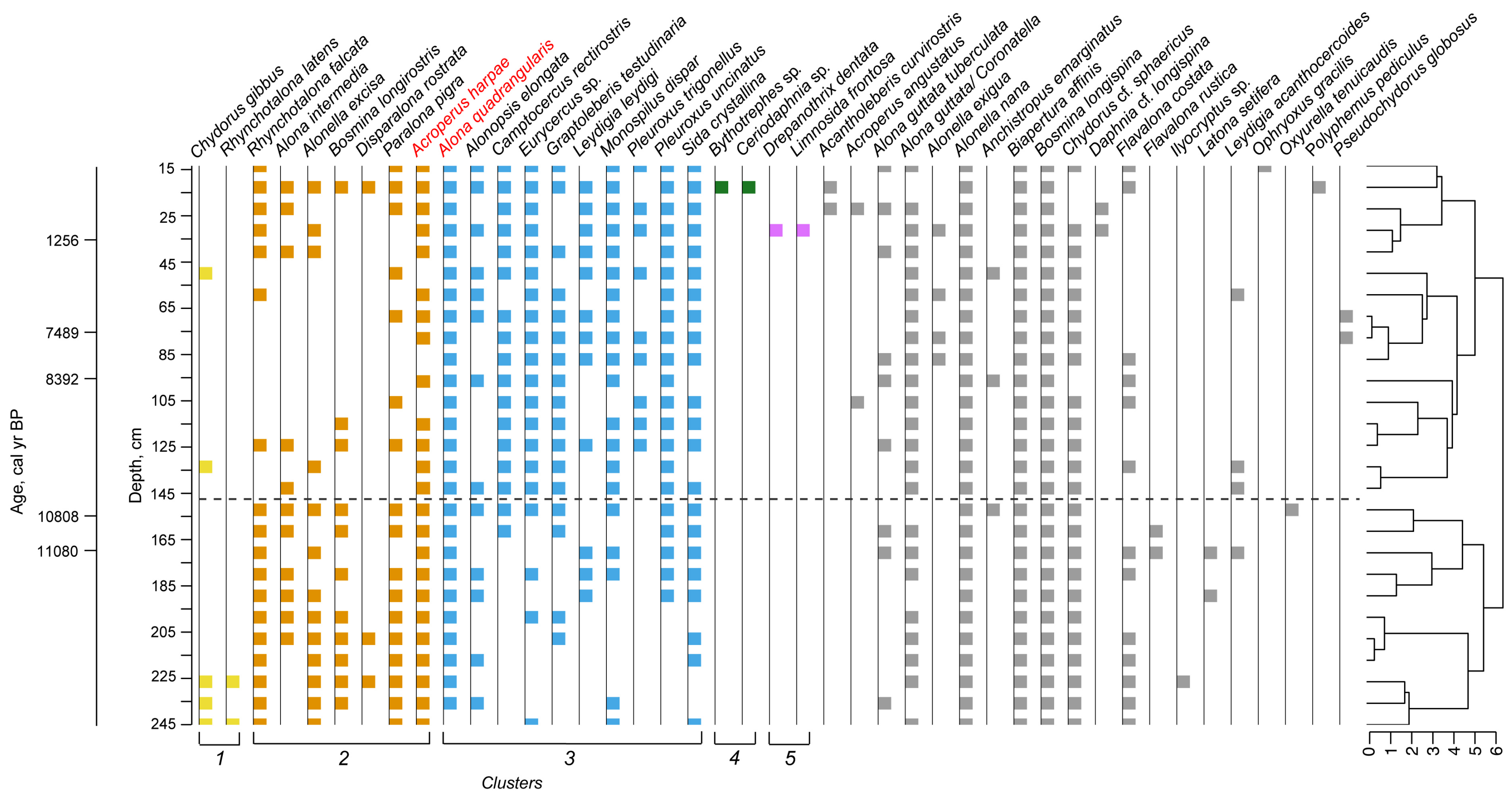

Fig. 2. Stratigraphic diagram of the cladoceran species occurrence in the taphocenosis of Lake Torosjarvi, with 1–5 clusters of associated species highlighted in different colours. Species not forming associated pairs are marked in grey. Sample clustering based on the CONISS of species occurrences is represented in the upper side.

Рис. 2. Стратиграфическая диаграмма встречаемости видов Cladocera в тафоценозе озера Торосярви с кластерами ассоциированных видов 1–5, выделенными разными цветами. Виды, не образующие ассоциированных пар, выделены серым цветом. Результаты CONISS-кластеризации образцов на основе встречаемости видов представлены в верхнейй части.

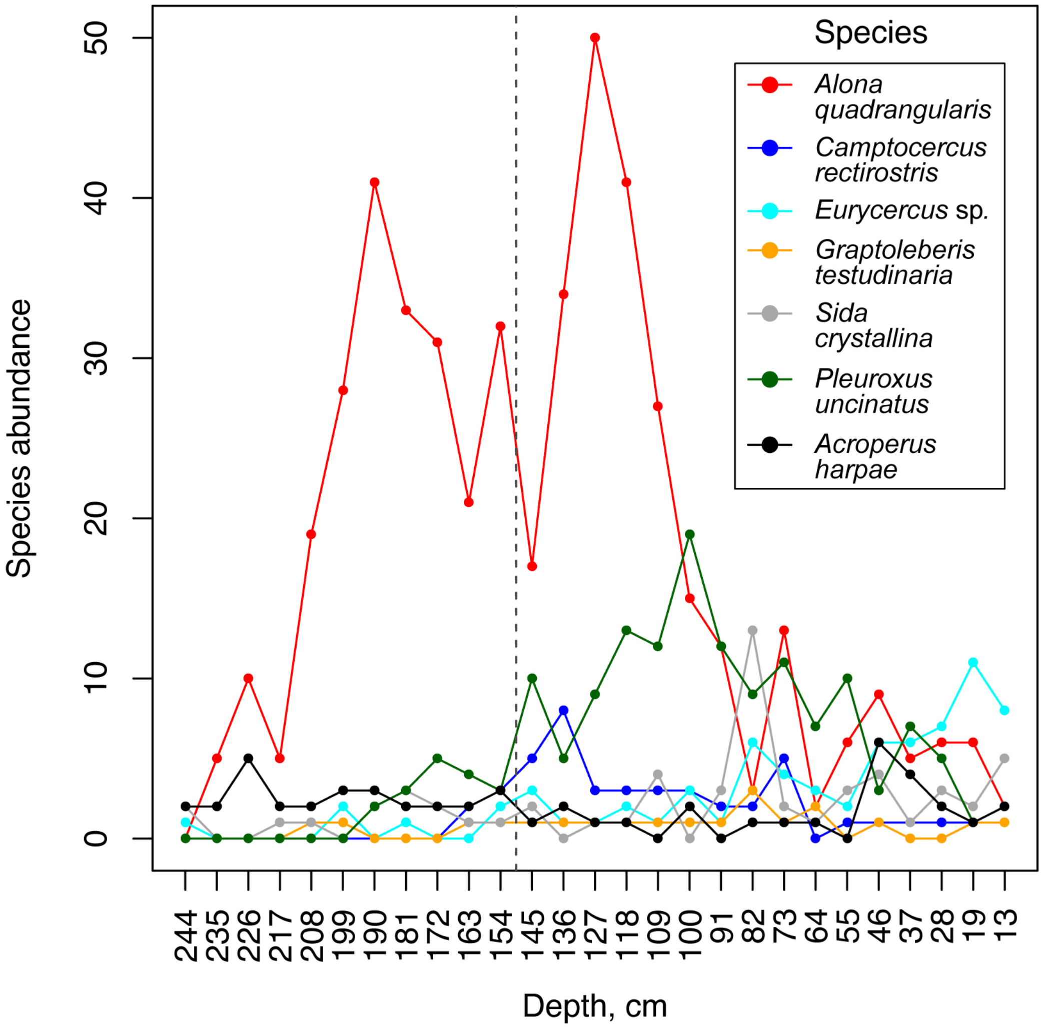

Fig. 3. Population dynamics of *Alona quadrangularis* and six associated species. The vertical dashed line indicates the boundary between the lower and upper parts of the core.

Рис. 3. Динамика численности *Alona quadrangularis* и шести ассоциированных видов. Вертикальная пунктирная линия обозначает границу между нижней и верхней частями колонки.

with a high occurrence in the core. Cluster 2 has a total connectivity strength [Seleznev *et al*., 2024] of 0.24 and contains seven species, while cluster 3 has a total connectivity strength of 0.42 and contains 10 species. These clusters are interconnected by a single inter-cluster edge. The remaining three clusters (1, 4, 5) are formed by a couple of species each, with a low or even single occurrences in the core (except of *Chydorus gibbus* in the cluster 1, relatively common in the samples).

The CONISS cluster analysis of the samples based on species occurrence (instead of species abundance in Part I, see Ibragimova *et al*. [2025]) revealed the existence of two distinct groups: a lower group comprising samples from depths of 245 to 150 cm, and an upper group comprising samples from depths of 150 to 15 cm (Fig. 2).

Results of the analysis of variance demonstrate that species belonging to cluster 2 are prevalent in the samples from the lower core part (p=0.0036), while species from cluster 3 are more frequently observed in the samples from the upper core part (p=0.0021). Conversely, species of the cluster 2 demonstrate no correlation with the division of the core into five sections in terms of abundance (p=0.13), whereas species of the cluster 3 are statistically significantly more abundant in the middle and upper part of the core (both values p<<0.001) (see Ibragimova *et al*. [2025]). Therefore, presence of species from the cluster 3 is correlated with the upper section of the core, and this cluster itself is larger and more compact as compared to the cluster 2. Species of the clusters 4 and 5 are sporadically found together in the uppermost part of the core, in Zone IIIb, which represents the most modern layers of Lake Torosjarvi sediments. In contrast, species of the cluster 1 are found in its lowest part (Zone I), which corresponds to the Late Pleistocene period.

Discussion

New cluster analysis of the samples, based on the occurrence of the cladoceran species, divided the core of Lake Torosjarvi into two distinct sections: the lower and upper sections. The boundary between the sections is located at a depth of approximately 1.5 m (4 m from the water's surface) and has an estimated age of 10.6 ka cal. yr BP. This boundary does not perfectly match the boundaries of the zones defined by abundance in Part I and falls within Zone IIb [Ibragimova *et al*., 2025]. A possible explanation for this discrepancy is that species abundance data contains more information than binary occurrence data. This allows for a comparison of the quantities of the two species, which in turn enables a more detailed analysis of the community change and the gradual reconstruction of environmental conditions by zone.

Cluster 1 was formed by only two species: *Chydorus gibbus* and *Rhynchotalona latens* inhabited the northern and alpine regions. Both species are among the first lake settlers and both demonstrate a tolerance to unfavourable environmental conditions, i.e. low temperature and organic matter content [Smirnov, 2010; Nevalainen *et al*., 2019; Ibragimova *et al*., 2024]. At the same time, while the remains of *C. gibbus* were identified in more recent samples of the Lake Torosjarvi core, *R. latens* was entirely absent there. In other studied cladoceran taphocenoses of glacial lakes in the European part of Russia, the remains of *R. latens* also were found mainly at the initial stages of lake formation [Ibragimova, 2021].

It is noteworthy that *C. gibbus* and *R. latens* were present together in the samples corresponding to the Late Pleistocene, in Zone I (when the core is divided into five zones by abundance, see Ibragimova *et al*. [2025]). In this case, the association analysis is more precise as compared to the cluster analysis based on occurrence (Fig. 1A, B).

Based on the associations revealed here we can conclude that at the period corresponding to the lower part of the core (Fig. 1B, C), Lake Torosjarvi had a developed littoral zone with sparce patches of aquatic vegetation. It was an oligotrophic (potentially acidified) cold-water body with a significant glacial cover impact and a low organic matter content. The bottom sediments during this period were primarily composed of clayey, organic-poor matter. Species of cluster 2 (which is confined to the lower part of the core) included the stenothermic *Alona intermedia* and *Bosmina longirostris*, oligo-mesotrophic *Paralona pigra*, and *Acroperus harpae* and *Alonella excisa*, which are associated with aquatic vegetation.

The glacial cover no longer had a pronounced cooling effect at the times represented by the upper section of the core (Fig. 1A, B). Perhaps, it was a period of increased water level, temperature, and the trophic state of the lake. During this period, the macrophyte zone continued to develop, and there was also a possible increase in the lake's water level. The Cluster 3 of associated species, observed in the upper section of the core, included phytophilous *Camptocercus rectirostris*, *Leydigia leydigi*, *Sida crystallina*, *Eurycercus* sp., *Graptoleberis testudinaria*, as well as the eurybiont *Alona quadrangularis*. Abundance increase of the latter taxon may indicate the acidification of the lake, according to Van Damme & Dumont [2008].

The period from 11.7 to 10 ka cal. BP marked the end of the last glacial period, accompanied by a retreat of glaciers [Rasmussen *et al*., 2006]. At that time, Lake Torosjarvi was separated from a larger Lake Segozero, which belonged to the palaeobasin of the Onega Glacial Lake [Biské, 1959]. The level of organic matter increased with the sedimentation rate. Increased trophic status of the lake and the change in sedimentation character were a consequence of weakening of the glacial cover due to general warming [Subetto *et al.*, 2017, 2022]. It can be assumed that the main changes in Cladocera community were caused by a general increase in temperature. In the Preboreal period, the proportion of phytophilic species was increased, indicating the development of the macrophyte zone. The increase in the proportion of these species in the Boreal period can be explained by the expansion of the lake area and the concomitant increase in the size of the zone accessible to higher aquatic vegetation. It is assumed that the development of aquatic vegetation, along with temperature, had a greater impact on the formation of the cladoceran community of the Lake Torosjarvi.

A. harpae and *A. quadrangularis* (Fig. 2, highlighted in red) were positively associated with each other ($p < 0.004$), belonging to clusters 2 and 3, respectively. They constituted the only inter-cluster association between the two major clusters. These two species are often observed as the first settlers in post-glacial lakes [Smirnov, 2010; Ibragimova, 2021]. Although *A. harpae* is a species common in the northern regions, it is confined to a well-developed zone of aquatic vegetation that is present in the lake during both cold-water and warm-water periods. It is regarded as an indicator of low temperatures and is considered an "Arctic" species due to its frequent occurrence in Arctic lakes [Harmsworth, 1968; Flössner, 2000]. In reality, *A. harpae* is widespread in the Holarctic, it has been recorded in tropical regions, and occurs in every region of Russia [Kotov *et al*., 2011; Kotov, 2016]. The taxon inhabits the littoral zone, shallow river backwaters and floodplains, and swamps, often among vegetation. *Alona quadrangularis* is found on a wide range of littoral substrates in a variety of environmental conditions, in water bodies of different types, and is often present in temporary water bodies [Smirnov, 2010]. This taxon is not associated with a specific substrate; however, it is more often found in association with vegetation, on rocks or detritus in waters rich in organic matter. *A. quadrangularis* demonstrates a tolerance to acidification and an increase in its proportion in Cladocera taxocenosis may indicate eutrophication of the water body [Van Damme, Dumont, 2008]. The extensive ecological tolerance exhibited by these species enables them to coexist beyond the boundaries of their clusters (Fig. 3).

Cluster 4 consisted of the predator *Bythotrephes* sp. and its prey, *Ceriodaphnia* sp. *Bythotrephes* sp. is largely a generalist predator, but in some experimental feeding studies, cladocerans, including *Daphnia*, *Ceriodaphnia* and *Bosmina* (*Eubosmina*) spp., were identified as the preferred prey of *Bythotrephes* [Vanderploeg *et al*., 1993]. These species were present in Subatlantic period (Zone IIIb), as described by Ibragimova *et al*. [2025] (Fig. 1A, B).

It is noteworthy that in previous studies of benthic and zooplankton communities, the predator-prey pairs also were included into a single associated cluster [Kurina *et al*., 2019; Prokin *et al*., 2021]. However, a distinct cluster comprising solely a predator and a prey was identified for the first time in this study. This is probably due to the fact that spatially distributed samples represent a snapshot of the community of living organisms, whereas each taphocenosis sediment sample covers a significant time interval and is an integral assessment of the cenosis over an extended period of time.

Cluster 5 was represented by single findings of *Drepanothrix dentata* and *Limnosida frontosa* in Zone IIIb. These species are regarded as indicators of oligotrophic conditions. The Subboreal period, corresponding to Zone IIIb, was characterised by a sharp cooling. The occurrence-based cluster analysis did not identify this zone as a discrete unit, and the association analysis, conversely, did not merge the species from Zone IIIb (clusters 4 and 5) with a major cluster confined to the upper part of the core. In this instance, the association analysis was more accurate than the broken stick model over the CONISS cluster analysis. Additionally, it is notable that species belonging to cluster 2, which occurred during the initial, cold-water period (*Rhynchotalona falcata*, *A. excisa*, *A. intermedia*), began to reappear in samples corresponding to Zone IIIb (Fig. 1A, B). Here, the results of the occurrence-based cluster analysis were more generalized compared to the abundance-based clustering, which was applied in the previous study [Ibragimova *et al*., 2025].

A. quadrangularis had a positive association with five species belonging to the cluster 3: *Pleuroxus uncinatus* (significance level of association p=0.003), *C. rectirostris* (p=0.018), *G. testudinaria* (p=0.018), *S. crystallina* (p=0.036) and *Eurycercus* sp. (p=0.047) (Fig. 3). *A. quadrangularis* was present in almost all samples (Ibragimova *et al.*, Part I), and predominated in two (IIa, IIb) out of five zones. The middle part of the core (IIa, IIb) accounted for 79% of this species abundance, while the upper part (IIIa, IIIb) accounted for 17%. The five species associated with *A. quadrangularis* also occurred mainly in the middle and upper part of the core, but the middle part accounts for 38% of their total abundance and the upper part for 60%. Thus, the increase in the abundance of the five associated species corresponded with a decrease in the abundance of the subdominant *A. quadrangularis*, while their occurrence in the middle and upper part of the core coincided. Given that the species association analysis was based on the occurrence of species, it grouped them into a single cluster, regardless of their abundances.

Conclusion

Comparison of the binary data analysis and previously made cluster analysis based on abundances allows us to make the following conclusions:

1) Cladoceran species occurrence analysis is less precise but reflects more general changes in the lake environment, whereas abundance analysis gives a more detailed and smoother representation of the changes in taphocenosis possibly reflecting changes in the environmental conditions.

2) Species association analysis is not limited to spatial data, as previously demonstrated; it can also be applied to temporal palaeodata. This approach enables the identification of a key set of species typical for certain environmental conditions. By comparing these groups of species with the periods identified during the clustering of samples in the sediment core, it is possible to provide or refine palaeoclimatic characteristics of these periods.

3) The analysis of qualitative data on the cladoceran taphocenosis enabled the identification of two significant periods in the history of Lake Torosjarvi. The transition between these periods occurred at ca. 10.6 thousand cal. yr BP and was accompanied by a warming trend and an increase in the lake trophic status, as well as the development of a macrophyte zone. These changes were associated with a shift in the cladoceran community from cold-water to warm-water species and an increase in the proportion of phytophilous species.

Compliance with ethical standards

CONFLICT OF INTEREST: The authors declare that they have no conflict of interest.

Ethical approval: No ethical issues were raised during our research.

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