

***ENVIRONMENTAL
RADIOECOLOGY
AND APPLIED
ECOLOGY***

Vol. 19 No.3-4 2013

Kazan (Volga Region) Federal University

with participation of the Ministry
of Protection of the Environment and
Natural Resources of the Republic of Tatarstan

ENVIRONMENTAL AND CLIMATIC FACTORS INFLUENCING THE DISTRIBUTION OF SUB-FOSSIL CLADOCERANS IN THERMOKARST LAKES IN NORTHEASTERN SIBERIA, RUSSIA

© Frolova L.*¹, Nazarova L., Nigamatzyanova G., Mukhametgaliev N.R., Krylov P., Frolova A.

Kazan (Volga Region) Federal University

Received 8 September, 2013

* Corresponding author: Frolova Larisa Alexandrovna, Kazan Federal University, Institute for fundamental biology and medicine, Department of Bioresources and Aquaculture, 420008, Kremlevskaya str., 18 Kazan.

Larissa.Frolova@mail.ru

Abstract. *Surface sediments of thermokarst lakes along the temperature gradient were sampled in northwestern Siberia. The lakes were distributed through three environmental zones: typical tundra, southern tundra and forest-tundra, which were all situated within the continuous permafrost zone. Our investigation showed that the cladoceran communities in the lakes of the region are represented by diverse, abundant communities as reflected by the taxonomic richness and high diversity indices. The differences in the cladoceran assemblages were related to the limnological and geographical position, vegetation type, climate and water chemistry. The constrained redundancy analysis (RDA) indicated that the T_{July} water depth and both sulphate (SO_4^{2-}) and silicium (Si^{4+}) concentrations statistically significant ($p \leq 0.05$) explained the variance in the cladoceran assemblage.*

INTRODUCTION

Climate change is emerging as the most far reaching and significant stressor on Arctic biodiversity. Thermokarst lakes act as “hot spots” of biological activity in northern regions with diverse and abundant microbial, plankton, benthic, aquatic plant, fish and bird communities [1]. It is expected that the warming climate will cause changes to or even decrease the distribution areas of animals living in Arctic regions. Due to strong seasonal climatic contrasts, the life cycles of many arctic species are synchronised to the onset of spring and summer to take advantage of seasonal peaks in productivity. The early melting of ice and snow, flowering of plants and emergence of invertebrates can cause a mismatch between the timing of reproduction and the availability of food. Furthermore, recent climate warming is expected to support biological invasions by species originating from warmer regions [2]. Hence, biological observations using the best available scientific methods are required to identify changes in the biodiversity, assess the implications of any observed changes and develop adaptation strategies.

Cladocera (Crustacea: Branchiopoda) is a key component of aquatic ecosystems; their community structure reflects a combination of the physical, chemical and biological characteristics of the ecosystem they inhabit [3] (Davidson et al. 2007). Their chitinous exoskeletal components (shell, head shield, postabdomen, postabdominal claws, antennal segments and mandibles) are usually well preserved

in sediments and most of them are identifiable to the species level. Hence, cladoceran subfossils preserved in lake sediments contain valuable information about the climatic and environmental conditions prevailing during the lifetime of those organisms, which allows cladocerans to be used in palaeoecological studies [4] (Kienast et al. 2011). However, to interpret subfossil cladoceran assemblages, a detailed ecological knowledge about their distribution and ecological preferences is required. Unfortunately, such information is still fragmentary and often restricted to calibration data sets from a limited geographical area [5, 6] (Lotter et al. 1997; Bigler et al. 2006).

The aim of the present investigation was to examine fossil cladoceran assemblages from the northeastern Siberia, Russia and portray their distribution within the region to reveal the influence of environmental variables in structuring the cladoceran communities. To do this, we examined the surface sediments of the lakes that spanned a long north–south transect across the modern treeline and numerically related the cladoceran spectra to the physical and chemical characteristics of these lakes.

MATERIAL AND METHODS

Samples were collected during the expedition in the summer of 2007. The study sites included 35 lakes distributed along a north–south transect across the Anabar region (71°30'10.8" to 73°23'13.5" N). To avoid disturbances in the sediment deposition we sampled only the lakes that are over 1.1 m deep, are not fed by large rivers and without anthropogenic impact. For the hydrochemical analyses for each site water was sampled from the lake centre at a depth of 0.5–1 m. Secchi-disk measurements were taken from the same location. The alkalinity and acidity were determined using titrimetric test kits (Macherey-Nagel, Visocolor series). We quantified the pH, water temperature, oxygen concentration and electrical conductivity (EC) using a handheld multi-parameter instrument (WTW 340i) equipped with the appropriate sensors (pH: SenTix 41; Oxygen: Cellox 325; EC and temperature: Tetracon 325). Water samples for ion analysis were passed through a cellulose-acetate filter (pore size 0.45 μm) in the field. Samples for elemental (cation) analysis were acidified using HNO_3 . Samples for anion analysis and residue samples were stored cool. Surface sediments were collected from the deepest point of each lake using an Eckman dredge. The sediments were stored in cold storage at 4°C prior to analysis for invertebrate remains.

The chemical analyses encompassed total phosphorus (TP), chloride (Cl^-), sulphate (SO_4^{2-}), nitrite (NO_2^-), nitrate NO_3^- , carbonate (HCO_3^-), Si^{4+} and certain metals (Al^{3+} , Ca^{2+} , Fe_{total} , Mg^{2+} , Mn^{2+} and Na^+). TP, Mn^{2+} and NO_3^- were eliminated from the analysis because their concentrations were mostly below the detection limits. The sample preparation method used for the cladocera analysis in our study was an adaptation of the subfossil cladocera preparation technique described by Korhola and Rautio [7] (2001) and the method of Jeppesen et al. [8] (Jeppesen et al. 2001). The chitinous remains of cladoceran (post-abdomens, claws, mandibles, sections of antennae, ephippia and remains of carapaces) were identified with reference to Flössner [9] (2000), Frey [10, 11] (1959, 1973), Smirnov [12, 13] (1974, 1996), Szeroczyńska and Sarmaja-Korjonen [14] (2007).

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Thermokarst lakes

At least 100 individuals per sample were counted from each sub-sample. All individuals were identified to the highest taxonomic level possible.

The environmental data included several physical, chemical and biological variables considered to be potentially important in structuring cladoceran communities. These included: the mean July air temperature, latitude, longitude, altitude, vegetation, water depth, Secchi depth, conductivity, pH, dissolved organic carbon (DOC) and the total phosphorus (TP), Cl⁻, SO₄²⁻, NO₂⁻, HCO₃⁻, Al³⁺, Si⁴⁺, Ca²⁺, Fe_{total}²⁺, Mg²⁺, Mn²⁺ and Na⁺ concentrations. Any environmental variables with a skewed distribution (altitude, conductivity, Secchi depth, Cl⁻, SO₄²⁻, NO₂⁻, Al³⁺, Fe_{total}²⁺) were ln (x+1) transformed, where x was the environmental variable under consideration. To reduce the variances across the cladoceran taxa, the percent abundances were square-root transformed prior to all numerical analyses.

A detrended correspondence analysis (DCA) was applied to the cladoceran data to calculate the sampled environmental gradient length. This was necessary to choose between unimodal or linear numerical techniques when estimating the relationship between the cladoceran assemblages and environmental variables [15] (Birks 1995). The DCA revealed a gradient length of 2.971 SD units, which is an intermediate gradient length and suggests either linear or unimodal ordination methods might be appropriate [16] (ter Braak and Šmilauer 2002).

Variance inflation factors (VIF) were used to identify the intercorrelated variables. Variables with high VIFs (>20) were eliminated one at a time beginning with the highest until all of the VIFs were below 20 [17] (ter Braak and Prentice 1988). The minimum number of environmental variables needed to explain significant (p<0.05) variations in the cladoceran data was then determined via forward selection in a redundancy analysis (RDA). To determine the relationships between the environmental variables and cladoceran taxa distribution and select those that best explained the cladoceran spectra variation, a set of RDAs separately constrained to each environmental variable was run. Any variables that were not significant were removed from the analysis. The significance of the variables was tested using a Monte Carlo test with 999 random permutations (p≤ 0.05) [18] (Hall and Smol 1996).

Ordinations were performed using CANOCO software, version 4.5 [16] (ter Braak and Šmilauer 2002). TILIA version 2.0.b.4 was used to generate a cladoceran percentage diagram [19] (Grimm 1993). The program CONISS was used to perform a stratigraphically constrained incremental sum-of-squares cluster analysis and identify the major groups in lake composition throughout the transect [20] (Grimm 1987).

Species diversity and evenness were calculated for each sample using the Shannon Index of Diversity (H) [21] (Shannon and Weaver 1963) and Pielou index (I) [22] (Pielou 1966).

RESULTS

A total of 28 cladoceran taxa belonging mostly to the family Chydoridae were identified. None of these taxa occurred in all lakes. The most common cladoceran taxa were *Chydorus sphaericus* (O.F. Müller, 1785), *Euryercus* spp., *Alona rectangula* Sars, 1861, *Acroperus harpae* (Baird, 1834) and *Daphnia pulex* agg. (frequency of occurrence > 50%). The species richness (the total number of taxa per lake) ranged between 5 (lakes 07-SA-05, 07-SA-14, 07-SA-18) and 20 (lake 07-SA-24) with a median of 9 which was not significantly correlated to any of the environmental variables measured. The most abundant cladoceran taxon in the modern samples was *Chydorus sphaericus*, which had a mean relative abundance of 44.6% ($\pm 4.5\%$) across all lakes and reached an abundance of over 50% in 13 of the 31 lakes (Fig. 1).

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Constrained cluster analysis (CONISS), based on the structure of cladoceran community and revealed three groups of lakes in the investigated area (Fig. 1). The clusters show a clear geographic pattern reflecting vegetation zonation into typical tundra, southern tundra and forest-tundra. However, the cladoceran assemblage from lake 07-SA-27 was clustered with the forest-tundra lakes, although this lake is situated in the tundra zone (30 km north of the tree line observed from helicopter in field) (Fig. 1).

The first cluster revealed by CONISS was formed by 9 northern lakes located in the typical tundra zone (mean $T_{\text{July}} = +10.6^{\circ}\text{C}$, range between $+10.2$ and $+10.9^{\circ}\text{C}$). Several littoral taxa, including *Chydorus sphaericus*, *Alona rustica* var. *tuberculata*, *Euryercus* spp. and *Daphnia pulex* agg. were the most abundant in this environment (Fig. 1). The species richness in this group of lakes (mean $N=7.78$, t-test $p \geq 0.01$) was lower than for southern tundra lakes; however, the other biodiversity indices were not smaller than in southern lakes (Table 1).

Lakes from the southern tundra (cluster II; mean $T_{\text{July}} = +11.2^{\circ}\text{C}$, range $+11.0$ to $+11.7^{\circ}\text{C}$) were dominated by diverse littoral and pelagic cladoceran assemblages (*Chydorus sphaericus*, *Bosmina longirostris* (O. F. Müller, 1785), *Eubosmina longispina* Leydig, 1860, *Eubosmona* spp., *Alona rectangula* Sars, 1862). The Shannon Index for this group of lakes was higher than for group I ($H = 1.99$). The evenness (I), which reflects the structural stability of the cladoceran communities, averaged at 0.82 (Table 1).

All of the lakes in cluster III, except lake 07-SA-27 were located in the forest-tundra zone (mean $T_{\text{July}} = +11.8^{\circ}\text{C}$, range $+11.7$ to $+12.1^{\circ}\text{C}$). The most common taxa were *Chydorus sphaericus*, *Alona rectangula* and *Daphnia longispina* agg. Interestingly, a dominant species in the northern part of the transect taxa from the family Daphnidae, *Daphnia pulex* agg., was replaced in the forest-tundra zone lakes by *Daphnia longispina* agg. (Fig. 2). Cladoceran assemblages in this cluster are more diverse and even ($N=9.15$, $H=1.72$) than in lakes in the typical tundra zone (Table 1).

Thermokarst lakes

Forward selection and Monte Carlo permutation tests (999 permutations) identified a minimal subset of four environmental variables that significantly ($p \leq 0.05$) and most effectively explained the taxonomic data variation: T_{July} , water depth, SO_4^{2-} and Si^{4+} (Fig. 2). RDA axis 1 ($\lambda = 0.174$) and axis 2 ($\lambda = 0.157$) were both significant ($p \leq 0.05$) and explained 85.8% of the relationships between the cladoceran taxa and the measured environmental variables. T_{July} and Si^{4+} correlated to RDA axis 1, while the water depth and SO_4^{2-} correlated to RDA axis 2.

Of the four identified significant environmental variables, T_{July} featured the highest percentage (17.4%) of explained variance and had the highest λ_1/λ_2 ratio (0.67) if tested in an RDA with only a single constraining environmental variable. The latter measure in particular indicates how effectively the variance in the species data was captured by a particular gradient (Korhola et al. 2000). The results suggest that the relationship between the cladoceran distribution in this data-set and T_{July} is sufficiently strong to be promising for the future development of a regional transfer function to reconstruct past mean July temperatures from cladoceran data in palaeoenvironmental investigations.

The sites with high axis 1 scores were clustered in the top right portion of the biplot. These lakes are located in the typical tundra zone in the North at low elevation and were shallower than the more southern lakes (water depth: mean 3.17 m, range 1.0-7.4 m).

Lakes with low axis 2 scores are relatively deep (mean >6.5 m, range 0.9- >10.0 m) and most are located in the southern tundra and characterised by diverse littoral and pelagic cladoceran assemblages (*Chydorus sphaericus*, *Bosmina longirostris*, *Eubosmina longispina*, *Eubosmona* spp. and *Alona rectangula*) (Fig. 2a, 2b).

Lakes with high axis 2 and low axis 1 scores also came from the southern part of the transect, though mostly from the forest-tundra zones with higher elevations and had high Si^{4+} ion concentrations (Fig. 2b).

There was a separation of littoral and pelagic cladocerans along the second RDA axis that was defined by lake depth. Littoral cladocerans generally occurred in shallow, coloured lakes (Fig. 2a: different taxa from the genus *Pleuroxus*, *Eurycerus* and *Alona*), whereas some pelagic cladocerans occurred in higher relative abundances in relatively deep, clear lakes (Fig. 2a: e.g., *Eubosmina* sp. and *Bosmina longirostris*). A typical profundal cladoceran species found in the deep lakes was *Leydigia leydigii* (Leydig, 1860). Only one pelagic taxa, the *D. pulex* complex, was abundant in the shallow coloured lakes (Fig. 2a).

Overall, the results obtained using the ordination methods supported the classification of the lakes made on the basis of constrained cluster analysis (COGNISS) (Fig. 1). Cladoceran assemblages have the strongest relationship to the climate related parameters (T_{July} , vegetation type) and lake water depth.

CONCLUSION

Surface sediments of thermokarst lakes were sampled and examined in north-eastern Siberia along the temperature gradient crossing the tree line. The lakes were distributed through three environmental zones: typical tundra, southern tundra and forest-tundra, which were all situated within the continuous permafrost zone. Our investigation showed that the cladoceran communities in the lakes are represented by diverse, abundant communities as reflected by the taxonomic richness and high diversity indices. Cluster analysis indicated that the Cladoceran communities in the three ecological zones (typical tundra, southern tundra and forest-tundra) differed in their taxonomic composition and structure. The differences in the cladoceran assemblages were related to the limnological and geographical factors, catchment characteristics, climate and water chemistry. The constrained redundancy analysis (RDA) indicated that the TJuly, water depth and both sulphate (SO_4^{2-}) and silicium (Si^{4+}) concentrations statistically significant ($p \leq 0.05$) explained the variance in the cladoceran assemblage.

One of the most significant changes in the structure of the cladoceran communities in the investigated transect was the replacement of closely related species along the latitudinal and vegetation gradient.

ACKNOWLEDGEMENTS

The authors thank the laboratory teams of the Alfred Wegener Institute for Polar and Marine Research (AWI) in Potsdam for general assistance during sample preparation and analysis. Larisa Frolova is especially thankful to Dr Thomas Davidson (Aarhus University) for his help and training her in slide preparation and identification of subfossil Cladocera. The group of authors also expresses sincere gratitude to the anonymous reviewers of this article for their valuable remarks and references. The project was funded by Federal Targeted Program "Scientific and Scientific-Pedagogical Personnel of the Innovative Russia" for 2009-2013.

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Thermokarst lakes

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