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Dynamics of Zooplankton Composition in the Lower Northern Dvina River and Some Factors Determining Zooplankton Abundance

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Abstract—The long-term dynamics of the taxonomic composition of zooplankton in the lower reaches of the Northern Dvina River and the effect of some hydrochemical factors on its abundance have been studied. It is found that the species list of the zooplankton has included 141 species over 50 years: it consisted of a total of 98 taxa in 1965 and 104 taxa in 2012–2019. The results of analyzing the spatiotemporal abundance distribution of the zooplankton and its taxonomic groups are presented. A significant increase in abundance (on account of copepods) and changes in the taxonomic structure of zooplankton have been revealed in the lower parts of the study water area. In 2019, changes in the structure-forming complex of zooplankton were noted for the first time over the study period. It is found that species diversity reaches high values in waters classified as "heavily polluted" and "dirty," which is evidence for a complex structure of zooplankton communities. The main factor influencing the horizontal distribution of the zooplankton abundance is the dissolved oxygen content of water.

Keywords: zooplankton, taxonomic composition, species diversity, abundance, long-term dynamics, Northern Dvina

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The study of water bodies in the Arctic zone of the Russian Federation is a priority in the state policy for the Arctic. This region is highly susceptible to climate changes; it is characterized by a low resistance of the natural environment to anthropogenic impacts, as well as by a slow recovery of disturbed ecosystems and landscapes. Therefore, the ecological monitoring of the state of Arctic freshwater ecosystems and their changes with time is currently of particular importance [1, 2].

Zooplankton is an important component of aquatic ecosystems that is involved in the transformation of organic matter and formation of matter and energy fluxes. Filter-feeding organisms are involved in the natural self-purification of water bodies, which is important under increased anthropogenic loads. The parameters of zooplankton species richness, diversity, size–weight structure, and dominance are sensitive indicators of anthropogenic changes in environmental conditions [3].

Among the mouths of the main Russian rivers in the Arctic, special attention should be paid to the mouth of the Northern Dvina River, which has been intensively developed in terms of industry and transport and is characterized by complex hydrochemical conditions due to the mixing of fresh river waters with saline waters of the White Sea [4].

The zooplankton of water bodies in Arkhangelsk oblast began to be studied in the late 19th–early 20th centuries [5]. Further studies of zooplankton in the lower reaches of the Northern Dvina River were carried out by the Department of Hydrology and Water Management of the Karelian Branch of the USSR Academy of Sciences in 1965–1966 and were included in the program of integrated research on the effect of industrial wastes from pulp and paper enterprises on zooplankton [6]. In the late 20th–first decade of the 21st centuries, the Northern Territorial Administration for Hydrometeorological and Environmental Monitoring (NTAHEM) carried out systematic hydrobiological observations in the water area of the entire Northern Dvina basin [7], and the results of studying the technogenic impact of large enterprises on the structure of planktonic fauna in the lower reaches of the Northern Dvina River were published [4, 8, 9]. The data on zooplankton in the lower reaches of the Northern Dvina were updated last time in 2013–2014 [10].

The above-mentioned reviews contain some discrepancies in the identification of zooplankton species. For example, representatives of the genus *Bosmina* were classified into 15 species in 1965 and five species in 2013–2014, while only two species of this genus from the waters of Russia were identified by molecular genetic methods. The taxonomic status of some rotifer, cladoceran, and copepod species has changed over the past period [11].

The river mouths are ecologically and socially significant productive ecosystems that support diverse life forms; however, the extinction rates of freshwater organisms have become much higher than those of terrestrial species due to the high impact of interacting stress factors [12, 13]. The effects of environmental factors and the mechanisms of formation of the zooplankton structure in river ecosystems have not been studied sufficiently [13]. Knowledge of spatiotemporal changes in functional traits is important for elucidating fundamental ecological processes that determine the diversity of species, structure of the community, and functioning of ecosystems [14]. Therefore, identification and description of specific features in structural organization of zooplankton are highly relevant, since they may provide a better understanding of its ecological role in the ecotonal aquatic system, and the large amount of available data on the composition of zooplankton in the lower reaches of the Northern Dvina River over a long time period provides a basis for analyzing the long-term dynamics of its composition and assessing probable climatogenic and anthropogenic trends.

The purpose of this study was to analyze the long-term dynamics of the composition, structure, biodiversity, and horizontal distribution of zooplankton in the lower reaches of the Northern Dvina River and assess the role of environmental factors (water temperature, acidity, and dissolved oxygen content) determining its abundance on a local scale.

MATERIAL AND METHODS

Long-term Dynamics of the Qualitative and Quantitative Composition of Zooplankton. Our analysis of the dynamics of zooplankton composition was performed using published data covering the summer periods of 1965 [6] and 1985 (limited to the values of zooplankton abundance and Shannon's index of species diversity) [8] and growing periods of 2012–2014 [7, 10, 15, 16], as well as materials collected from June to October 2018–2019 within the framework of the program of the NTAHEM and the state assignment to the Federal Center for Integrated Arctic Research, Russian Academy of Sciences, for conducting fundamental and applied studies in the lower reaches of the Northern Dvina River.

Samples were taken in 2012–2014 and 2018–2019 in a network of observation stations established according to the Regulation Document RD 52.24.309-2016 "Organization and Performance of Monitoring Observations of the State and Pollution of Inland Surface Waters": station 1, within the village of Ust-Pinega (the left and right banks and middle of the river); station 2, 1 km upstream of the Pinega River mouth (middle of the river); station 3, within the town of Novodvinsk (left and right banks); station 4, within the city of Arkhangelsk near the railway bridge (left and right banks); station 5, in the Kuznechikha duct (left and right banks); station 6, in the Korabelny branch (the middle of the river); station 7, in the Maimaksa duct (left and right banks); and station 8, in the Nikolsky branch, the village of Rikasikha (the middle of the river) (Fig. 1). During the study period, a total of 307 zooplankton samples were taken from the surface water horizon and analyzed at the observation stations according to the generally accepted hydrobiological methods [17], including 60 samples in 2012, 60 samples in 2013, 53 samples in 2014, 70 samples in 2018, and 64 samples in 2019. Species identification of zooplankton organisms was performed using appropriate identification keys [11].

Zooplankton communities were characterized with respect to species composition, species number, abundance (N), and the ratio of taxonomic groups ($N_{\text{Rotifera}}/N_{\text{Cladocera}}/N_{\text{Copepoda}}$). Dominant species in the communities were identified by their relative abundance at a level of no less than 10%. The species diversity of zooplankton communities was analyzed using Shannon's diversity index (H_N) [17] calculated based on the average abundance values for each study year (2012–2014 and 2018–2019).

Factors Determining the Current Abundance of Zooplankton in the Ecotonal Aquatic System of the Northern Dvina. The integrity of studies in 2018 was provided for by making simultaneous measurements of water temperature, acidity, and dissolved oxygen content at each observation station. Water samples were analyzed at the NTAHEM laboratory according to the certified methods: RD 52.24.496-2018 "Procedure for Measuring Temperature, Transparency, and Water Odor"; RD 52.24.495-2017 "Hydrogen Water Index. Potentiometric Measurement Procedure"; RD 52.24.419-2019 "Mass Concentration of Dissolved Oxygen in Waters: Iodometric Measurement Procedure."

Statistical processing of the results (arithmetic mean, error of the mean, and median) and analysis of correlations between environmental parameters and the abundance of zooplankton and its individual groups were performed with the SPSS Statistics software. The Pearson correlation coefficient was calculated using a set of hydrobiological and hydrological–hydrochemical data for 2018 (70 coupled samples).

RESULTS AND DISCUSSION

Long-term Dynamics of the Qualitative and Quantitative Composition of Zooplankton. The zooplankton in the lower reaches of the Northern Dvina River is represented by three major taxonomic groups of micro- and mesozooplankton: Rotifera, Cladocera, and Copepoda. A total of 141 species were identified over the study period, with 41.1% of these species

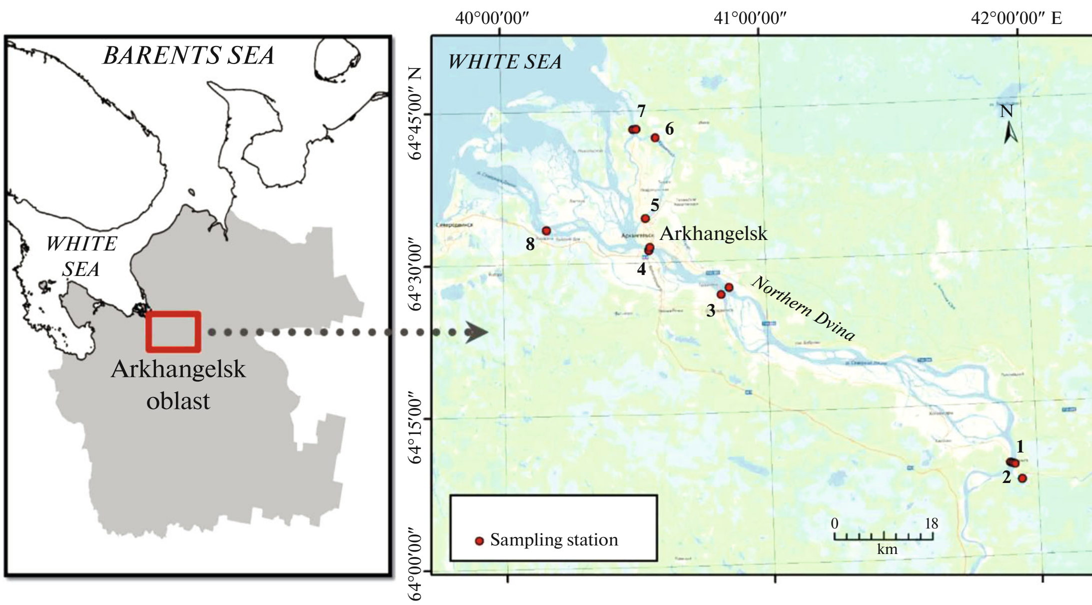

Fig. 1. Schematic map of the lower reaches of the Northern Dvina River and hydrobiological sampling stations.

belonging to the superorder Cladocera (Table 1). Analysis of the data shows that the composition of the zooplankton fauna of the surveyed water area has changed significantly during the period from 1965 to the present, which is probably due to increase in the anthropogenic load on the ecosystem and in the level of pollution of the aquatic environment [7, 15, 16, 18].

Five new Rotifera species, nine new Cladocera species, and six new Copepoda species not listed in the 1965 reports were recorded in the zooplankton. They appeared in the lotic system in the course of climatic and anthropogenic changes that occurred there over more than 45 years [19]. On the other hand, 11.3% of rotifer species identified in 1965 samples were no longer recorded in 2012–2019 samples. All Rotifera species that are new to the fauna are cosmopolitan. Among them, *Brachionus quadridentatus* deserves particular attention as an indicator of β-mesosaprobic conditions that can live in fresh, brackish, and sea waters; i.e., it is tolerant to significant fluctuations in water salinity.

Among the Cladocera, we found species with an undetermined saprobic valence: two cold-water species with a limited northern range (*Bythotrephes cederstroemii* and *Eurycercus* (*Teretifrons*) *glacialis*) and one species inhabiting peat bogs, *Ophryoxus gracilis*. All the other species were Holarctic and included both oligosaprobes and β-mesosaprobes.

With respect to representation in the total species list, copepods were the most constant group over many years. This is explained both by their trophic characteristics and relationships with the environment: this group is represented mainly by species that actively search for mobile prey and capture it in the water column [11] and can escape the attacks by predators due to their high motor activity [20].

Since 2012, the number of species recorded in the lower reaches of the Northern Dvina River varied from 42 to 66 in 2019, with cladocerans reaching the highest level of development in all years. When the pollution level increases, the species diversity index usually decreases and has low values [21, 22]. According to the integrated estimates of the NTAHEM, the waters of the lower reaches of the river correspond to quality classes IIIb and IVa and are characterized as "heavily polluted" or "dirty" [18]. Shannon's index of species diversity, calculated by the average annual abundance throughout the water area for a single year, varied in the range from 2.00 (in 1985) to 3.88 bit/ind. (in 2014); its values in 2018 and 2019 were 3.55 and 3.67, respectively. On the whole, the values of this index in the lower reaches of the river were high, indicating the evenness of the community structure and significant species richness of the zooplankton.

The chaotic pattern of the dynamics of zooplankton is its intrinsic and natural property, which can be used to characterize the realized adaptive potential of the community [3]. The zooplankton of the ecotonal aquatic system of the Northern Dvina was characterized by its quantitative diversity: the abundance of organisms varied in a wide range both along the river profile and over the study years (Table 2).

The highest indices of zooplankton abundance in the long-term dynamics were observed in 2013–2014, which is probably explained by a favorable combined effect of factors on the development of plankton animals in the study years [7, 16]. The structure-forming complex of species was quantitatively represented by

Table 1. Taxonomic composition of zooplankton in the lower reaches of the Northern Dvina River

Species	Study years					
	1965*	2012**	2013**	2014**	2018	2019
Rotifera						
Asplanchna priodonta Gosse, 1850	+	+	+	+	+	+
A. herricki Guerne, 1888	+		+	+	+	+
Asplanchna sp.	+			+	+	+
Brachionus angularis Gosse, 1851	+					
Br. calyciflorus calyciflorus Pallas, 1776	+		+	+	+	+
Br. diversicornis (Daday, 1883)	+					
Br. quadridentatus Hermann, 1783				+		
Brachionus sp.	+				+	
Cephalodella sp.					+	
Conochilus unicornis Rousselet, 1892	+					+
Euchlanis dilatata Ehrenberg, 1832	+			+	+	+
Euchlanis sp.	+			+		
Filinia longiseta (Ehrenberg, 1834)	+					+
Kellicottia longispina (Kellicott, 1879)	+			+		+
Keratella cochlearis (Gosse, 1851)	+		+	+	+	+
K. cruciformis (Thompson, 1892)	+					
K. quadrata (O.F. Müller, 1786)	+			+	+	+
Lecane cornuta (Müller, 1786)						+
L. luna (Müller, 1776)	+					
Lecane sp.					+	+
Lepadella ovalis (Müller, 1786)	+					
Mytilina sp.					+	
Notholca acuminata (Ehrenberg, 1832)	+				+	
Notholca sp.					+	
Ploesoma hudsoni (Imhof, 1891)	+					+
Ploesoma truncatum (Levander, 1894)	+					
Ploesoma sp.				+	+	+
Polyarthra dolichoptera Idelson, 1925	+					
P. luminosa Kutikova, 1962	+					
P. vulgaris Carlin, 1943	+				+	
Polyarthra sp.				+	+	+
Synchaeta baltica Ehrenberg, 1834	+					
S. grandis Zacharias, 1893	+					
S. stylata Wierzejski, 1893	+					
Synchaeta sp.	+				+	+
Testudinella sp.					+	
Trichocerca cylindrica (Imhof, 1891)	+					
Tr. porcellus (Gosse, 1851)	+					
Tr. pusilla (Jennings, 1903)	+					
Trichocerca sp.	+			+	+	+
Trichotria curta (Skorikov, 1914)	+					
Tr. pocillum (Müller, 1766)	+					
Cladocera						
Acroperus harpae (Baird, 1834)	+	+	+		+	
Alona affinis (Leydig, 1860)	+	+	+		+	+
A. costata G.O. Sars, 1862	+					
A. guttata G.O. Sars, 1862	+				+	
A. quadrangularis (O.F. Müller, 1776)	+	+	+	+	+	+
Alona sp.				+	+	+
Alonella exigua (Lilljeborg, 1853)		+				

Table 1. (Contd.)

Species	Study years					
	1965*	2012**	2013**	2014**	2018	2019
Al. nana (Baird, 1843)	+					+
Alonopsis elongatus G.O. Sars, 1862	+	+				
Bythotrephes cederstroemii Schoedler, 1877					+	
Bosmina (Eubosmina) coregoni Baird, 1857	+	+	+	+	+	+
B. (Bosmina) longirostris (O.F. Müller,1785)	+	+	+	+	+	+
Bosmina sp.	+	+	+	+	+	+
Bosminopsis sp.	+					
Camptocercus fennicus Stenroos, 1898	+					
Ceriodaphnia dubia Richard, 1894		+	+	+	+	+
C. quadrangula (O.F. Müller, 1785)	+	+	+	+		+
C. pulchella G.O. Sars, 1862	+					
Ceriodaphnia sp.			+		+	+
Chydorus sphaericus (O.F. Müller, 1785)	+	+	+	+	+	+
Ch. ovalis Kurz, 1875	+	+	+			
Chydorus sp.			+			
Coronatella rectangula (G.O. Sars, 1862)	+				+	+
Daphnia (Daphnia) cucullata G.O. Sars, 1862	+	+	+	+	+	+
D. (D.) cristata G.O. Sars, 1862	+	+	+		+	+
D. (D.) hyalina Leydig, 1860	+					
D. (D.) longiremis G.O. Sars, 1862	+	+				
D. (D.) longispina (O.F. Müller, 1776)	+					+
D. (D.) pulex Leydig, 1860	+					
Daphnia sp.			+	+		+
Diaphanosoma brachyurum (Liévin, 1848)	+	+		+	+	+
Disparalona rostrata (Koch, 1841)	+					+
Disparalona sp.					+	+
Eurycercus (Teretifrons) glacialis Lilljeborg, 1887			+		+	
E. lamellatus (O.F. Müller, 1776)	+					
Graptoleberis testudinaria (Fischer, 1851)	+					
Holopedium gibberum Zaddach, 1855	+					
Ilyocryptus acutifrons G.O. Sars, 1862	+		+	+		+
Il. sordidus (Liévin, 1848)		+	+			
Ilyocryptus sp.	+					
Leptodora kindtii (Focke, 1844)	+		+		+	
Leydigia leydigi (Schödler, 1863)	+		+			+
Limnosida frontosa G.O. Sars, 1862	+	+	+	+	+	
Macrothrix hirsuticornis Norman & Brady, 1867		+	+	+	+	+
M. laticornis (Jurine, 1820)	+	+	+	+		
Macrothrix sp.					+	
Moina sp.	+					
Monospilus dispar G.O. Sars, 1862	+	+				
Ophryoxus gracilis (G.O. Sars, 1862)				+		
Peracantha truncata (O.F. Müller, 1785)	+					+
Picripleuroxus laevis (G.O. Sars, 1862)	+					
Pleuroxus aduncus (Jurine, 1820)						+
Pl. trigonellus (O. F. Müller, 1776)		+				
Pl. uncinatus (Baird, 1850)	+	+				
Polyphemus pediculus (Linnaeus, 1761)	+		+	+	+	+
Scapholeberis mucronata (O.F. Müller, 1776)	+		+		+	+
Sida crystallina (O.F. Müller, 1776)	+		+		+	
Simocephalus vetulus (O.F. Müller, 1776)	+	+				

Table 1. (Contd.)

Species	Study years					
	1965*	2012**	2013**	2014**	2018	2019
Copepoda						
Acanthocyclops vernalis vernalis (Fischer, 1853)	+			+	+	+
A. venustus venustus (Norman & Scott T., 1906)	+					
Acanthocyclops sp.			+			
Calanoida sp.		+	+	+	+	+
C. scutifer scutifer Sars G.O., 1863		+	+	+	+	+
C. strenuus strenuus Fischer, 1851	+	+	+	+	+	+
C. vicinus vicinus Uljanin, 1875	+					
Cyclops sp.		+			+	+
Cyclopoida sp.			+	+		+
Diacyclops bicuspidatus (Claus, 1857)	+	+	+			
D. languidoides languidoides (Lilljeborg, 1901)	+					
D. nanus nanus (Sars G.O., 1863)	+					
Diacyclops sp.					+	+
Ectinosoma sp.				+		+
Eudiaptomus gracilis (Sars G.O., 1863)	+					
E. graciloides (Lilljeborg, 1888)	+					+
Eudiaptomus sp.		+				
Eucyclops macruroides macruroides (Lilljeborg, 1901)	+					
E. macrurus macrurus (Sars G.O., 1863)	+					
E. serrulatus serrulatus (Fischer, 1851)	+	+	+	+		+
Eucyclops sp.						+
Eurytemora affinis (Poppe, 1880)	+	+	+	+	+	+
E. gracilis (Sars G.O., 1898)	+	+	+	+	+	+
E. lacustris (Poppe, 1887)		+	+	+	+	+
Eurytemora sp.		+	+	+	+	+
Harpacticoida sp.					+	+
Harpacticus uniremis uniremis Krøyer in Gaimard, 1842–1845?				+		
Harpacticus sp.				+		
Heterocope appendiculata Sars G.O., 1863	+				+	
Heterocope sp.			+			
Macrocyclops albidus albidus (Jurine, 1820)	+	+				
Macrocyclops sp.					+	+
Megacyclops viridis viridis (Jurine, 1820)	+	+		+	+	+
Mesocyclops leuckarti leuckarti (Claus, 1857)	+	+	+	+	+	+
Paracyclops affinis (Sars G.O., 1863)		+	+	+		+
P. fimbriatus fimbriatus (Fischer, 1853)	+	+	+		+	+
Paracyclops sp.					+	+
Platycyclops phaleratus (Koch, 1838)	+		+			+
Thermocyclops crassus crassus (Fischer, 1853)	+					
Th. oithonoides (Sars G.O., 1863)	+	+	+	+	+	
Rotifera: 43	33	1	4	13	19	17
Cladocera: 58	43	24	26	17	25	26
Copepoda: 40	22	17	17	17	18	23
Total: 141	98	42	47	47	62	66

* According to [6]; ** according to [7, 10, 15, 16].

one to four species in 2012–2019. The background of the plankton composition was formed by copepods; crustaceans of the genus *Eurytemora*, which can live in brackish waters, were common to all study years; in some years, they reached 52.0% of the total abundance (see Table 2). In 2019, the species structure of zooplankton underwent transformation manifested in the replacement of the superdominant species and the entire dominant taxonomic group by *Bosmina* (*Bosmina*) *longirostris.* In terms of abundance, this cosmopolitan eurybiontic species indicative of eutrophic conditions [23] formed the core of the plankton in that year. We do not attempt here to reveal factors responsible for this structural transformation, since this issue requires special study.

Similar species composition and structure-forming complex were described for the lower reaches of the Sacramento and San Joaquin rivers in North America. The brackish-water component of the zooplankton was represented by copepods of the genus *Eurytemora* and rotifers of the genus *Synchaeta*. The common representatives of freshwater zooplankton included species typical for rivers of the temperate zone rivers: *Bosmina* sp. and *Cyclops* sp. among crustaceans and species of the genera *Keratella*, *Polyarthra*, *Trichocerca* and *Synchaeta* among rotifers [24].

It should be noted that rotifers absolutely dominate in the zooplankton fauna of most of the big European rivers, such as the Elbe, Danube, Loire, Vistula, and Rhine [25, 26]. It is considered that representatives of the rotifer complex more easily adapt to the hydrodynamic conditions of the rivers, since they have a shorter generation period and are less intensively consumed by fish.

In the spatial aspect, the abundance of organisms at the station on the Northern Dvina within Novodvinsk decreased by factors of 1.5 (2019) up to 6 (2013), compared to 1985, which can be explained by continuous discharge of wastewaters that contain a large amount of toxic substances suppressing the functioning of biocenoses [4, 9]. The abundance of zooplankton at the station on the Kuznechikha duct in 2018–2019 increased up to threefold, compared to 1965. To some extent, this may be explained by differences in the dates of sampling. In addition, some major facilities such as the Arkhangelsk Hydrolysis Plant and Solombala Pulp and Paper Mill were put out of operation in the 2000s, which alleviated anthropogenic pressure on the aquatic ecosystem.

Analysis of the general structure of zooplankton and contribution of individual taxonomic groups to its abundance throughout the study period provided evidence for a succession of dominant groups, with Copepoda gaining prevalence beginning from station 5 on the Kuznechikha duct. In the upper parts of the water area, cladocerans contributed most to the development of zooplankton (47.3% at station 4 to 60.1% at station 2); in the lower parts of the water area, they were replaced by copepods (up to 90.3% at station 5) whose abundance was many times higher than the total values for all groups at stations nos. 1 to 4. This was accounted for mainly by brackish-water species of the genus *Eurytemora* (Table 3), which indicated their significant effect on the freshwater ecosystem of the Northern Dvina River.

Copepods of the genus *Eurytemora* reach significant densities in coastal waters all over the world and dominate in zooplankton communities, in particular, in the Gulf of Mexico and Chesapeake Bay, at the mouth of the Columbia River, and in many European rivers, where they occupy main trophic positions [27–29]. Of great scientific interest is the invasive species *Eurytemora affinis* identified in the lower reaches of the Northern Dvina, which can transmit water-borne diseases [30]. The sequencing of the *E. affinis* microbiome revealed some pathogenic and potentially pathogenic taxa, including *Vibrio cholerae*, *Salmonella*, *Shigella*, *Campylobacter*, *Corynebacterium diphtheriae*, *Yersinia*, *Aeromonas hydrophila*, and *Acinetobacter hausoul*, while these bacteria were absent in areas where *Eurytemora* samples were taken. Tidal events in the river mouths allow *E. affinis* to easily migrate from coastal to inland waters, which is accompanied by its rapid physiological evolution and changes in the microbiome, and these changes in the species composition of microbial community may have serious consequences in terms of disease transmission [30].

Factors Determining the Current Abundance of Zooplankton in the Ecotonal Aquatic System of the Northern Dvina

The dependence of the annual average abundance of zooplankton in the lower reaches of the Northern Dvina on temperature, pH, and the dissolved oxygen content is addressed in this study for the first time based on the 2018 data. To determine the effect of abiotic environmental factors on the development of zooplankton, we performed correlation analysis of the abundance of zooplankton as whole and its separate groups with the above hydrological and hydrochemical characteristics. It was found that the annual average total abundance of zooplankton was inversely correlated with the dissolved oxygen content and had a weak direct correlation with water pH value and temperature (Table 4).

In the lower reaches of the Northern Dvina River, the numerical parameters of Copepoda showed an inverse correlation of medium strength with the dissolved oxygen content and a weak direct correlation with water temperature. Similar correlations have been described for the Novosibirsk Reservoir [31], arctic lakes in the Anabar River basin [2], and the small Il'd River [32].

Table 2. Spatiotemporal dynamics of zooplankton abundance (ind./m^3) in the lower reaches of the Northern Dvina River

Statistical parameters	St. 1, Ust-Pinega	St. 2, 1 km upstream of the Pinega mouth	St. 3, Novodvinsk	St. 4, Arkhangelsk near railway bridge	St. 5, Kuznechikha duct	St. 6, Korabelny branch	St. 7, Maimaksa duct	St. 8, Nikolsky branch, Rikasikha
1965 (summer low water period)*								
M	No data				810	No data	740	350
1985 (summer low water period)**								
M	No data		1040	220	No data	840	440	620
2012***								
$M \pm m$	245 ± 61	76 ± 22	265 ± 88	303 ± 62	437 ± 116	252 ± 78	398 ± 201	No data
(min–max)	(30–690)	(20–150)	(40–920)	(50–610)	(50–1230)	(50–480)	(40–2130)	
Average number of species ± m	5.8 ± 0.8	4.4 ± 1.4	5.6 ± 0.6	5.8 ± 0.7	6.9 ± 1.1	6.8 ± 1.5	5.1 ± 0.6	
(min–max)	(2–10)	(2–10)	(2–8)	(3–10)	(2–11)	(3–12)	(3–9)	
Dominant species (%)	*Eurytemora affinis* (16.3), *Bosmina (Eubosmina) coregoni Baird, 1857* (13.9), *Mesocyclops leuckarti leuckarti* (12.2), *Eurytemora lacustris* (11.8)							
2013***								
$M \pm m$	658 ± 257	228 ± 149	632 ± 417	1406 ± 656	7242 ± 4707	644 ± 476	3010 ± 1758	No data
(min–max)	(40–1980)	(60–820)	(80–4320)	(60–5380)	(60–43 600)	(80–2540)	(40–18 200)	
Average number of species ± m	5.6 ± 1.6	4.0 ± 1.5	4.2 ± 0.6	5.0 ± 1.1	5.6 ± 0.9	5.6 ± 1.7	6.3 ± 1.1	
(min–max)	(2–15)	(2–10)	(3–9)	(2–12)	(2–10)	(2–12)	(2–11)	
Dominant species (%)	*Eurytemora lacustris* (52.0)							
2014***								
$M \pm m$	1375 ± 478	350 ± 41	304 ± 59	3274 ± 1587	5988 ± 2747	1440 ± 735	1045 ± 396	No data
(min–max)	(320–4300)	(260–460)	(100–740)	(120–13 200)	(440–23 820)	(140–3960)	(140–3440)	
Average number of species ± m	6.9 ± 0.9	4.3 ± 0.8	5.4 ± 0.9	8.6 ± 1.7	7.6 ± 1.1	8.6 ± 1.9	6.6 ± 0.7	
(min–max)	(4–11)	(2–5)	(2–11)	(3–17)	(4–14)	(3–14)	(4–10)	
Dominant species (%)	*Eurytemora lacustris (24.1), Brachionus calyciflorus calyciflorus* (12.8), *Eurytemora gracilis* (11.1)							
2018								
$M \pm m$	421 ± 292	176 ± 99	340 ± 169	548 ± 177	2628 ± 784	480 ± 267	1766 ± 718	708 ± 359
(min–max)	(0–4440)	(40–560)	(0–1520)	(40–1780)	(0–7860)	(20–1420)	(0–6540)	(40–1880)
Average number of species ± m	3.1 ± 0.7	3.4 ± 0.9	4.3 ± 1.7	7.6 ± 1.9	5.6 ± 1.0	4.8 ± 1.8	6.0 ± 1.7	6.2 ± 2.4
(min–max)	(0–7)	(1–6)	(0–14)	(1–18)	(0–9)	(1–11)	(0–17)	(1–12)
Dominant species (%)	Nauplii Copepoda (27.7), *Eurytemora affinis* (20.2)							
2019								
$M \pm m$	422 ± 149	148 ± 125	678 ± 305	417 ± 178	2004 ± 1215	180 ± 156	734 ± 473	435 ± 202
(min–max)	(0–1280)	(0–640)	(0–3020)	(10–1580)	(0–10 960)	(0–800)	(0–4920)	(40–900)
Average number of species ± m	5.1 ± 1.6	3.2 ± 2.3	4.6 ± 1.2	5.2 ± 1.4	5.7 ± 1.9	2.4 ± 1.6	5.5 ± 1.6	5.5 ± 2.2
(min–max)	(0–14)	(0–12)	(0–9)	(0–11)	(0–17)	(0–8)	(0–15)	(1–11)
Dominant species (%)	*Bosmina (Bosmina) longirostris* (23.7), *Eurytemora affinis* (17.1), *Asplanchna priodonta* (11.3), *Bosmina (Eubosmina) coregoni* (10.8)							

$M \pm m$ (min–max), arithmetic mean and its error (minimum and maximum values); * according to [6]; ** according to [8]; *** according to [7, 10, 15, 16].

Table 3. Long-term average abundance (N, ind./m^3) of zooplankton taxonomic groups in the lower reaches of the Northern Dvina River

Stations	$N_{Rotifera}$	$N_{Cladocera}$	$N_{Copepoda}$	$N_{Rotifera + Cladocera + Copepoda}$
No. 1, Ust-Pinega	215	332	128	675
No. 2, 1 km upstream the Pinega mouth	41	125	42	208
No. 3, Novodvinsk	70	200	115	385
No. 4, Arkhangelsk near railway bridge	435	654	294	1383
No. 5, Kuznechikha duct	54	339	3681	4074
No. 6, Korabelny branch	158	305	241	704
No. 7, Maimaksa duct	50	290	1216	1556
No. 8, Nikolsky branch, Rikasikha	68	184	456	708
$M \pm m$ (min–max)	136 ± 48 (41–435)	304 ± 57 (125–654)	772 ± 436 (42–3680)	1212 ± 440 (208–4074)
m_e	69	298	267	706

$M \pm m$ (min–max), arithmetic mean and its error (minimum and maximum values of abundance); m_e is median.

Table 4. Correlation coefficients of the abundance of zooplankton and its taxonomic groups with environmental factors (2018)

Group	O_2	pH	T, °C
$N_{Rotifera}$	–0.34 ($p < 0.01$)	0.29 ($p < 0.05$)	0.37 ($p < 0.01$)
$N_{Cladocera}$	–0.26 ($p < 0.05$)	0.26 ($p <0 .05$)	0.33 ($p < 0.01$)
$N_{Copepoda}$	–0.48 ($p < 0.01$)	0.21 ($p > 0.05$)	0.26 ($p < 0.05$)
$N_{Rotifera+Cladocera+Copepoda}$	–0.56 ($p < 0.01$)	0.31 ($p < 0.05$)	0.38 ($p < 0.01$)

The abundance dynamics of cladocerans and rotifers had a weak direct correlation with water pH and temperature and a weak inverse correlation with the dissolved oxygen content. Apparently, the development and distribution of hydrobionts in the studied water system are also dependent on other factors, including food supply [3, 20].

CONCLUSIONS

At the current stage, the zooplankton of the ecotonal aquatic system of the Northern Dvina comprises a moderate number of species and represents a stable and balanced community. Among its constituents, the highest species richness in all study years is characteristic of cladocerans. On the whole, the zooplankton community is characterized by quantitative diversity both along the river profile and over the study years. The abundance dynamics of its different groups have specific features determined by the regime of the lotic aquatic system, ecological conditions of the aquatic environment, and adaptive features of hydrobionts themselves. The structure of the zooplankton has undergone transformation manifested in the replacement of the superdominant species and the dominant taxonomic group as a whole. According to the results of correlation analysis, the main factor among the climate-dependent variables influencing the distribution of zooplankton is the content of dissolved oxygen. The obtained data on the zooplankton fauna in the lower reaches of the Northern Dvina River cannot be considered exhaustive; it is necessary to carry out further monitoring studies, including additional, more detailed analysis of the phylum Rotifera in general and of structural transformations that occurred in the zooplankton community in 2019.

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COMPLIANCE WITH ETHICAL STANDARDS

Statement on the welfare of animals. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

Conflict of interest. The authors declare that they have no conflict of interest.

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