Трансформация экосистем
Ecosystem Transformation

ISSN 2619-094X Print
ISSN 2619-0931 Online
www.ecosysttrans.com

Article

The structure of zooplankton community in different biotopes of small rivers in the Kologrivsky cluster of the Natural State Reserve "Kologrivsky Forest"

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Received: 11.03.2022
Revised: 11.04.2022
Accepted: 27.05.2022
Published online: 17.10.2022

DOI: 10.23859/estr-220311
UDC 574.52; 574.583

Translated by D.M. Martynova

Abstract. Structure of zooplankton community was studied in different biotopes of streams and beaver ponds in the Kologrivsky cluster of the State Nature Reserve "Kologrivsky Forest" named after M.G. Sinitsyn. Forty-five zooplankton species were recorded, namely, Cladocera (20), Rotifera (17), and Copepoda (8). Zooplankton was represented mostly by phytophilic ecological group (46–61% of the total number of species). Species composition of zooplankton, trophic group ratio, zooplankton abundance and biomass differed in the medium-small river, the smallest and most insignificant watercourses. In near-shore river area (ripal) and beaver ponds, overgrown by macrophytes, higher quantitative indicators of zooplankton were registered comparing to central area of the river. In addition, high zooplankton abundance and biomass were observed in permanent beaver ponds at streams.

Keywords: ecological groups of zooplankton, macrophytes, Kostroma Oblast, protected areas, beaver ponds

To cite this article. Sirotin, A.L., Sirotina, M.V., 2022. The structure of zooplankton community in different biotopes of small rivers in the Kologrivsky cluster of the Natural State Reserve "Kologrivsky Forest". *Ecosystem Transformation* **5** (4), 37–47. https://doi.org/10.23859/estr-220311

Introduction

Zooplankton is the most important link in the functioning of aquatic ecosystems; zooplankton organisms are consumers at several trophic levels, they serve as a food base for juveniles of many fish species and play a significant role in the processes of water self-purification. Conventionally, much attention has been paid to the study of zooplankton in lentic systems, since in most cases the environmental conditions in such ecosystems are more favorable for zooplankters, since no flow is present there. However, to date, there are many studies of zooplankton in various watercourses (Ermolaeva, 2008; Krylov, 2002, 2005, 2008; Krylov et al., 2010; Sirotina et al., 2014; Sirotina and Sirotin, 2021).

Small rivers are the most represented lotic ecosystems in Russia (Krylov, 2005). In the near-shore areas of many small rivers of the European part of Russia, there are thickets of higher aquatic vegetation (macrophytes), which contribute significantly to the formation of the primary production in aquatic ecosystems. Macrophytes are also ecosystem engineers for a large number of aquatic invertebrates. Aquatic plants reduce the flow velocity, provide heterogeneity of the environment, and form many refugia for zooplankton living among them, as reflected in a number of publications (Gavrilko, 2017; Gavrilko et al., 2018; Krylov et al., 2003; Krylov and Zhgareva, 2007; Kurbatova et al., 2017; Lobunicheva, 2008; Mukhortova, 2011; Sirotina et al., 2020; Stolbunova, 2011). Simultaneously with the positive role of higher aquatic vegetation for the development of zooplankton communities, other biotic effects of macrophytes on zooplankters are also noted in the scientific literature, for example, allelopathy. Some authors indicate that alkaloid substances secreted by the yellow water-lily (*Nuphar lutea* L.) have an inhibitory effect on planktonic crustaceans (Balanda et al., 2004; Zimbalevskaya et al., 1987).

The activity of the European beaver (*Castor fiber* L., 1758) has a significant impact on the development of zooplankton communities in small rivers. Much attention is paid to the impact of this factor on zooplankton in the publications by A.V. Krylov (Krylov, 2002, 2005, 2008; Krylov et al., 2016) and other authors (Sirotina, 2019; Zaitsev et al., 2018). Beavers, being ecosystem engineers, transform the aquatic communities of small rivers and influence the vector of succession in aquatic and near-water ecosystems. In this regard, it is very important to study the structure of plankton and benthic communities in protected areas in order to predict the changes in the lentic and lotic systems. The analysis of the structural and functional characteristics of phytophilic zooplankton in pristine areas also attracts much attention; the obtained data may be used in the monitoring of anthropogenically modified communities. In addition, the aquatic communities of small rivers are poorly studied in the southern taiga zone in the Kostroma Trans-Volga region, so such work is of high demand.

The study aims to describe the structure of zooplankton communities in small rivers of a protected area, as well as to assess the influence of both the activity of the European beaver and the presence of higher aquatic vegetation.

Materials and methods

State Nature Reserve "Kologrivsky Forest" named after M.G. Sinitsyn was established in 2006 in the north of the Kostroma Oblast (European Russia) to preserve the southern taiga natural complexes of the Russian Plain. The reserve consists of two clusters: Kologrivsky and Manturovsky; the rivers flowing through the territory of the reserve are tributaries of a different orders of the Volga River.

The studies were performed in the Kologrivsky cluster of the reserve in June 2021 as part of a long-term monitoring of the aquatic communities in small rivers (Sirotina, 2019; Sirotina et al., 2014, 2020) at 14 sampling sites at the Londushka, Sekha, Ponga, Nelka, and Chernaya rivers, as well as on two permanent beaver ponds at streams (Fig. 1). A different number of stations at each river is due to the inaccessibility of many sections of watercourses in the conditions of the southern taiga. The study sites were reached on a Trekol-39294 all-terrain vehicle, then, by walking.

The beaver ponds were studied at the Sekha, Londushka, Nelka, and Chernaya rivers; these ponds have appeared as a result of blocking the river channel by a dam (ponds in the channel). Here, a significant slowdown of the current was observed, but the presence of a high floodplain did not allow a large spill to form. The ponds formed as a result of blocking streams by beaver dams were analyzed for comparison. Here, as a rule, a significant area was flooded, and beaver settlements existed in these areas for a long time (up to 10 years). At each sampling site, different biotopes were studied, formed by thickets of various macrophytes, such as clasping-leaved pondweed (*Potamogeton perfoliatus* L.), sago pondweed (*Stuckenia pectinata* (L.) Börner), broad-leaved pondweed (*Potamogeton natans* L.), whitestem pondweed (*Potamogeton praelongus* Wulf.), yellow water-lily (*Nuphar lutea* (L.) Sm.), straight vallisneria (*Vallisneria spiralis* L.), and water horsetail (*Equisetum fluviatile* L.). In addition, mixed biotopes of *Potamogeton praelongus / Vallisneria spiralis, Equisetum fluviatile / Vallisneria spiralis, Equisetum fluviatile / Nuphar lutea* were studied. Samples were also taken in the areas free from higher aquatic vegetation in the near-shore zone and the central zone of the river.

Zooplankton was sampled by filtering 50 L of water through the Juday plankton net (mesh size of 76 μm). In total, 152 quantitative and qualitative samples were taken and fixed with 4% formaldehyde aqueous solution. Samples were processed according to generally accepted methods (Salazkin et al., 1982) under an *MBS-10* stereomicroscope. Species were identified under a *Micromed 2 var. 3–20 inf* trinocular microscope with mounted digital camera *ToupCam 3/1 MP*. The species were identified according to the up-to-date taxonomic keys (Alekseev, 2010; Opredelitel'..., 1995).

The individual mass of crustaceans and rotifers was calculated according to the weight-size dependence (Balushkina and Vinberg 1979; Puttner-Kolisko, 1976).

Trophic structure of zooplankton was assessed by the presence and ratio of the following groups (Krivenkova, 2018): 1 – freely swimming verticators; 2 – swimming and crawling verticators; 3 – filter-feeders, consuming fine particles; 4 – freely swimming filter-feeders, consuming coarse particles; 5 – primary filter-feeders, consuming both fine and coarse particles,

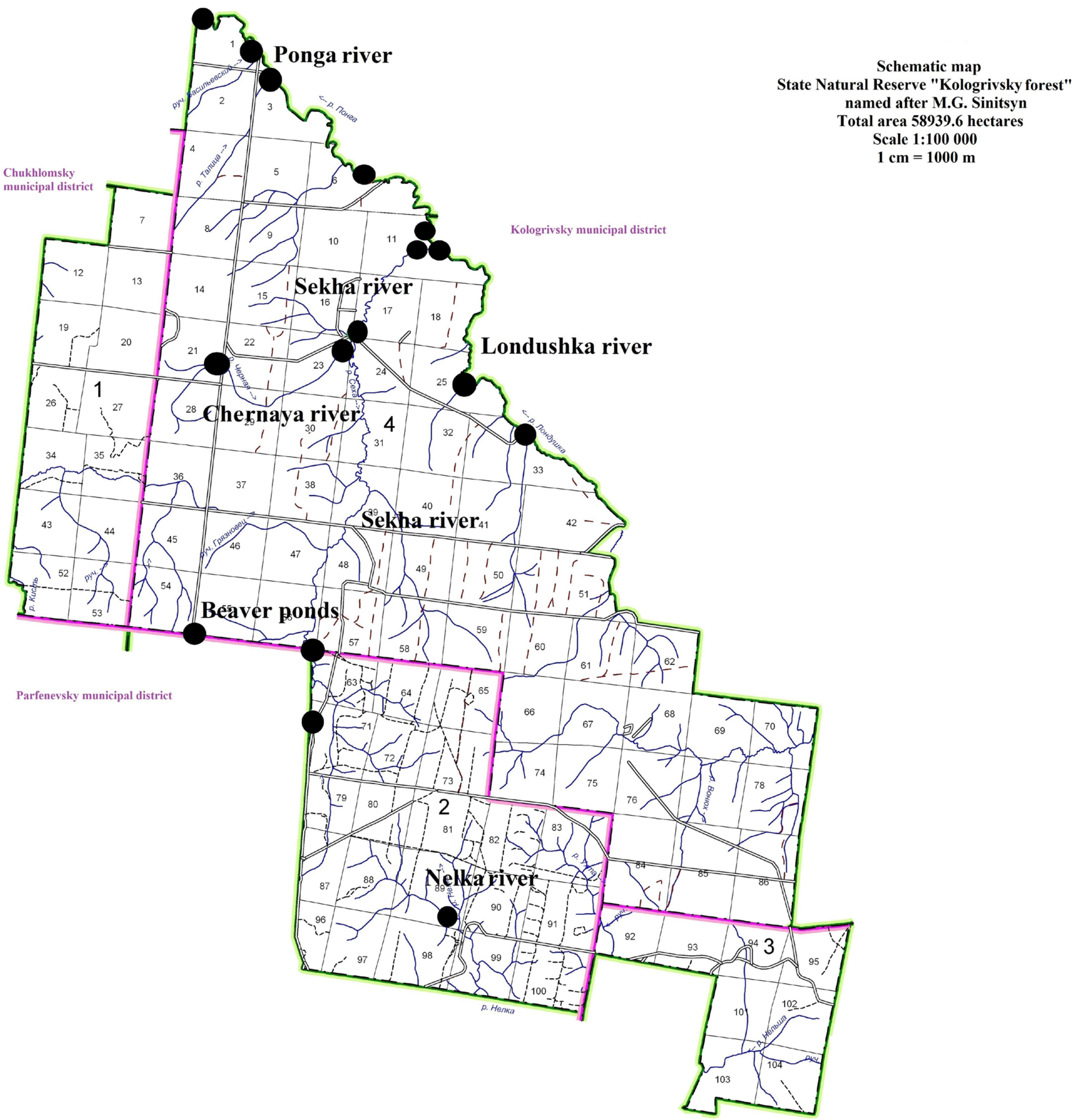

Fig. 1. Main zooplankton sampling stations in the Kologrivsky cluster of the Natural State Reserve “Kologrivsky Les”.

freely swimming and/or attached to the substrate or water surface; 6 – primary filter-feeders, consuming both fine and coarse particles, freely swimming; 7 – freely swimming and crawling secondary filter-feeders, scrapers, and detritus-feeders; 8 – crawling, freely swimming gatherers and euryphagous; 10 – swimming active predators, euryphagous; 11 – swimming predator-grabbers with incudate mastax type; 12 – active swimming predators.

The species structure of zooplankton communities was assessed using the Paliya – Kownacki dominance index (Shitikov et al., 2003). The Sørensen index was applied to determine the similarity of species composition (Shitikov et al., 2003; Sørensen, 1948); samples were classified by the cluster analysis.

Hydrological studies were performed in accordance to generally accepted methods (Davydov et al., 1973). A tape measure and measuring rods were used. The average river width and depth, the depths of river profiles in the studied areas were determined, the area of natural and of the estimated cross-section of the watercourse, and the water flow were calculated. The flow velocity was measured by setting the gates and calculating the speed of the float passing through the system of gates. In addition, several water indicators were determined at sampling sites. The amount of dissolved oxygen was measured by an amperometric sensor of dissolved oxygen with a thermoelectric converter *DKTP-02* and a combined liquid analyzer *Expert-001-2.0.1*. Water transparency was determined using a Secchi disk. The water pH was measured with a pocket waterproof pH meter *HI 98127 pHep4* (Hanna Instruments, USA).

Results

According to the Rokhmistrov – Naumov classification (Rokhmistrov and Naumov, 1984), the studied rivers belong to several types of the watercourses: medium-small (Ponga River), the smallest (Sekha and Londushka rivers), and insignificant (Nelka and Chernaya rivers). Rivers have winding channels; relatively shallow sections of rifts are combined with deeper hollows, bays, and oxbow lakes. Many sections of the rivers are zoogenically transformed, i.e., blocked by beaver dams. The channels in many places are overgrown with macrophytes, which form the thickets of different density and various projective cover.

The Ponga River (73-km long, catchment area of 824 km^2) is the widest and the deepest one (Ershov and Sirotina, 2021). It is formed by the confluence of the Sekha and Londushka rivers. Sampling has been carried out at five stations: two in the upper reaches and three in the middle reaches.

The Sekha River (34-km long, catchment area of 198 km^2) is a left tributary of the Ponga River. In upper, middle, and lower reaches, the sampling was performed at one station each.

The Chernaya River (7-km long) is a left tributary of the Sekha River. Sampling was carried out at its middle and lower reaches.

The Londushka River (26-km long, catchment area of 206 km^2) is a right tributary of the Ponga River. Research was carried out in the middle and lower reaches of the river.

The Nelka River is 13-km long, with a catchment area of 58 km^2. Sampling was performed at the monitoring station with coordinates N 58.44919° E 43.53816°.

In general, the width of the rivers in the studied areas varied from 2.23 to 10.80 m, the depth, as 0.28–0.59 m, the area of the natural current, as 1.55–5.10 m^2, water discharge, 0.03–1.86 m^3/s (Table 1). Water transparency ranged as 0.48–0.72 m, flow velocity, as 0.02–0.37 m/s. It was not possible to measure the water transparency in the Chernaya River, since the Secchi disk was still visible when laying on the bottom.

In the Sekha River, water acidity varied from slightly acidic (pH = 5.60 in the upper and 6.25 in the middle reaches) to neutral (pH = 6.56 in the lower reaches) at the sampling sites. In the Ponga River, pH values ranged from 4.75 (acidic) to 6.96 (neutral), in the Londushka River, from 4.86 (acidic, in the middle reaches) to6.70 (neutral, in the lower reaches). In the Nelka River, pH varied as 6.23–6.88; in the Chernaya River, pH = 4.80. The studied beaver ponds were characterized by acid water (pH = 4.20).

The studied rivers were characterized by a low oxygen content (4.33–6.99 mg/L). The lowest oxygen content was noted for sections of rivers blocked by beaver dams and beaver ponds, the highest, at the confluence of the Londushka and Sekha rivers.

In total, 45 species of zooplankton were found in the studied watercourses and reservoirs of the Kologrivsky Reserve (Table 2); representatives of Cladocera predominated (20 species), followed by Rotifera (17 species) and Copepoda (8 species). The largest number of species was noted in the Sekha River (28 species), the lowest, in the Nelka

Table 1. Morphometric and hydrological parameters of the studied watercourses (mean ± error of mean). For the Nelka River, average values are not indicated, because the studies have been carried out at one station.

Parameter	Ponga River	Sekha River	Londushka River	Nelka River	Chernaya River
River length, km	73	34	26	13	7
Drainage basin area, km^2	824	198	206	58	no data
Channel width, m	10.80 ± 1.05	5.27 ± 1.25	3.84 ± 0.93	4.45	2.23 ± 0.80
Depth, m	0.48 ± 0.07	0.36 ± 0.05	0.55 ± 0.06	0.59	0.28 ± 0.04
River cross-sectional area, m^2	5.10 ± 0.90	3.29 ± 1.50	3.52 ± 1.50	1.55	1.81 ± 0.70
Water consumption, m^3/s	1.86 ± 0.70	0.60 ± 0.40	1.54 ± 0.70	0.03	0.60 ± 0.30
Flow velocity, m/s	0.37 ± 0.10	0.14 ± 0.07	0.04 ± 0.10	0.02	0.33 ± 0.10
Transparency, m	0.72 ± 0.06	0.62 ± 0.06	0.53 ± 0.14	0.48	–

River (15 species). In beaver ponds, 27 species of zooplankton were found.

In all the studied streams and reservoirs, the ecological group of phytophilic zooplankton prevailed, accounting for 46–61% of the total number of zooplankter species (Fig. 2). Representatives of the genera *Lecane, Mytilina, Platyias, Trichotria, Acroperus, Alona, Eurycercus, Pleuroxus, Scapholeberis, Simocephalus, Eucyclops*, *Macrocyclops* were found. Phytophilic-planktonic species were also widespread (26–35%): *Brachionus quadridentatus, Euchlanis dilatata, Chydorus sphaericus, Polyphemus pediculus, Mesocyclops leuckarti, Thermocyclops crassus, T. oithonoides,* and *Ceriodaphnia* sp. Obligate planktonic species (representatives of the genera *Filinia, Keratella, Polyarthra,* and *Daphnia)* were registered in much smaller numbers.

It should be noted that the largest share of holoplankton species is observed in beaver ponds located on streams (19%), where significant areas of open water with sufficient development of semi-submerged and submerged vegetation in the littoral zone are present. In addition, almost the same share of holoplankton species was noted for the Ponga River (18%). This may be explained by the fact that this river is larger than others, it is characterized by more pronounced central and near-shore areas free from macrophytes than observed in other rivers. The Londushka River was almost completely overgrown with higher aquatic vegetation (at the study sites); therefore, the share of holoplankton species was the lowest here (9%). The demersal species were noted only in the Sekha River, where they amounted to 3%.

The species composition of zooplankton was compared for different biotopes of the Ponga and Sekha rivers by Sørensen similarity index. These rivers were the largest in the Kologrivsky section of the reserve, and the largest number of sampling stations were located here, so this preconditioned such a choice. The merging distance between stations, typical for different zooplankton habitats, is presented at dendrograms (Fig. 3; Fig. 4).

The smallest similarity distance at the Ponga River was recorded between stations nos. 4 and 5 (*Vallisneria spiralis* and *Potamogeton praelongus / Vallisneria spiralis*), as well as stations nos. 9 and 10 (*Vallisneria spiralis* and *Potamogeton natans*) (Fig. 3). Generally, stations nos. 5–10 formed a single group, where "pondweed" biotopes were located. The biotopes characterized by the absence of macrophytes outlie at a much greater distance (stations nos. 1–3 located in the central zone of the river). A separate cluster was formed by "pondweed" biotopes in the middle reaches of the river, at stations nos. 13 and 14 (*Potamogeton perfoliatus* and *Potamogeton natans*). Perhaps, this was due to the difference in environmental conditions in this area, in particular, due to low pH values (4.75).

The lowest merging distance at the Sekha River was noted for at sampling stations nos. 7 and 8 (*Equisetum fluviatile* and *Equisetum fluviatile / Nuphar lutea*) (Fig. 4). In general, a cluster of stations nos. 4–9 was distinguished here, characterized by the thickets of *Equisetum fluviatile* and *Vallisneria spiralis* (including a mixed biotope of *Equisetum fluviatile / Nuphar lutea*).

Station nos. 1 and 3 (located medially, without macrophytes) and station no. 2 (with thickets of sago pondweed) had at a greater distance between each other. The stations nos. 1—9 were located in the upper reaches of the Sekha River. A separate cluster is formed by stations nos. 10 and 11 (*Vallisneria spiralis* and *Potamogeton praelongus / Vallisneria spiralis*), located in the middle reaches of the river; the station nos. 12 (central stream, lower reaches) in the Sekha River was the most distanced at the dendrogram.

Different biotopes were regularly distributed into separate clusters on the dendrograms in accordance with the similarity index. Groupings of clusters with and without macrophytes were noted; biotopes located in different parts of the river were also distinguished.

According to Palia – Kownacki index of dominance (*D)*, rotifers of the genus *Euchlanis* (*D* = 12.0–83.08), juvenile stages and adult Copepoda (*D* = 10.28–22.22 for nauplii, 11.14–42.5 for copepodites, and 10.67–21.94 for adults), and cladocerans *Acroperus harpae* (*D* = 10.21–14.42) dominated in the near-shore areas, overgrown with macrophytes, at the Ponga River; nauplii, copepodites, and adult Copepoda were subdominants. At the Sekha River, nauplii (*D* = 10.10–23.70), copepodites (*D* = 20.35–40.70), and adult representatives of the *Eucyclops* genus (*D* = 15.99–34.17) dominated in macrophyte thickets, followed by *Acroperus harpae,* representatives of the *Ceriodaphnia* genus, *Polyphemus pediculus,* and *Simocephalus vetulus.* In the Londushka River, in the thickets of higher aquatic vegetation, copepodites dominates (*D* = 12.33–31.02), followed by representatives of the *Daphnia* genus and *Polyphemus pediculus.* In vegetation-free areas, dominants and subdominants included juvenile and adult Copepoda; *D* values for nauplii ranged from 15.48 to 60.00, for copepodites, 15.48–63.30, and for adults, 9.69–10.83. In permanent beaver ponds on streams, Copepoda of different age groups dominated (*D* = 20.52–58.02 for nauplii, 12.82–29.20 for copepodites), as well as representatives of the *Daphnia* genus did (*D* = 10.77–11.34). Subdominants were represented *Keratella serrulata, Polyarthra vulgaris,* nauplii and copepodites of Copepoda, and the species of *Ceriodaphnia* genus.

In the studied areas of small rivers, various structure of zooplankton communities was observed in biotopes of a different nature and ecological conditions. Generally, in most biotopes, almost all trophic groups

Table 2. Quantitative indicators of zooplankton in different biotopes of the studied rivers (mean ± error of mean).

No.	Species	Ponga River	Sekha River	Londushka River	Nelka Rivera	Chernaya River	Ponds on streams
	Cladocera						
1	*Ceriodaphnia reticulata* (Jurine, 1820)	–	+	+	–	–	–
2	*Ceriodaphnia megops* Sars, 1862	+	+	–	+	+	+
3	*Ceriodaphnia pulchella* Sars, 1862	–	+	+	–	+	–
4	*Daphnia longispina* O.F. Müller, 1785	–	+	++	+	+	++
5	*Daphnia cristata* Sars, 1862	–	+	–	–	–	–
6	*Daphnia pulex* Leydig, 1860	–	–	+	–	–	–
7	*Simocephalus vetulus* (O.F. Müller, 1776)	+	+	+	+	–	+
8	*Simocephalus exspinosus* (De Geer, 1778)	–	–	+	–	–	–
9	*Simocephalus serrulatus* (Koch, 1841)	–	–	+	–	+	–
10	*Scapholeberis mucronata* (O.F. Müller, 1776)	+	+	+	+	–	+
11	*Acroperus harpae* (Baird, 1834)	++	+	+	–	+	–
12	*Acantholeberis curvirostris* (O.F. Müller, 1776)	–	+	–	–	–	–
13	*Alona affinis* (Leydig, 1860)	–	+	–	–	+	–
14	*Alona quadrangularis* (O.F. Müller, 1776)	–	–	+	–	–	+
15	*Alonella exigua* (Lilljeborg, 1853)	–	+	–	–	–	–
16	*Chydorus sphaericus* (O.F. Müller, 1776)	+	+	–	–	+	+
17	*Macrothrix laticornis* (Fischer, 1851)	–	+	–	–	–	–
18	*Pleuroxus truncatus* (O.F. Müller, 1785)	–	+	+	–	+	+
19	*Eurycercus lamellatus* (O.F. Müller, 1776)	+	+	+	–	+	+
20	*Polyphemus pediculus* (L., 1761)	–	+	+	+	+	+
	Copepoda						
21	*Eucyclops serrulatus* (Fischer, 1851)	++	+	++	+	+	++
22	*Eucyclops macrurus* (G.O. Sars, 1863)	–	+	+	+	+	+
23	*Macrocyclops albidus* (Jurine, 1820)	+	+	+	–	+	+
24	*Macrocyclops fuccus* (Jurine, 1820)	+	+	+	+	+	+
25	*Mesocyclops leuckarti* (Claus, 1857)	+	+	+	–	–	+
26	*Paracyclops poppei* (Rehberg, 1880)	–	–	–	–	–	+
27	*Thermocyclops oithonoides* (Sars, 1863)	+	+	+	+	+	+
28	*Thermocyclops crassus* (Fischer, 1853)	–	+	+	–	+	+
	Rotifera						
29	*Lecane luna* (Müller, 1776)	–	+	–	+	+	+
30	*Lecane ungulata* Gosse, 1887	–	–	–	–	–	+
31	*Euchlanis dilatata* Ehrenberg, 1832	++	+	+	+	+	+

No.	Species	Ponga River	Sekha River	Londushka River	Nelka Rivera	Chernaya River	Ponds on streams
32	*Euchlanis incisa* Carlin, 1939	+	–	–	–	–	+
33	*Rotaria neptunia* (Ehrenberg, 1830)	–	–	–	+	–	–
34	*Brachionus quadridentatus* (Ehrenberg, 1832)	–	–	–	–	–	+
35	*Keratella quadrata* (Müller, 1786)	–	–	–	–	+	–
36	*Keratella serrulata* (Ehrenberg, 1838)	–	–	–	+	–	++
37	*Keratella cochlearis tecta* (Gosse, 1851)	–	–	–	–	–	–
38	*Platyias quadricornis* (Ehrenberg, 1832)	–	–	–	–	–	+
39	*Trichotria truncata* (Whitelegge, 1889)	+	+	–	–	–	–
40	*Trichocerca longiseta* (Schrank, 1802)	–	–	+	–	–	–
41	*Mytilina mucronata* (Müller, 1773)	+	–	+	+	–	–
42	*Filinia longiseta* (Ehrenberg, 1834)	+	–	–	–	–	+
43	*Polyarthra dolichoptera* Idelson, 1925	–	+	–	+	–	–
44	*Polyarthra vulgaris* Carlin, 1943	+	–	+	–	–	++
45	*Synchaeta pectinata* Ehrenberg, 1832	–	+	+	–	–	+
	Total	**17**	**28**	**25**	**15**	**19**	**27**

were registered, except swimming predators armed with an incudate mastax. However, representatives of various trophic groups may predominate in different biotopes in terms of abundance. For example, floating and crawling verticators (representatives of the genus *Euchlanis*) predominated in the thickets of pondweeds at the Ponga River, followed by thin filter feeders (naupliar stages of Copepoda) and swimming and crawling euryphages. In the areas overgrown with *Vallisneria spiralis*, along with floating and crawling verticators, there were mainly floating and crawling collectors (euryphagous species, floating and crawling secondary filter feeders, scrapers, and detritus-feeders). In the areas covered with *Equisetum fluviatile*, mainly copepods were found, representing four trophic groups: filter feeders consuming fine particles (nauplii), swimming filter feeders consuming coarse particles (copepodites of 1–3 stages), swimming active euryphagous predators (copepodites of 4–5 stages), crawling and floating euryphagous collecting animals (adult specimens of genus *Eucyclops)*. Along with these trophic groups, floating primary filter feeders consuming thin and coarse particles (genus *Ceriodaphnia)*, floating and crawling secondary filter feeders, scrapers, and detritophagous animals (genus *Acroperus)* were common in the thickets of *Nuphar lutea*. It should be noted that no representatives of freely swimming verticators, were found in the macrophyte thickets, but they were noted in pelagic areas and in the areas free from higher aquatic vegetation (*Keratella* and *Polyarthra* genera).

Quantitative indicators of zooplankton in the studied small rivers are presented in Table 3. They depend on the morphological, hydrological, and hydrochemical features of the watercourse, on the species composition, morphological features of macrophytes, the degree of overgrowing of river sections with higher aquatic vegetation, and on the presence of zoogenic transformation of watercourses (Gavrilko, 2017; Gavrilko et al., 2018; Kurbatova et al., 2017; Kurbatova et al., 2018; Lobunicheva, 2008; Mukhortova, 2011).

The Ponga River is wider compared to other studied rivers, it has a higher flow rate and pronounced sections of the medial stream and near-shore macrophyte-free areas. Due to the hydrological features of the river, the abundance and biomass of zooplankton was significantly lower than in other rivers; in addition, quantitative indicators of zooplankton differed in different biotopes. In macrophyte thickets, zooplankton abundance was 3.87 times higher, biomass, 1.87 times higher, comparing to vegetation-free areas. The highest abundance of zooplankton was noted in areas with pondweeds, for example,

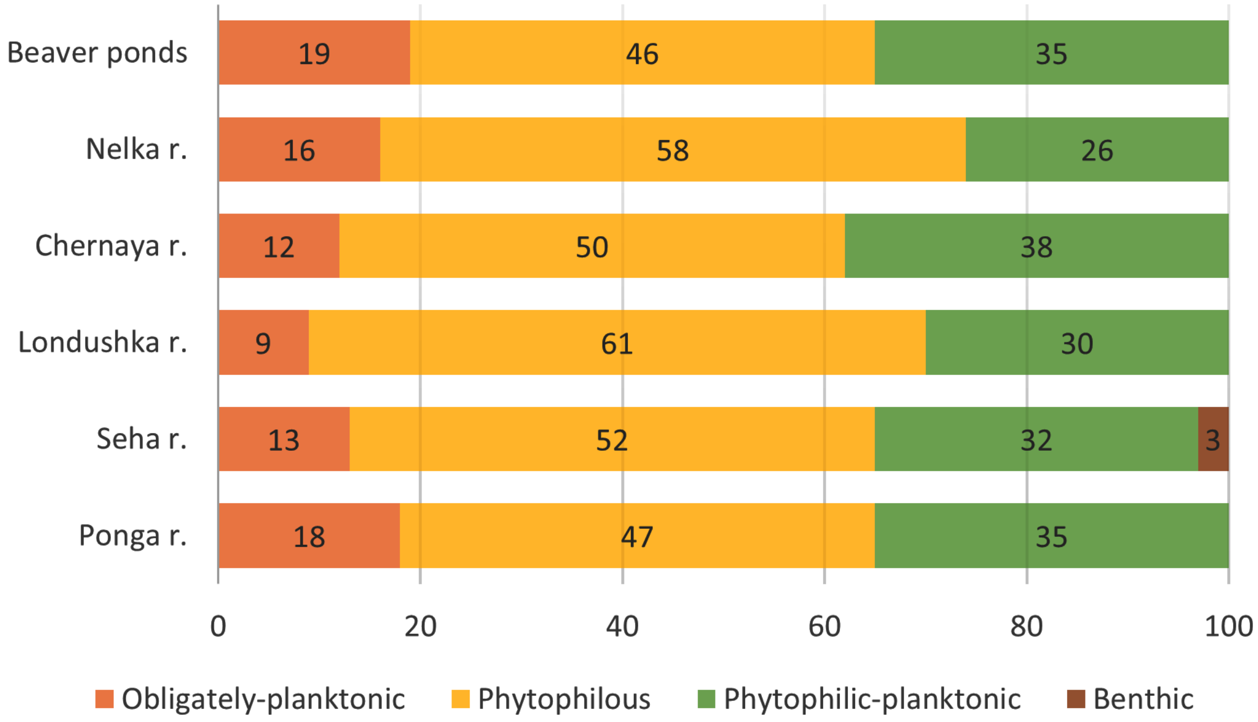

Fig. 2. Ecological groups of zooplankton in the studied streams and reservoirs, %.

Potamogeton perfoliatus (on average, 33.41 thousand ind./m^3) and *Potamogeton praelongus* (13.65 thousand ind./m^3). Here, higher numbers were provided by the presence of a significant number of *Euchlanis dilatata.* The highest zooplankton biomass was observed in the thickets of *Nuphar lutea* (0.30 g/m^3), represented mainly by Cladocera (genus *Ceriodaphnia* and *Simocephalus vetulus*).

At the sampling sites, the Sekha River is half as much narrower than the Ponga River, it has even lower flow rate; the channel is blocked by beaver dams in many places along the river. For these reasons, the quantitative indicators of zooplankton community were higher here comparing to the Ponga River; however, they were different in different biotopes as well. The maximum zooplankton abundance (about 88.85 thousand ind./m^3) was recorded in areas covered with *Stuckenia pectinata* due to the presence of a large number of juvenile and adult copepods. The highest biomass was noted for *N. lutea* thickets (3.15 g/m^3 on average), due to Cladocera (genera *Ceriodaphnia* and *Pediculus)*. The lowest indicators of zooplankton from mono-species thickets were observed in areas overgrown with *Equisetum fluviatile*; even lower abundance and biomass of zooplankton were registered in mixed thickets of *E. fluviatile* and *Vallisneria spiralis*. In addition, low rates were observed in the thickets of *E. fluviatile* on the Chernaya River.

In the studied areas of the Londushka River, the highest biomass of zooplankton was also characteristic of *N. lutea* thickets. Here, cladocerans (*Daphnia longispina*) were presented in high numbers.

In the studied sections of the rivers, blocked by beaver dams (beaver ponds in the channel), the quantitative indicators of zooplankton were much higher due to a flow slowdown in these biotopes and with other environmental conditions formed as a result of the activity of beavers (Krylov, 2002, Krylov et al., 2016; Sirotina, 2019). Even higher rates were observed in beaver ponds formed as a result of blocking forest streams. Here, the zooplankton biomass averaged 4.02 g/m^3, abundance, 163.27 thousand ind./m^3. Cladocerans *Polyphemus pediculus, Simocephalus vetulus,* representatives of the genus *Ceriodaphnia* brought main contribution to biomass*;* copepods dominated by abundance. It should be noted that zooplankton was represented mainly by cladocerans and copepods in beaver ponds that existed for a short period (2–3 years). At the same time, in the plankton of long-term (about 10 years) functioning communities, rotifers are widely represented (*Keratella serrulata, Polyarthra vulgaris, Lecane moon, Brachionus quadridentatus, Synchaeta pectinata,* and *Euchlanis incisa*), some species were a part of the subdominant complex (the coordinates of these ponds: N 58.82199° E 43.73437°; N 58.82204° E 43.73421°; N 58.82286° E 43.73442°).

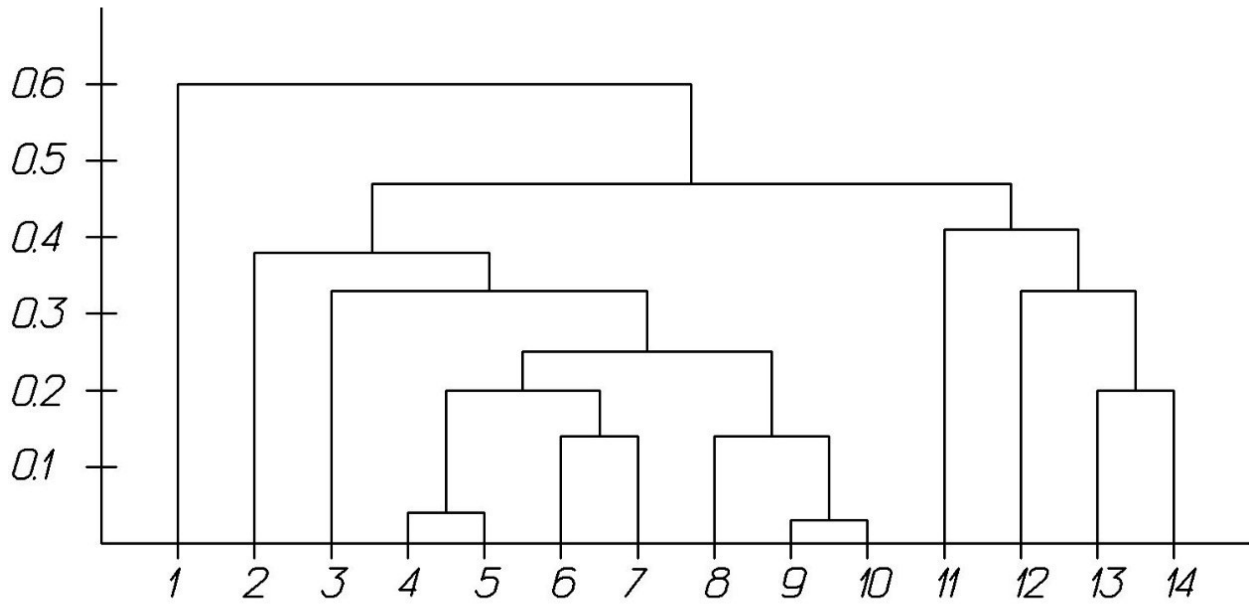

Fig. 3. Dendrogram of the hierarchical clustering of the species composition of different zooplankton biotopes on the Ponga River according to the Sørensen index. Numbers indicate different biotopes in accordance with edificator species (or their absence) and the location of sampling stations; Y-axis represents the distance. 1 — stream midline (middle reaches); 2 — stream midline (middle reaches); 3 — stream midline (upper reaches); 4 – *Vallisneria spiralis* (middle reaches); 5 – *Potamogeton praelongus* / *Vallisneria spiralis* (middle reaches); 6 – *Potamogeton praelongus* (middle reaches); 7 – *Stuckenia pectinata* (upper reaches); 8 – *Potamogeton natans* (upper reaches); 9 – *Potamogeton praelongus* (upper reaches); 10 – *Potamogeton natans* (upper reaches); 11 – *Nuphar lutea* (middle reaches); 12 – *Vallisneria spiralis* (middle reaches); 13 – *Potamogeton natans* (middle reaches); 14 – *Potamogeton perfoliatus* (middle reaches).

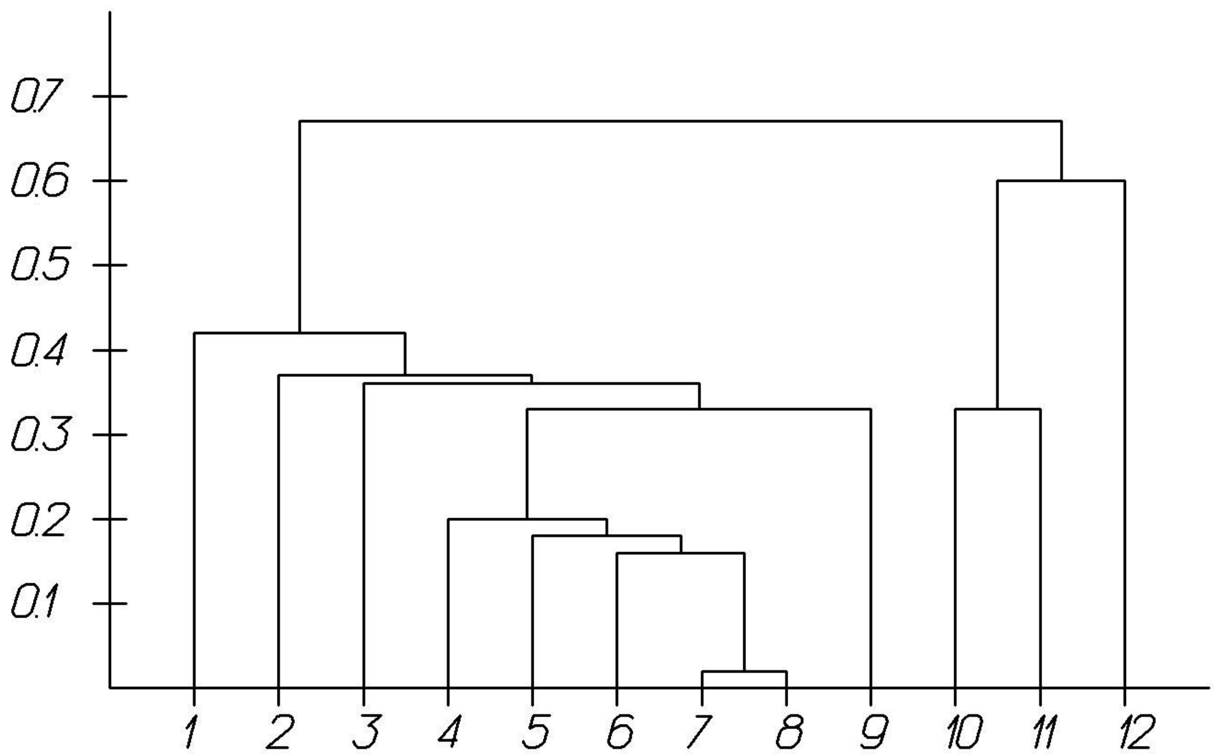

Fig. 4. Dendrogram of the hierarchical clustering of the species composition of different zooplankton biotopes on the Sekha River according to the Sørensen index. Numbers indicate different biotopes in accordance with edificator species (or their absence) and the location of sampling stations; Y-axis represents the distance. 1 – stream midline (upper reaches); 2 – *Stuckenia pectinata* (upper reaches); 3 – stream midline (upper reaches); 4 – *Vallisneria spiralis* (upper reaches); 5 – *Equisetum fluviatile* (upper reaches); 6 – *Vallisneria spiralis* (upper reaches); 7 – *Equisetum fluviatile* (upper reaches); 8 – *Equisetum fluviatile* / *Nuphar lutea* (upper reaches); 9 – *Equisetum fluviatile* I (upper reaches); 10 – *Vallisneria spiralis* (middle reaches); 11 – *Equisetum fluviatile* / *Vallisneria spiralis* (middle reaches); 12 – stream midline (lower reaches).

Table. 3. Quantitative indicators of zooplankton in different biotopes of the studied rivers (mean ± error of mean).

Macrophyte species / Sampling station	Abundance, thousand ind./m^3	Biomass, g/m^3
Ponga River		
Potamogeton praelongus	13.65 ± 4.21	0.04 ± 0.01
Potamogeton perfoliatus	33.41 ± 3.03	0.07 ± 0.01
Stuckenia pectinata	3.80 ± 0.71	0.02 ± 0.004
Nuphar lutea	6.95 ± 1.14	0.30 ± 0.14
Vallisneria spiralis	7.16 ± 0.87	0.04 ± 0.01
Without macrophytes	3.35 ± 1.42	0.05 ± 0.02
Sekha River		
Stuckenia pectinata	88.85 ± 30.51	1.87 ± 0.68
Nuphar lutea	48.26 ± 6.51	3.15 ± 0.95
Vallisneria spiralis	17.94 ± 3.87	1.24 ± 0.44
Equisetum fluviatile	6.23 ± 1.20	0.22 ± 0.12
Equisetum fluviatile / Nuphar lutea	33.42 ± 0.20	2.33 ± 0.32
Equisetum fluviatile / Vallisneria spiralis	0.24 ± 0.06	0.004 ± 0.003
Beaver ponds in the riverbed	33.39 ± 2.79	2.80 ± 0.20
Londushka River		
Nuphar lutea	105.70 ± 7.53	3.16 ± 0.82
Without macrophytes	129.20 ± 17.20	2.04 ± 0.26
Beaver ponds in the riverbed	11.84 ± 4.13	1.83 ± 0.87
Nelka River		
Without macrophytes	30.72 ± 7.76	0.36 ± 0.04
Beaver ponds in the riverbed	76.80 ± 22.83	1.10 ± 0.21
Chernaya River		
Equisetum fluviatile	10.72 ± 0.62	0.70 ± 0.14
Beaver ponds in the riverbed	22.16 ± 3.61	2.14 ± 0.45
Beaver ponds on streams		
Without macrophytes	163.26 ± 21.51	4.02 ± 0.45

Discussion

Macrophytes are of key importance in the formation of refugia for the habitat of zooplankton organisms in the small rivers of the Kologrivsky Reserve in the Kostroma Oblast, Russia. The Sørensen species similarity index makes it possible to outline certain clusters of stations united both by the presence or absence of macrophytes and the species lists. In the thickets of higher aquatic plants, phytophilic zooplankter species predominate. Quantitative indicators of zooplankton, dominant species, and diversity of trophic groups depend both on the hydrological and hydrochemical conditions of the watercourse, and on the species composition of macrophytes in near-shore areas.

In the *Nuphar lutea* biotopes (Ponga, Sekha, and Londushka rivers), the zooplankton biomass is the highest compared to other biotopes due to development of cladocerans *Eurycercus lamellatus* (floating and crawling secondary filter feeders, scrapers and detritus feeders) and *Simocephalus vetulus* (primary filter feeders, consuming fine and coarse particles, floating and attaching to the substrate and/or surface water film), as well as representatives of the genus *Ceriodaphnia* (floating primary filter feeders, consuming fine and coarse particles). It is possible that the allelopathic effect of plants (in particular, of *N. lutea*) is compensated by the presence of water flow in the studied areas of small rivers.

When the river bed is blocked by beaver dams, both abundance and biomass of zooplankton increase; the maximum indicators are noted for long-term existing beaver ponds at streams. In these areas, rotifers reach significant development, contributing to a high abundance of total zooplankton.

Unlike the ponds on streams, many of the beaver ponds at riverbeds are washed with melt water every year during the flood period. As a result, seasonal succession of the zooplankton community starts here every year, from dominating naupliar and copepodite stages of copepods in spring to the development of a summer community represented by primary filter feeders (mainly large cladocerans), which are gradually eaten away by active predators. Rotifers are poorly represented in this case (Sirotina, 2019).

Conclusions

The zooplankton communities in five small rivers and two beaver ponds in the Kologrivsky Forest Nature Reserve named after M.G. Sinitsyn, located in the southern taiga zone in the Kostroma Oblast, Russia, have been studied. The community structure, species diversity, dominant species, abundance and biomass, the presence of certain trophic and other ecological groups of zooplankton are associated with the conditions prevailing in certain biotopes. The species composition and quantitative indicators of zooplankton differ in the medium-small river (Ponga), the smallest (Sekha and Londushka) and insignificant rivers (Nelka and Chernaya) due to a number of morphological and hydrological characteristics of watercourses. The presence of thickets of higher aquatic vegetation, as well as the zoogenic activity of the European beaver are of particular importance. Areas overgrown with macrophytes are characterized by higher biomass and abundance. In addition, these indicators are higher in beaver ponds compared to unregulated river sections.

In most of the studied biotopes, almost all trophic groups are found, except swimming grabbing predators with an incudate mastax. However, the medium-small Ponga River is characterized by the predominance of floating and creeping freely swimming verticators, in the thickets of macrophytes (representatives of the river *Euchlanis)*. In addition, filter feeders, consuming fine particles, and floating and crawling euryphagous species are dominants and subdominants. The phytophilic zooplankton of the smallest and insignificant rivers is mostly represented by filter feeders, consuming fine particles, swimming filter feeders, consuming coarse particles, swimming active euryphagous predators, crawling and swimming euryphagous foragers. Filter feeders, consuming fine particles, and floating filter feeders, consuming coarse particles dominate in permanent beaver ponds at streams; the subdominants include freely swimming verticators and floating primary filter feeders, consuming fine and coarse particles.

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