ZOOPLANKTON, ZOOBENTHOS,
AND ZOOOPERIPHYTON

Zoobenthos of Pools of Rapid Rivers: Composition, Abundance, and Trophic Structure (Based on the Example of Eastern Fennoscandia)

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Abstract—The species composition and abundance of zoobenthos are studied to reveal the structure of bottom invertebrate communities under the effect of biotopical, hydrological, and climatic factors. One hundred and six quantitative samples were collected from 15 pools of rapid rivers (61.6°–67.1° N) from 2003 to 2017 in eastern Fennoscandia. The basic part of the fauna is formed by 151 species, including 36 Diptera species, 23 Trichoptera species, 21 Bivalvia species, and 19 Ephemeroptera species. Representatives of Chironomidae, Oligochaeta, Sphaeriidae, Ephemeroptera, and Trichoptera occurred most frequently in the samples (89, 72, 58, 40, and 28%, respectively). The diversity of bottom communities of the pools was low when compared to that in the riffles. The abundance of zoobenthos varies greatly from site to site (from 0.06 to 42.6 thousand spec./m² and from 0.06 to 100.8 g/m²). The average values (3106 ± 642 spec./m² and 6.6 ± 1.27 g/m²) are comparable with the abundance of zoobenthos in the riffles. The basic biomass was formed by Bivalvia (*Euglesa* spp.), Gastropoda (*Radix intermedia* and *Gyraulus borealis*), Diptera (Chironominae spp. and *Dicranota bimaculata*), and Trichoptera (*Brachycentrus subnubilus* and *Hydropsyche contubernalis borealis*). The lowest zoobenthos biomass was detected in brooks (1.4 ± 0.37 g/m²) and the highest was in the medial zone of rivers (9.5 ± 2.52 g/m²). Local aggregations of large mollusks (*Anodonta cygnea*, *Unio pictorum*, and *U. tumidus*) with a multiple biomass (0.5–3.6 kg/m²) and a density of 80–120 spec./m² were found in the study area (4% of samples, mainly in the medial zone). Gatherer–collectors were dominant in the trophic structure (32–60% of biomass); the proportions of groups varied depending on the characteristics of the biotope, in particular, the pattern of the bottom substrate. An increase in the zoobenthos biomass was recorded in the southern part of the region: from 2.7 ± 0.48 g/m² north of 65° N to 8.6 ± 1.82 g/m² south of 63° N. Comparison of the structure of the zoobenthos of rapid river pools in Fennoscandia with that in lowland rivers in other areas did not reveal any fundamental differences, which indicates the importance of local hydrological and other factors in the formation of the composition and abundance of bottom invertebrate communities.

Keywords: bottom invertebrates, fauna, communities, biomass, Republic of Karelia, Kola Peninsula

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INTRODUCTION

Fennoscandia is an unspoiled land located on the Baltic Crystal Shield. The Quaternary sediment layer is relatively small (Biske, 1959). The young age of the landscape (the glacier broke 8000–14000 years ago) and numerous outcrops of crystalline rocks determine the formation of branching lake–river systems, which are characterized by a large number of riffles alternating with pools and flowage lakes. The watercourses of this area are distinguished as a separate Kola hydrobiological type (Zhadin, 1950). The northern location (60°–70°N) determines its harsh climate. The dependence of the characteristics of the bottom population of the rivers on the features of the hydrographic network, determined by the Quaternary history of the basins, has been previously revealed (Zvereva, 1969).

Thus, the rivers that flow along stable platform formations for a long period and are characterized by developed longitudinal profiles look flat; alluvial soils play a great role in the channel (Bogatov and Fedorovskii, 2017). Many rivers of the European northeast of Russia (Middle and Lower Pechora), Izhma, and Vychegda, where pools and riffles with soft soils are the prevailing type of biotope, serve as an example (Zvereva, 1969). In Fennoscandia, pools are formed in areas between riffles. It can be assumed that the transit of organisms and organic matter between riffles and pools significantly influences the zoobenthos of both biotopes.

The zoobenthos of the rivers of eastern Fennoscandia has been studied many times; however, the main attention was paid to riffles (Baryshev, 2016). The

pool areas have not been specifically studied; the data on the zoobenthos structure are fragmentary (Belyakov, 2006; Ryabinkin, 2003, 2008; Yakovlev, 2004, 2005). At the same time, these areas can occupy a significant part of a river; here, special communities of bottom invertebrates are formed, which play a great role in maintaining the biological diversity of watercourses.

The purpose of this research was to identify the main structural characteristics of benthos in the pools of rivers in Karelia and Murmansk oblast and determine and analyze the trophic structure of the zoobenthos of different biotopes and substrates.

MATERIALS AND METHODS

The study material includes 106 quantitative samples that were collected in the river pools in the Russian part of Fennoscandia (the Republic of Karelia and Murmansk oblast) from 2003 to 2017. The stations were located in the area of 15 river basins (from 61.6° N to 67.1° N); five of these rivers (Ponoy, Pongoma, Kovda, Kem, and Letnyaya) are included in the catchment of the White Sea and ten of them (Chebinka, Kumsa, Unitsa, Lizhma, Suna, Shuya, Lososinka, Orzega, Bolshaya Uya, and Okunya Tonya) in the catchment of Lake Onega. We investigated brooks in areas with a decelerated flow (12 samples) and the medial (50 samples) and ripal (44 samples) zones of river pools. The brooks are characterized by sandy and sandy pebble soils; the medial zone is characterized by stony, clay, or sandy pebble soils; and the ripal zone has detritus deposits on silty, sandy, or clay substrates. The current velocity was 0.02–0.3 m/s.

Samples were taken in the second half of summer using a DAK-250 bottom grab with a capture area of 0.025 m² (two lifts per sample); in small watercourses, we used a scraper that had a trap net with a gas mesh of 0.06 mm (the area was 0.05 m²). Samples were fixed in 70% ethanol. At the laboratory, organisms were sorted by taxonomic groups using a binocular microscope and then weighed with an accuracy of 0.1 mg. Species were identified according to contemporary guides (*Opredelitel' zooplanktona i zoobentosa* ..., 2016; *Opredelitel' presnovodnykh bespozvonochnykh* ..., 1997, 1999, 2001). Species of the family Sphaeriidae (Bivalvia) were identified by A.A. Frolov (Murmansk Marine Biological Institute, Kola Research Center, Russian Academy of Sciences); species of the class Gastropoda were identified by M.V. Vinarski (St. Petersburg State University). Large representatives of Bivalvia (family Unionidae) were considered separately from the rest of zoobenthos. The names of the species (except Mollusca) are given using the Fauna Europea database (De Jong et al., 2014). The names of the Gastropoda and Bivalvia species are given according to (Vinarski and Kantor, 2016). Saprobity was assessed by the Pantle–Buk method with

modification taking into account the “indicator weight” of the species (Sladeczek, 1973). The biodiversity indices were calculated using standard formulas (Magurran, 1998).

To assess the abundance and biomass differences between the samples, we used the Mann–Whitney *U*-test ($p \leq 0.05$), which makes it possible to work with log-normal distributed data; the Student's *t*-test ($p \leq 0.05$) was used for the diversity and saprobity indices (with a distribution that is usually close to normal) (Shitikov et al., 2003). The trophic structure of communities was assessed according to the pattern of food consumption by bottom invertebrates using the published data (Cummins and Klugg, 1979; Sladeczek, 1973). This research provides mean values with the indication of the standard error.

RESULTS

We recorded 151 specific and superspecific taxa of zoobenthos in the river pools. The list of species with the indication of their habitat biotopes is given in Table 1. The identified species belong to 5 types, 10 classes, 25 orders, 57 families, and 117 genera. Taxa of Chironomidae, Oligochaeta, Sphaeriidae, Ephemeroptera, and Trichoptera occurred most frequently in the samples (89, 72, 58, 40, and 28%, respectively). It was not always possible to identify representatives of the first three groups to the species level; therefore, we failed to determine the frequency of occurrence for some species. The highest occurrence was observed for *Baetis fuscatus* (11%), *Serratella ignita* (11%), *Eclyonurus joernensis* (8%), and *Ephemera vulgata* (7%) in the order Ephemeroptera and *Brachycentrus subnubilus* (6%) and *Neureclipsis bimaculata* (6%) in the order Trichoptera. We also often recorded separate representatives of Plecoptera (*Leuctra fusca*, 14%) and Coleoptera (*Elmis* spp., 9%; *Oulimnius tuberculatus*, 8%). The average values of the diversity indices were 1.03 ± 0.057 according to Shannon and 0.50 ± 0.026 according to Simpson; the differences between the biotopes were statistically insignificant with respect to these characteristics (Student's test).

The abundance of zoobenthos significantly varied from site to site (from 0.06 to 42.6 thousand spec./m² and from 0.06 to 100.8 g/m²); the mean values reached 3106 ± 642 spec./m² and 6.6 ± 1.27 g/m². The abundance and biomass of the main taxa for the identified biotopes (without representatives of Unionidae) are given in Table 2.

The zoobenthos of brooks was characterized by a low abundance compared to the medial and ripal zones of the rivers (Mann–Whitney test). The highest biomass and abundance of zoobenthos were determined in the medial zone. Representatives of Bivalvia (*Euglesa* spp.) and Gastropoda (*Radix intermedia*, *Gyraulus borealis*, and *G. stelmachetius*) and larvae of dipterans (*Dicranota bimaculata*) prevailed in the

Table 1. Taxonomic composition of zoobenthos in the river pools of eastern Fennoscandia

Taxon	Brooks	Rivers	
		medial zone	ripal zone
Type Porifera			
<i>Spongilla lacustris</i> (Linnaeus, 1758)	—	+	+
Type Nematoda	+	+	+
Type Annelida, class Oligochaeta			
<i>Eiseniella tetraedra</i> (Savigny 1826)	—	+	+
<i>Enchytraeidae</i> sp.	—	+	—
<i>Lamprodrilus isoporus</i> Michaelsen, 1901	—	—	+
<i>Limnodrilus hoffmeisteri</i> Claparède, 1862	—	—	+
<i>Lumbricus variegatus</i> Müller, 1774	+	+	—
<i>Spirosperma ferox</i> Eisen, 1879	+	+	+
<i>Tubifex tubifex</i> (Müller, 1774)	+	—	—
<i>Uncinaiis uncinata</i> (Ørsted, 1842)	—	+	—
Subclass Hirudinea			
<i>Erpobdella octoculata</i> (Linnaeus, 1758)	—	+	—
<i>Glossiphonia complanata</i> (Linnaeus, 1758)	—	+	+
<i>Helobdella stagnalis</i> (Linnaeus, 1758)	+	+	+
<i>Theromyzon tessulatum</i> (O.F. Müller, 1774)	—	+	—
Type Mollusca, class Bivalvia			
<i>Anodonta cygnea</i> (Linnaeus, 1758)	—	+	+
<i>Euglesa</i> (<i>Cingulipisidium</i>) <i>nitida</i> (Jenyns, 1832)	—	+	+
<i>E.</i> (<i>Cyclocalyx</i>) <i>lapponica</i> (Clessin in Westerlund, 1873)	—	+	—
<i>E.</i> (<i>Cyclocalyx</i>) <i>scholtzii</i> (Clessin, 1873)	+	—	—
<i>E.</i> (<i>Euglesa</i>) <i>curta</i> (Clessin, 1874)	—	+	+
<i>E.</i> (<i>E.</i>) <i>ponderosa</i> (Stelfox, 1918)	—	+	+
<i>E.</i> (<i>Henslowiana</i>) <i>henslowana</i> (Sheppard, 1825)	—	+	+
<i>E.</i> (<i>H.</i>) <i>liljeborgii</i> Clessin in Esmarket Hoyer, 1886	—	+	+
<i>E.</i> (<i>H.</i>) <i>polonica</i> Anistratenko et Starobogatov, 1990	—	+	—
<i>E.</i> (<i>Hiberneuglesa</i>) <i>normalis</i> (Stelfox, 1929)	—	+	+
<i>E.</i> (<i>H.</i>) <i>parvula</i> (Clessin in Westerlund, 1873)	—	—	+
<i>E.</i> (<i>Pseudeupera</i>) <i>subtruncata</i> (Malm, 1855)	—	+	+
<i>E.</i> (<i>P.</i>) <i>turgida</i> (Clessin in Westerlund, 1873)	—	—	+
<i>E.</i> (<i>Pulchelleuglesa</i>) <i>acuticostata</i> Starobog. et Korn., 1989	—	+	+
<i>E.</i> (<i>Roseana</i>) <i>globularis</i> (Clessin in Westerlund, 1873)	+	—	—
<i>E.</i> (<i>Tetragonocyclas</i>) <i>baudoniana</i> (de Cessac, 1855)	—	—	+
<i>E.</i> (<i>T.</i>) <i>milium</i> (Held, 1836)	—	+	—
<i>Pisidium amnicum</i> (Müller, 1774)	—	+	—
<i>Sphaerium westerlundi</i> Westerlund, 1873	—	+	+
<i>Unio pictorum</i> (Linnaeus, 1758)	—	+	+
<i>U. tumidus</i> Retzius, 1788	—	—	+
Class Gastropoda			
<i>Bathymorphalus crassus</i> (Da Costa, 1778)	—	—	+
<i>Gyraulus</i> (<i>Gyraulus</i>) <i>borealis</i> (Lovén in Westerlund, 1875)	+	+	+
<i>G.</i> (<i>G.</i>) <i>stelmachoetius</i> (Bourguignat, 1860)	+	+	+
<i>Lymnaea</i> (<i>Lymnaea</i>) <i>stagnalis</i> (Linnaeus, 1758)	—	—	+

Table 1. (Contd.)

Taxon	Brooks	Rivers	
		medial zone	ripal zone
<i>Planorbis (Planorbis) planorbis</i> (Linnaeus, 1758)	—	+	+
<i>Radix (Peregrina) intermedia</i> (Lamarck, 1822)	+	+	+
<i>Valvata (Cincinna) piscinalis</i> O.F. Müller, 1774	+	—	—
<i>V. (Sibirovalvata) confusa</i> Westerlund, 1897	—	—	+
Type Arthropoda, class Grustacea			
<i>Asellus aquaticus</i> (Linnaeus, 1758)	—	+	+
<i>Eurycerus lamellatus</i> (O.F. Müller, 1776)	—	+	—
<i>Gammarus lacustris</i> G.O. Sars, 1863	—	+	+
Class Ostracoda	+	+	—
Class Arachnida, Hydracarina group	+	+	+
Class Insecta			
Order Hemiptera <i>Aphelocheirus aestivalis</i> (Fabricius, 1794)	—	+	—
Order Coleoptera			
<i>Agabus</i> sp.	+	—	—
<i>Donacia</i> sp.	—	+	+
<i>Elmis aenea</i> (Müller, 1806)	+	+	—
<i>E. maugetii</i> Latreille, 1802	+	+	—
<i>Halipus</i> sp.	—	+	+
<i>Hydrophilus</i> sp.	—	+	—
<i>Limnius volckmari</i> (Panzer, 1793)	—	+	+
<i>Oulimnius tuberculatus</i> (Müller, 1806)	+	+	+
Order Megaloptera			
<i>Sialis sordida</i> Klingstedt, 1933	—	+	+
<i>S. fuliginosa</i> Pictet, 1836	+	+	+
<i>S. lutaria</i> (Linnaeus, 1758)	—	+	+
Order Neuroptera			
<i>Sisyra fuscata</i> (Fabricius, 1793)	—	+	—
Order Ephemeroptera			
<i>Baetis fuscatus</i> (Linnaeus, 1761)	+	+	—
<i>B. rhodani</i> (Pictet, 1843)	+	—	+
<i>B. vernus</i> Curtis, 1834	+	+	—
<i>Caenis horaria</i> (Linnaeus, 1758)	—	+	—
<i>Centroptilum luteolum</i> Müller, 1776	+	—	—
<i>Cloeon (Procloeon) bifidum</i> Bengtsson, 1912	—	+	—
<i>C. sp.</i>	—	+	+
<i>Ecdyonurus joernensis</i> Bengtsson, 1909	—	+	—
<i>Ephemerella danica</i> Müller, 1764	—	+	—
<i>E. vulgata</i> Linnaeus, 1758	—	+	+
<i>Ephemerella aurivillii</i> (Bengtsson, 1909)	—	+	—
<i>E. mucronata</i> (Bengtsson 1909)	—	+	—
<i>Habrophlebia lauta</i> McLachlan, 1884	+	+	+
<i>Heptagenia dalecarlica</i> Bengtsson, 1912	—	+	—
<i>H. sulphurea</i> (Müller, 1776)	—	+	—
<i>Metretopus borealis</i> (Eaton, 1871)	+	+	—

Table 1. (Contd.)

Taxon	Brooks	Rivers	
		medial zone	ripal zone
<i>Nigrobaetis digitatus</i> (Bengtsson, 1912)	—	+	—
<i>Paraleptophlebia submarginata</i> (Stephens, 1835)	—	+	—
<i>Serratella ignita</i> (Poda, 1761)	+	+	+
Order Plecoptera			
<i>Amphinemura borealis</i> (Morton, 1894)	—	+	—
<i>Arcynopteryx compacta</i> (McLachlan, 1872)	—	+	—
<i>Diura nanseni</i> (Kempny, 1900)	+	+	—
<i>Isoperla difformis</i> (Klapalek, 1909)	—	+	—
<i>Leuctra digitata</i> Kempny, 1899	—	+	+
<i>L. fusca</i> (Linnaeus, 1758)	+	+	+
<i>Nemoura cinerea</i> Stephens, 1836	—	+	+
<i>Taeniopteryx nebulosa</i> (Linnaeus, 1758)	—	+	—
Order Trichoptera			
<i>Agraylea multipunctata</i> Curtis, 1834	—	+	—
<i>Arctopsyche ladogensis</i> (Kolenati, 1859)	—	+	—
<i>Athripsodes aterrimus</i> (Stephens, 1836)	—	+	—
<i>A. cinereus</i> (Curtis, 1834)	—	+	—
<i>Brachycentrus subnubilus</i> Curtis, 1834	—	+	—
<i>Ceraclea</i> sp.	—	+	+
<i>Ceratopsyche newae</i> (Kolenati, 1858)	—	+	—
<i>Cyrnus trimaculatus</i> (Curtis, 1834)	—	—	+
<i>Halesus</i> sp.	—	—	+
<i>Hydropsyche borealis</i> Martynov, 1926	—	+	—
<i>H. pellucidula</i> (Curtis, 1834)	—	+	—
<i>Hydroptila</i> sp.	—	+	—
<i>Lepidostoma hirtum</i> (Fabricius, 1775)	—	+	—
<i>Limnephilus</i> sp.	—	+	—
<i>Neureclipsis bimaculata</i> (Linnaeus, 1758)	—	+	+
<i>Oecetis</i> sp.	—	+	—
<i>Oligostomus reticulata</i> (Linnaeus, 1761)	+	—	—
<i>Oxyethira</i> sp.	+	+	—
<i>Plectrocnemia conspersa</i> (Curtis, 1834)	+	—	—
<i>Polycentropus flavomaculatus</i> (Pictet, 1834)	+	+	—
<i>Potamophylax</i> sp.	—	—	+
<i>Rhyacophila nubila</i> Zetterstedt, 1840	+	+	+
<i>Stenophylax</i> sp.	+	+	+
Order Odonata			
<i>Aeshna cyanea</i> Müller, 1764	—	—	+
<i>Cordulegaster boltonii</i> Donovan, 1807	—	+	+
<i>Gomphus vulgatissimus</i> Linnaeus, 1758	—	+	+
<i>Onychogomphus forcipatus</i> Linnaeus, 1758	—	+	—
Order Diptera			
Family Athericidae			
<i>Atherix ibis</i> (Fabricius, 1798)	—	+	—

Table 1. (Contd.)

Taxon	Brooks	Rivers	
		medial zone	ripal zone
Family Ceratopogonidae	+	+	+
Family Pediciidae			
<i>Dicranota bimaculata</i> (Schummel, 1829)	+	—	+
<i>Tricyphona immaculata</i> (Meigen, 1804)	—	+	—
Family Limoniidae			
<i>Hexatoma</i> sp.	—	+	+
<i>Phylidorea</i> sp.	+	—	+
Family Tabanidae	—	—	+
<i>Chrysops</i> sp.	—	+	—
Family Tipulidae	—	—	+
<i>Eleophila</i> sp.	—	—	+
Family Simuliidae			
<i>Cnetha</i> sp.	+	—	—
<i>Odagmia</i> sp.	—	+	—
<i>Simulium morsitans</i> Edwards, 1915	—	+	—
<i>S.</i> sp.	+	+	—
Family Chironomidae			
Subfamily Tanypodinae			
<i>Clinotanypus</i> sp.	—	+	—
<i>Procladius (Holotanypus)</i> sp.	+	+	+
Tanypodinae spp.	+	+	+
<i>Tanypus punctipennis</i> Meigen, 1818	—	—	+
Subfamily Ortoclaadiinae			
<i>Corynoneura carriana</i> group sp.	—	+	—
Ortocladeinae spp.	+	+	+
<i>Psectrocladius simulans</i> (Johannsen, 1937)	+	+	—
Subfamily Chironominae			
<i>Chironomus</i> sp.	—	+	+
<i>Cladopelma goetghebueri</i> Spies & Saether, 2004	—	—	+
<i>Cladotanitarsus mancus</i> group sp.	—	—	+
<i>Fleuria lacustris</i> Kieffer, 1924	—	—	+
<i>Harnischia curtilamellata</i> (Malloch, 1915)	—	—	+
<i>Heterotrissocladius marcidus</i> (Walker, 1856)	—	+	—
<i>H. subpilosus</i> group sp.	—	+	—
<i>Microchironomus tener</i> (Kieffer, 1918)	—	—	+
<i>Microtendipes pedellus</i> group sp.	—	+	+
<i>Polypedilum convictum</i> group sp.	—	+	+
<i>P. nubeculosum</i> (Meigen, 1804)	—	—	+
<i>P. scalaenum</i> (Schränk, 1803)	—	—	+
<i>Stictochironomus crassiforceps</i> (Kieffer, 1922)	—	+	+
<i>Tanytarsus</i> sp.	—	+	—
<i>Tribelos intextus</i> (Walker, 1856)	—	+	—
Total	42	115	79

Table 2. Number (*N*) and biomass (*B*) of the main taxa of zoobenthos of river pools in eastern Fennoscandia

Taxon	<i>N</i> , spec./m ²			<i>B</i> , g/m ²		
	Brooks	Rivers		Brooks	Rivers	
		medial zone	ripal zone		medial zone	ripal zone
Nematoda	25	12	1	0.018	0.008	0.000
Oligochaeta	107	245	515	0.135	0.619	0.468
Hirudinea	2	14	4	0.014	0.221	0.053
Bivalvia	169	185	138	0.374	2.602	0.493
Gastropoda	17	32	15	0.277	0.305	0.149
Crustacea	40	50	32	0.013	0.056	0.021
Hydracarina	8	7	1	0.005	0.009	0.001
Ephemeroptera	23	208	26	0.031	0.328	0.168
Plecoptera	73	118	6	0.036	0.129	0.007
Trichoptera	21	1261	11	0.030	2.528	0.108
Coleoptera	44	93	6	0.037	0.062	0.007
Heteroptera	0	27	0	0.000	0.497	0.000
Odonata	0	8	5	0.000	0.703	0.924
Megaloptera	0	7	18	0.000	0.101	0.211
Chironomidae	191	1187	2294	0.073	1.053	1.860
Diptera others	196	173	43	0.369	0.284	0.193
Total	916 ± 185	3627 ± 1069	3113 ± 952	1.4 ± 0.37	9.5 ± 2.52	4.7 ± 0.89

brooks with respect to their biomass. There were numerous larvae of caddis flies (*Brachycentrus subnubilus* and *Hydropsyche contubernalis borealis*), bivalve mollusks (*Euglesa* spp.), and chironomid larvae of the subfamily Chironominae in the medial zone. The zoobenthos of the ripal zone was dominated by larvae of chironomids (subfamily Chironominae).

Large bivalves—representatives of the family Unionidae (*Anodonta cygnea*, *Unio pictorum*, and *U. tumidus*)—were locally distributed and recorded in 11.3% of samples. At the same time, these species could form a large biomass in some areas (4% of samples, mainly in the medial zone): 0.5–3.6 kg/m² at a density of 80–120 spec./m².

The abundance of zoobenthos significantly increases in the southern part of the region. Thus, the average values were 1.0 ± 0.22 thousand spec./m² and 2.7 ± 0.48 g/m² north of 65° N, 0.8 ± 0.13 thousand spec./m² and 1.9 ± 0.59 g/m² from 63° N to 65° N, and 4.1 ± 0.92 thousand spec./m² and 8.6 ± 1.82 g/m² south of 63° N. The difference between the abundance of river zoobenthos south of 63° N (73 samples) from that to the north of this parallel (34 samples) was significant both in number and biomass (Mann–Whitney test).

The trophic structure of the zoobenthos of the pools is represented by shredders, collectors (filterer–collectors and gatherer–collectors), scrapers, and predators. The biomass proportion of collectors is the

highest (50–75%); i.e., the studied areas can be classified as a rithral zone.

We revealed differences in the ratio of functional trophic groups with respect to the biotope (brooks, medial zone, or ripal zone) and type of bottom substrate (silty, sandy, or stony bottom). Thus, the ripal and medial zones of relatively large rivers are dominated by gatherer–collectors (40–60% of the zoobenthos biomass). The trophic structure of the zoobenthos of the brooks significantly differs from that in larger watercourses, primarily by a high proportion of scrapers. The proportions of predators, shredders, and filterer–collectors are comparable, while the proportion of gatherer–collectors is 2 times lower than that in the ripal zoobenthos. The proportion of shredders in the trophic structure of the zoobenthos of pools is relatively low and rarely exceeds 10% of biomass (Table 3).

The type of bottom influenced the trophic structure of zoobenthos. Thus, the proportion of scrapers increased from 2% on silty bottoms to 30% on stony bottoms (Table 4). The proportion of shredders also increased with growth in the bottom fraction (from 3 to 11%). At the same time, the proportion of predators was high on the silty bottom (24%). Large bivalve mollusks (of the family Unionidae), classified as filterer–collectors, were recorded mainly on silty bottoms; however, they can also form aggregations on stones (in particular, in areas with a significant current at the beginning of pools).

Table 3. Proportion of trophic groups of zoobenthos (% of total biomass) in different biotopes of river pools of eastern Fennoscandia

Trophic group	Biotope		
	Brooks	Rivers	
		medial zone	ripal zone
Shredders	2 ± 0.9	9 ± 2.3	3 ± 1.4
Filterer—collectors	27 ± 8.9	25 ± 4.3	14 ± 2.9
Gatherer—collectors	32 ± 9.3	40 ± 4.7	60 ± 4.9
Scrapers	24 ± 11.0	11 ± 3.3	3 ± 1.5
Predators	14 ± 4.7	15 ± 3.7	20 ± 3.8

Table 4. Proportion of trophic groups of zoobenthos (% of total biomass) on different bottoms of river pools in eastern Fennoscandia

Trophic group	Bottom		
	silty	sandy	stony
Shredders	3 ± 1.7	5 ± 1.9	11 ± 3.7
Filterer—collectors	20 ± 4.5	25 ± 3.8	10 ± 3.9
Gatherer—collectors	50 ± 6.0	48 ± 4.4	40 ± 8.4
Scrapers	2 ± 1.5	8 ± 2.8	29 ± 8.6
Predators	24 ± 5.1	13 ± 2.5	10 ± 5.6

DISCUSSION

With respect to the hydrological characteristics, pattern of the bottom substrate, and flowage, the pools of the rivers occupy an intermediate position between riffles and channel lakes. Therefore, both typical river species and typical lake species can be found in the zoobenthos of the pools. At the same time, a significant part of specialized rheophilic and limnophilic species can be absent in the river pools. The complete list of species of the rheophilic and limnophilic freshwater zoobenthos for the northern part of the area (Murmansk oblast) includes about 600 species (Yakovlev, 2005). Species diversity increases to the south. Thus, the limnophilic benthic fauna of the water bodies of the Republic of Karelia can include about 1100 species without taking into account bottom plankton crustaceans (Popchenko and Aleksandrov, 1983). About 500 species are known for the flowage lakes of the Kem River basin (Ryabinkin, 2003). By comparison, the fauna of waters in the Republic of Komi includes about 700 species (Zvereva, 1969). About 850 species are known for the benthos of Ural and Timan rivers (Shubina, 2006). However, the basic fauna of bottom communities is formed only by 25–30% of taxa of the species list, while the rest of them occur much less frequently (Popchenko and Aleksandrov, 1983). Thus, we previously identified 137 taxo-

nomic groups for the rapid parts of the rivers in eastern Fennoscandia without a detailed identification of chironomids and oligochetes (Baryshev, 2017). A detailed investigation has recorded 222 species in the zoobenthos of the Ild River tributary (the basin of the Rybinsk Reservoir), which is located much farther south and characterized by high saprobity (Perova, 2016). One hundred and fifty-six invertebrate species were identified in the zoobenthos of the lower reaches of the Sylva River (the Kama River basin) (Pan'kov, 1997).

This research failed to identify some of the hydrobionts (primarily those belonging to the Oligochaeta, Chironomidae, and Hydracarina groups) to the species level, which significantly reduced the faunal list. In addition, this study concerns only part of river biotopes (pool areas). Therefore, the number of identified taxa (151) seems quite natural. The number of species recorded in the selected biotopes (brooks, medial zone, and ripal zone) significantly varies (Table 1) what can be explained different number of samples, because the comparison of diversity using the Shannon and Simpson indices did not show statistically significant differences.

The set of species that form the basic zoobenthos biomass of the pools significantly differs from the set that was previously identified in the communities in the rapid parts of the rivers (Baryshev, 2014, 2015). The prevailing number of Bivalvia, Gastropoda, and Chironominae invertebrates that was found in the zoobenthos of the pools is also largely characteristic of the zoobenthos of lakes (Ryabinkin, 2008; Yakovlev, 2005).

The values of the Shannon index (0.94–1.17) and Simpson index (0.45–0.51) show a relatively low diversity of bottom invertebrate communities in the pools. At the same time, the values of the Shannon index varied from 1.20 to 2.77 and the values of the Simpson index varied from 0.09 to 0.33 in the rapid parts of different rivers of eastern Fennoscandia (except for the mountain rivers) (Baryshev, 2014, 2015; Baryshev and Khrennikov, 2016; Komulainen et al., 2013). The relatively high species diversity of lithoreophilic communities in the rapid parts of the rivers against the background of the diversity of habitats within the biocenosis was previously noted quite many times (Shubina, 2006).

The average values of the abundance and biomass of zoobenthos in the pools of the rivers (3106 ± 642 spec./m² and 6.6 ± 1.27 g/m²) are comparable with the previously determined values for the riffles of eastern Fennoscandia (Baryshev, 2014, 2015; Baryshev and Khrennikov, 2016; Komulainen et al., 2013). An extremely high abundance variability was recorded, which is presumably determined by the diversity of microhabitats within the pools. A similar mosaic pattern of zoobenthos with multiple fluctuations in abundance was recorded on the Pechora River (Zvereva, 1969).

The high proportion of gatherer–collectors in the trophic structure of bottom invertebrate communities in rivers is common not only for the rivers of Fennoscandia, but also for rivers of other regions (Kocharina, 2005; Baryshev, 2017; Tiuniva, 2006). The differences in the trophic structure of zoobenthos between the selected biotopes may be related to the specific conditions in each of them. Thus, silty bottoms are formed in areas with moderate currents and are mainly characteristic of the ripal zone. The absence of a solid substrate determines the minimum proportion of scrapers and a certain level of development of gatherer–collectors. Sandy soils are present in brooks and ripal zones of rivers. The trophic structure of benthos in these biotopes is close to that on silty bottoms; however, the proportion of filterer–collectors and scrapers increases here. The large stony bottom that is characteristic of areas with significant currents creates favorable conditions for scrapers (Table 4).

The study region stretches from north to south over thousands of kilometers; the climate significantly differs in the Kola Peninsula and southern Karelia. Therefore, the increase in the abundance of river zoobenthos towards the south appears quite natural. We previously recorded a similar dynamics for the rapid parts of Fennoscandian rivers (Baryshev, 2014).

The general composition of the zoobenthos of pools of the lake–river systems of Fennoscandia is similar to that in lowland rivers. The zoobenthos of watercourses in the European northeast of Russia (Middle Pechora and Vychegda) is also dominated by chironomid larvae, oligochaetes, mollusks, and nematodes, as well as caddis larvae in some areas (Zvereva, 1969). A significant species diversity of Chironomidae, Mollusca, and Oligochaeta was recorded in more southern regions, namely, at the mouth of the Ild River (the basin of the Rybinsk Reservoir) and in the lower reaches of the Sylva River (the Kama River basin) (Pan'kov, 1997; Perova, 2016). In the zoobenthos of the pools of Fennoscandian rivers, where rapid rivers periodically occur almost throughout the entire channel, we also found typical rheophilic species penetrating from main streams. However, in rivers where the lower pools have no riffles, such species can penetrate from the upper reaches (Zvereva, 1969). The significant variation in the zoobenthos abundance that we revealed for the pools of lake–river systems was also recorded in lowland rivers with low lake percentage and without rapid waters. Thus, the watercourses of the European northeast of Russia in the middle and lower reaches (Middle Pechora and Vychegda) are characterized by a relatively low zoobenthos biomass (about 1–4 g/m²); however, there are also areas with the biomass of 40 g/m² (Zvereva, 1969). The zoobenthos biomass is 2–70 g/m² in the estuary zone of the lowland Ild river (the basin of the Rybinsk reservoir) (Perova, 2016). Similar values were obtained for the

zoobenthos of the lower reaches of the Sylva River: 11–44 g/m² (Pan'kov, 1997).

CONCLUSIONS

We have identified 151 invertebrate taxa in the zoobenthos of the pools of rivers in eastern Fennoscandia. Representatives of the Chironomidae, Oligochaeta, Sphaeriidae, Ephemeroptera, and Trichoptera groups are most numerous. The species diversity of invertebrate communities in the pool areas has proven to be low compared to the areas with rapid parts; however, the abundance, which is formed primarily by representatives of Bivalvia, Gastropoda, Diptera, and Trichoptera, is quite comparable. The lowest zoobenthos biomass among the studied biotopes was determined in the brooks, while the highest was in the medial zone of the rivers. The abundance of zoobenthos significantly increases towards the south. The trophic structure of zoobenthos is dominated by gatherer–collectors; the ratio of trophic groups varies with respect to the type of biotope and pattern of bottom. The comparison of the structure of zoobenthos of the rapid river pools with that of the lowland rivers in Fennoscandia has not shown fundamental differences, which indicates the importance of local hydrological and other factors in the formation of the composition and abundance of bottom invertebrate communities.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interests. The author declares that he has no conflict of interest.

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

REFERENCES

Baryshev, I.A., Factors of formation of macrozoobenthic communities of rocky rapids and rifts of watercourses of

- Eastern Fennoscandia, *Zh. Obshch. Biol.*, 2014, vol. 75, no. 2, p. 124.
- Baryshev, I.A., Features of formation of the macrozoobenthos structure in rift areas of rivers of the Karelian coast of the White Sea, *Tr. Karel. Nauchn. Tsentra Ross. Akad. Nauk*, 2015, no. 1, p. 29.
- Baryshev, I.A., The history of the study of macrozoobenthos of rivers of Karelia and Murmansk oblast, *Tr. Karel. Nauchn. Tsentra Ross. Akad. Nauk, Ser. Ekol. Issled.*, 2016, no. 4, p. 3.
<https://doi.org/10.17076/eco98>
- Baryshev, I.A., Taxonomic composition and trophic structure of benthic fauna in rocky rapids and riffles in rivers of the Republic of Karelia and Murmansk oblast, *Inland Water Biol.*, 2017, vol. 10, no. 4, p. 405.
<https://doi.org/10.1134/S1995082917040034>
- Baryshev, I.A. and Khrennikov, V.V., Quantitative characteristics of macrozoobenthos of rapids of rivers of the Kandalaksha coast of the White Sea as the basis of food resources for juvenile salmonids, *Povolzh. Ekol. Zh.*, 2016, no. 3, p. 255.
<https://doi.org/10.18500/1684-7318-2016-3-255>
- Belyakov, V.P., Composition and structure of zoobenthos of Lake Ladoga tributaries, in *Otsenka ekologicheskogo sostoyaniya rek basseina Ladozhskogo ozera po gidrokhimicheskim pokazatelyam i strukture gidrobiotsenozov* (Assessment of the Environmental State of Rivers of Ladoga Lake Basin by Hydrochemical Indices and Hydrobiocenosis Structure), St. Petersburg: Lema, 2006, p. 108.
- Biske, G.S., *Chetvertichnaya geologiya i geomorfologiya Karelii* (Quaternary Geology and Geomorphology of Karelia), Petrozavodsk: Gos. Izd. Karel. ASSR, 1959.
- Bogatov, V.V. and Fedorovskii, A.S., *Osnovy rechnoi gidrologii i gidrobiologii* (Fundamentals of River Hydrology and Hydrobiology), Vladivostok: Dal'nauka, 2017.
- Cummins, K.W. and Klugg, M.J., Feeding ecology of stream invertebrates, *Annu. Rev. Ecol. Syst.*, 1979, vol. 10, p. 147.
- De Jong, Y., Verbeek, M., Michelsen, V., et al., Fauna Europaea—all European animal species on the web, *Biodiversity Data J.*, 2014, vol. 2.
<https://doi.org/10.3897/BDJ.2.e40342014>
- Kocharina, S.L., Trophic structure of invertebrates of some watercourses of the Pravaya Sokolovka River basin (Upper Ussuri Station, Primorsky Krai), in *Chteniya pamyati Vladimira Yakovlevicha Levanidova* (Lectures in Memory of Vladimir Yakovlevich Levanidov), Vladivostok: Dal'nauka, 2005, vol. 3, p. 49.
- Komulainen, S.F., Kruglova, A.N., and Baryshev, I.A., Structure of communities of aquatic organisms of tributaries of the Vygozero Reservoir, *Povolzh. Ekol. Zh.*, 2013, no. 3, p. 261.
- Magurran, A.E., *Ecological Diversity and Its Measurement*, Princeton: Princeton Univ. Press, 1998.
<https://doi.org/10.1007/978-94-015-7358-0>
- Opredelitel' presnovodnykh bespozvonochnykh Rossii i sprovedel'nykh territorii* (Identification Guide to Freshwater Invertebrates of Russia and Adjacent Countries), vol. 3: *Paukoobraznye i nizshie nasekomye (Arachnida and Lower Insects)*, St. Petersburg: Nauka, 1997.
- Opredelitel' presnovodnykh bespozvonochnykh Rossii i sprovedel'nykh territorii* (Identification Guide to Freshwater Invertebrates of Russia and Adjacent Countries), vol. 4: *Vysshie nasekomye. Dvukrylye (Higher Insects. Diptera)*, St. Petersburg: Nauka, 1999.
- Opredelitel' presnovodnykh bespozvonochnykh Rossii i sprovedel'nykh territorii* (Identification Guide to Freshwater Invertebrates of Russia and Adjacent Countries), vol. 5: *Vysshie nasekomye (rucheiniki, cheshuekrylye, zhestkokrylye, setchatokrylye, bol'shekrylye, pereponchatokrylye)* (Higher Insects (Trichoptera, Lepidoptera, Coleoptera, Neuroptera, Megaloptera, and Hymenoptera)), St. Petersburg: Nauka, 2001.
- Opredelitel' zooplanktona i zoobentosa presnykh vod Evropeiskoi Rossii* (Identification Guide to Freshwater Zooplankton and Zoobenthos of European Russia), vol. 2: *Zoobentos (Zoobenthos)*, Moscow: Tov. Nauchn. Izd. KMK, 2016.
- Pan'kov, N.N., Structural and functional characteristics of zoobenthic communities of the Sylva River (Kama River basin), *Cand. Sci. (Biol.) Dissertation*, Perm: Perm State Univ., 1997.
- Perova, S.N., Structure of the macrozoobenthos of the estuarine area of the Rybinsk Reservoir tributary, *Tr. Inst. Biol. Vnutr. Vod Ross. Akad. Nauk*, 2016, no. 74 (77), p. 113.
- Popchenko, V.I. and Aleksandrov, V.M., Benthic fauna of Lake Onega and its biocenosis, in *Presnovodnye gidrobioty i ikh biologiya* (Freshwater Aquatic Animals and Their Biology), Leningrad: Nauka, 1983, p. 102.
- Ryabinkin, A.V., Macrozoobenthos of water bodies of the Kem River Basin (Karelia) and its dynamics under conditions of anthropogenic impact, *Cand. Sci. (Biol.) Dissertation*, Petrozavodsk: Petrozavodsk State Univ., 2003.
- Ryabinkin, A.V., Fauna of benthic invertebrates of the Kem River basin, *Tr. Karel. Nauchn. Tsentra, Biogeogr.*, Petrozavodsk: Karel. Nauchn. Tsentr Ross. Akad. Nauk, 2008, no. 12, p. 134.
- Shitikov, V.K., Rozenberg, G.S., and Zinchenko, T.D., *Ko-lichestvennaya gidroekologiya: metody sistemnoi identifikatsii* (Quantitative Hydroecology: System Identification Techniques), Tolyatti: Inst. Ekol. Volzhsk. Basseina Ross. Akad. Nauk, 2003.
- Shubina, V.N., *Bentos lososevykh rek Urala i Timana* (Benthos of Salmon-Rich Rivers of the Urals and Timan), St. Petersburg: Nauka, 2006.
- Sladeczek, V., System of water quality from the biological point of view, *Arch. Hydrobiol. Ergebn. Limnol.*, 1973, vol. 7, p. 1.
- Tiunova, T.M., Trophic structure of invertebrate communities in ecosystems of salmon rivers in the southern far east, *Russ. J. Ecol.*, 2006, vol. 37, no. 6, p. 419.
<https://doi.org/10.1134/S10674136060060099>
- Vinarski, M.V. and Kantor, Y.I., *Analytical Catalogue of Fresh and Brackish Water Mollusks of Russia and Adjacent Countries*, Moscow: Severtsov Inst. Ecol. Evol. Ross. Akad. Nauk, 2016.
- Yakovlev, V.A., Faunistic review of freshwater zoobenthos of the northeastern part of Fennoscandia, *Biol. Vnutr. Vod*, 2004, no. 3, p. 16.
- Yakovlev, V.A., *Presnovodnyi zoobentos Severnoi Fennoskandii (raznoobrazie, struktura i antropogennaya dinamika)* (Freshwater Zoobenthos of North Fennoscandia (Diversity, Structure, and Anthropogenic Dynamics)), Apatity: Kol'sk. Nauchn. Tsentr Ross. Akad. Nauk, 2005.
- Zhadin, V.I., Life in rivers: benthos, in *Zhizn' presnykh vod SSSR* (Life of Freshwaters of the USSR), Moscow: Akad. Nauk SSSR, 1950, vol. 3, p. 149.
- Zvereva, O.S., *Osobennosti biologii glavnykh rek Komi ASSR v svyazi s istoriei ikh formirovaniya* (Characteristics of Biology of the Major Rivers of the Komi ASSR in Connection with the History of Their formation), Leningrad: Nauka, 1969.

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