Oligochaete (Annelida, Clitellata) communities in lakes of the Ural Mountains (Russia)

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Abstract

The oligochaete fauna of 25 lakes located in the Polar and Subpolar regions of the Ural Mountains in Russia was studied. In total, 46 oligochaete taxa were collected, 32 of them identified to species level. Naididae had the highest number of taxa (19); the other taxa belonged to Pristinidae (2), Enchytraeidae (6), Tubificidae (10), Lumbriculidae (8) and Lumbricidae (1). Canonical correspondence analysis (CCA) was used to characterize the relationship between abundance of oligochaete species, abundance and biomass of all oligochaetes, abundance of separate families and environmental factors. Latitude, elevation, silt, detritus, moss and algal periphyton and depth were found to be factors influencing the distribution of oligochaetes.

Key words: oligochaetes, fauna, distribution, mountain water bodies, Ural Mountains, Komi Republic, Russia

Introduction

The European high-mountain water bodies represent an important resource of unpolluted water for the future but are becoming increasingly threatened by local (e.g. tourism and water extraction) and global (climate change) environmental impacts (McGregor et al. 1995; Lencioni et al. 2004). The geographical position of the Ural Mountains on the border of Europe and Asia contributes to a great interest in the fauna of this region. The investigated lakes are situated within the National Park "Yugyd Va", one of the largest territories protected as natural areas in the European Northeast, and also included on the list of the UNESCO's World Heritage sites.

The local benthic fauna has been regularly studied over the last two decades by researchers at the Institute of Biology of the Komi Branch of Ural Division of the Russian Academy of Sciences within the framework of two projects: "Biodiversity of terrestrial and aquatic ecosystems of the Subpolar Ural Mountains: mechanisms of formation, a modern condition, the forecast of natural and antropogenic dynamics" and the UNDP/GEF project "Strengthening Protected Areas System of the Komi Republic to Conserve Virgin Forest Biodiversity in the Pechora River Headwaters Region" (2008–2013).

In this paper, we compare the oligochaete fauna of 25 lakes in the Polar and the Subpolar Ural Mountains. We also assessed some ecological factors responsible for differences in the distribution of oligochaete communities (e.g., depth, elevation, bottom sediment).

Study area

The 25 lakes under study are located in the Komi Republic of the Russian Federation on the western slope of the Polar Urals (PU area, 10 lakes) and Subpolar Urals (SPU area, 15 lakes), in the extreme Northeast of Europe. All of these lakes are located in areas ranging from latitude 64°00' to 68°08' N, and longitude 59°40' to 65°21' E; the elevation of the PU lakes range from 200 to 500 m a.s.l. in PU, while the elevation of the SPU lakes range from 200 to 1000 m a.s.l.

Two of these lakes belong to the Kara River basin while the others are drained by tributaries of the Pechora River (Fig. 1, Table 1).
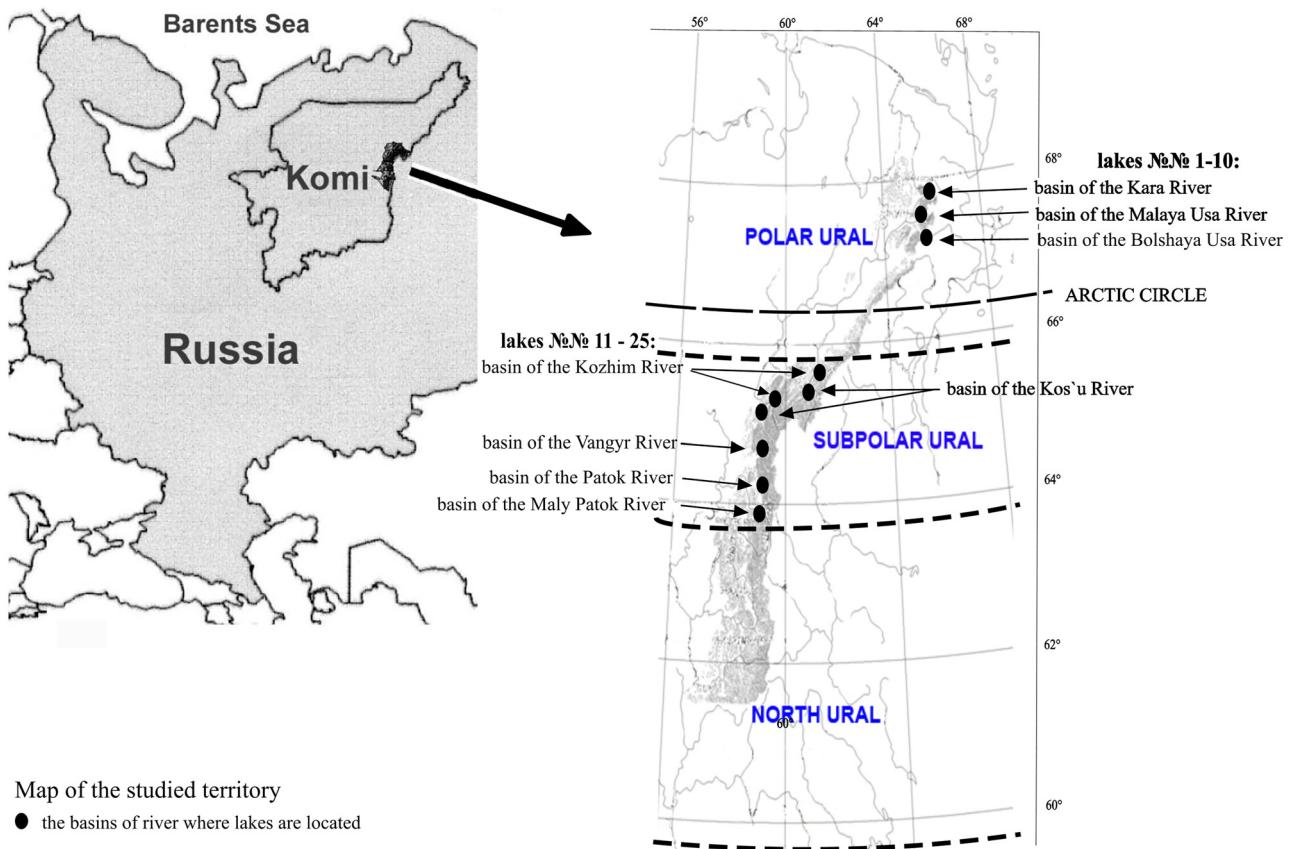
FIGURE 1. Location of the study area.

These lakes are of diverse origin: tarns, glacial, thermokarst, floodplain lakes. They are frozen for most of the year; only ice-free during the months of June through September. The surface water temperature of most of these lakes ranges from 10 to 15 ℃ in summer, although the temperature in floodplain lakes can reach 25 ℃. The lakes vary in size (in PU 0.22–1.5 km^2, SPU 0.05–1.45 km^2), depth (in PU 1.3–37 m, SPU 2.0 –21 m), and water transparency (5–11 m). The substrates of these lakes vary, including rocks, pebbles, gravel, sand and mud (silt). They are ultraoligotrophic and oligotrophic. In the investigated lakes the hydrogen ion concentration (as pH) measured usually fluctuates from slightly acidic to weakly alkaline. For example, during the sampling period the lowest pH (4.6) was observed just after the end of snowmelt (early in June) in a lake of the Maly Patok River basin, while the highest recorded pH values (8.6) were seen in August. Water mineralization and conductivity are very low; saturation with oxygen is typical, during the observation period dissolved oxygen being always present in the profundal zone of the lake.

Most of the lakes are pristine, without any direct human impact. They can be reached only with helicopter or special cross-country vehicles. Severe climate conditions and inaccessibility are the reasons that the fauna of these local lakes has not been investigated until the recent time.

Methods

The Polar and Subpolar Ural lakes were studied during summer seasons of 1998 through 2010. Quantitative zoobenthos samples (46 from PU lakes and 54 from SPU lakes) were taken with a Petersen dredge (sampling area 0.040 m^2) on soft bottoms and with a hydrobiological scraper (S = 0.09 m^2, 230 μm mesh size net) on stony and gravel bottoms. The zoobenthos samples were taken from different depths. After the samples had been sorted, oligochaetes were prepared for identification. The worms were mounted in a glycerin-water solution and identified to species level under a light microscope (Leica DM 4000 B), following the methodologies and keys presented in Timm (2009). Some part of the material remained unidentified, including several taxa in the family Enchytraeidae and juvenile individuals. These individuals were determined only to family level. Oligochaete biomass was determined as a wet weight using a torsion balance (WT-250, Poland).

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TABLE 1. List of the lakes under study.

№	Name of lake	River basin	Coordinates	Area (km²)	Elevation above sea level (m)	Depth (max / widespread)	Substrate type
Polar Ural							
1	Lake № 1-B.U.	Bol'shaya Usa	N 67°28'; E 65°45'	0.25	154.7	7 / 3.5	rk, pb
2	Bol'shoe Kuz-ty	Bol'shaya Usa	N 67°36'; E 65°39'	1.5	289.1	4.6 / 2	rk, pb
3	Chan-ty	Malaya Usa	N 67°42'; E 65°42'	0.5	244.3	37 / 20	rk, pb
4	Maloe Shuch`e	Malaya Usa	N 67°48'; E 66°10'	4.0	270.0	36 / 20–30	sd, rk
5	Usva-ty	Malaya Usa	N 67°44'; E 65°59'	1.8	245.4	12 / 1.3	rk, pb, sd
6	Gnet-ty	Kara	N 67°58'; E 65°34'	0.8	189.7	7 / 3	rk, pb, sd, sl
7	Koma-ty	Kara	N 68°08'; E 65°21'	0.9	91.5	4 / 2	sd, sl
8	Plaun-ty	Malaya Usa	N 67°45'; E 65°40'	0.44	175.8	13 / 3.5	rk
9	Bezymyannoe-U	Malaya Usa (near Lake Usva-ty)	N 67°28'; E 65°38'	0.22	154.1	5.2 / 3	rk, sd
10	Protochnoe	Malaya Usa	N 67°46'; E 65°35'	1.31	172.5	1.3 / 0.8	rk, pb, sl
Subpolar Ural							
11	Bol'shoe Balban-ty	Kozhim	N 65°12'; E 60°14'	0.92	654.9	15 / 8	sl, rk
12	Maloe Balban-ty	Kozhim	N 65°09'; E 60°13'	0.5	687.6	10 / 8	sd, sl, rk
13	Verkhnee Balban-ty	Kozhim	N 65°03'; E 60°09'	0.12	1007.0	12 / 8	sl, sd, rk
14	Trubka	Kozhim (small river of Limbeko-yu)	N 65°05'; E 60°08'	0.1	850.0	2 / 1	sd, pb
15	Padezha-ty	Kozhim (small river of Limbeko-yu)	N 65°11'; E 60°03'	1.45	694.3	21 / 9	sl, rk
16	Forel`noe	Kozhim (small river of Limbeko-yu)	N 65°16'; E 59°55'	0.42	757.4	14 / 4	rk, sl
17	Lake № 1-K	Kos`u (small river of Lomes-vozh)	N 64°54'; E 59°54'	0.2	1048.3	5.7 / 2.5	rk, sl, sd
18	Lake № 2-K	Kos`u (small river of Lomes-vozh)	N 64°55'; E 59°54'	0.34	1010.2	6.3 / 2	rk, sl, sd
19	Lake № 3-K	Kos`u (small river of Lomes-vozh)	N 64°56'; E 59°55'	0.17	785.2	11 / 8.5	rk, pb, sd, sl
20	Nom-ty	Maly Patok	N 64°39'; E 59°40'	0.08	562.0	16 / 9	rk, sd
21	Patok	Maly Patok	N 64°40'; E 59°41'	0.24	560.6	16 / 5	rk, pb, sd, sl
22	Losinoe	Vangyr	N 64°58'; E 59°10'	0.06	274.8	2 / 1	sl
23	Lake № 1-V	Vangyr	N 64°59'; E 59°10'	0.05	278.5	8.5 / 6	rk
24	Lake № 2-V	Vangyr	N 64°59'; E 59°09'	0.15	278.0	2 / 1	rk
25	Mezhgornoe	Kos`u (small river of Nidysej)	N 65°15'; E 59°41'	0.03	601.7	9 / 2.4	rk, sl, sd

Abbreviation used: sl – silt, sd – sand, pb – pebbles, rk – rocks (boulders)

During the sampling period, water depth, temperature, hydrogen ion concentration (as pH), conductivity and oxygen content were measured using the portative analyzer Multi 340i/SET (Germany). The substrate components were classed according to grain-size as silt (0.01–0.1 mm), sand (0.1–1.0 mm), gravel (1.0–10.0 mm), pebbles (10.0–100.0 mm) and boulders (100.0–1000 mm) (Konstantinov 1972). Substrates with a mixture of several different fractions are defined as follows – silted sand, sand-gravel, boulder-pebble, and boulder-gravel.

The similarity of the oligochaete fauna identified from each of these lakes was estimated according to the Sørensen's similarity coefficient (Sørensen 1948). For the characterization of community evenness, the Pielou index (Pielou 1969) was used. Species' domination was characterized using the Kownacki index (d): d>10 – dominant, 1<d>10 – sub-dominant (Kownacka 1971).

The relationships between oligochaetes and environmental variables were investigated with canonical correspondence analysis (CCA) followed by Monte Carlo tests and cluster analysis with Euclidean distance measure and Ward`s group linkage method using PC-ORD for Windows (McCune & Meffod 1999). Eleven environmental variables were included in these analyses. These included substrate sizes, sampling depth (m), maximum depth (m) and area of lakes (m^2), as well as the qualitative characteristics such as presence and absence of visually distinguishable plants, moss, algae, detritus, and silt, and the geographical coordinates (elevation, latitude and longitude). Abundance of 31 identified species of oligochaetes, the total abundance and biomass of oligochaetes, abundance and number of Naididae, Tubificidae, Lumbriculidae, Enchytraeidae and Lumbricidae were used. The species identified only to family or genus level as "sp." were included, too. Species found in only one lake were omitted.

Results

Species composition

A total of 46 oligochaete taxa were found, 32 of them identified to species level (Table 2). Naididae was the most diverse group (with 19 taxa); the other taxa belonged to Pristinidae (2), Enchytraeidae (6), Tubificidae (10), Lumbriculidae (8) and Lumbricidae (1).

Numerous juvenile specimens of Enchytraeidae and Tubificidae (with hair chaetae) were found but remained unidentified due to the absence of genital organs. The majority of oligochaete species were cosmopolitan or widely distributed. There were 33 oligochaete taxa in the PU lakes, and 32 taxa in the SPU lakes, but similarity of their oligochaete fauna was low, the Sørensen index of similarity being only 0.36 between the all lakes of Polar and Subpolar Urals. The total number of species per lake was low, between 5 and 16 in PU and between 1 and 13 in SPU.

The greatest species number in both groups of lakes belonged to Naididae (17 species in PU and 11 in SPU). The number of Naididae species per lake varied from 1 (mostly in SPU lakes) to 8 (e.g., in the lakes of Gnet-ty and Koma-ty—PU, and Bol'shoe Balban-ty—SPU). *Chaetogaster diaphanus*, *Nais pseudobtusa*, *N. barbata* and *N. communis* were the most frequent species in PU, *N. variabilis* and *Uncinais uncinata* in SPU.

Enchytraeidae (5 taxa) and Lumbriculidae (6 taxa) were most diverse in the SPU lakes. The genus *Cernosvitoviella* was the most frequently encountered enchytraeid taxon in SPU lakes while *Cognettia glandulosa* and *Mesenchytraeus armatus* were found in PU lakes.

Only 10 taxa of Tubificidae were found in the Ural lakes, 1–5 species per lake. No tubificids were found in the samples of SPU lakes Bol'shoe Balban-ty and Trubka (Kozim River basin) and Lake № 1-K (Kos`u River basin). *Spirosperma ferox* was the most common tubificid in both PU and SPU lakes.

The Pielou index varied in different lakes (Table 3). In some lakes of Subpolar Ural (Maloe Shuch`e, Usva-ty, Plaun-ty, Bezymyannoe-U) and Polar Ural (Losinoe, Verkhnee Balban-ty, Patok) the evenness of community was greater. The index of domination "d" indicated that oligochaete communities had one or two dominants and a large number of subdominants. In these lakes the share of dominating species varied from 20 to 35 % in oligochaete abundance, while abundance of the other oligochaete species was more than 50 %. In the lakes with low evenness of community, Lake № 1-B.U. and Chan-ty in the SPU lake group, and Lake № 1-K, Lake № 2-K, and Maloe Balban-ty in the PU lake group, the share of the dominating species varied from 50 to 80 % from the abundance of all oligochaetes.

TABLE 2. List of oligochaete taxa found in the Polar and Subpolar Ural Mountain lakes under study (taxonomy follows Timm 2009).

Species	Polar Ural lakes (n = 10) Average abundance in all lakes (min – max, ind. m^{-2})	Numbers of the lakes (from Table 1) where the species were found	Subpolar Ural lakes (n = 15) Average abundance in all lakes (min – max, ind. m^{-2})	Numbers of the lakes (from Table 1) where the species were found
Naididae				
Chaetogaster diaphanus (Gruithuisen, 1828)	64.6 (0.0 – 456.0)	2, 6, 7, 8	13.1 (0.0 – 166.8)	11, 16, 23
Ch. diastrophus (Gruithuisen, 1828)	14.5 (0.0 – 75.1)	4, 6, 7		
Nais alpina Sperber, 1948	2.7 (0.0 – 26.7)	4, 7	1.3 (0.0 – 18.9)	11
N. behningi Michaelsen, 1923			2.1 (0.0 – 31.7)	21
N. communis Piguet, 1906	20.7 (0.0 – 79.6)	1, 3, 4, 5, 6, 7, 10		
N. elinguis Müller, 1774	16.1 (0.0 – 17.3)	7, 9		
N. pseudobtusa Piguet, 1906	66.2 (0.0 – 425.5)	1, 2, 6, 7, 8, 9	37.4 (0.0 – 222.3)	11, 13, 16, 20, 23
N. variabilis Piguet, 1906	25.3 (0.0 – 194.3)	1, 2, 5, 6	39.8 (0.0 – 360.8)	11, 15, 20, 21, 23
N. pardalis Piguet, 1906	22.1 (0.0 – 176.6)	1, 2, 3, 9	0.7 (0.0 – 11.1)	25
N. barbata Müller, 1774	121.2 (0.0 – 549.5)	3, 6, 7, 9		
N. bretscheri Michaelsen, 1899			0.4 (0.0 – 5.6)	25
N. simplex Piguet, 1906			22.3 (0.0 – 258.3)	11, 19, 21, 25
Nais sp.	8.6 (0.0 – 70.3)	4,		
Specaria josinae (Vejdovský, 1884)	2.7 (0.0 – 30.0)	1		
Piguetiella blanci Piguet, 1906	0.3 (0.0 – 3.7)	7	0.9 (0.0 – 13.3)	11
Uncinais uncinata (Oersted, 1842)	12.9 (0.0 – 50.1)	2, 7, 8, 9, 10	68.9 (0.0 – 513.8)	11, 12, 15, 20, 25
Vejdovskyella comata (Vejdovský, 1884)	17.9 (0.0 – 114.7)	6, 7	1.8 (0.0 – 26.7)	11
V. macrochaeta (Lastočkin, 1921)	36.4 (0.0 – 400.0)	1		
Slavina appendiculata (Udekem, 1855)	4.0 (0.0 – 400.0)	7		
Pristinidae				
Pristina bilobata (Bretscher, 1903)	0.6 (0.0 – 6.7)	5		
Pristina sp.			0.9 (0.0 – 13.3)	12
Enchytraeidae				
Cognettia glandulosa (Michaelsen, 1888)	12.9 (0.0 – 101.0)	8, 9, 10	15.1 (0.0 – 111.0)	15, 19, 23
Mesenchytraeus armatus (Levinsen, 1884)	13.2 (0.0 – 103.6)	6, 7	2.7 (0.0 – 40.0)	14
Cernosvitoviella sp.			91.8 (0.0 – 680.0)	14, 15, 23

Species	Polar Ural lakes (n = 10)		Subpolar Ural lakes (n = 15)	
	Average abundance in all lakes (min – max, ind. m^{-2})	Numbers of the lakes (from Table 1) where the species were found	Average abundance in all lakes (min – max, ind. m^{-2})	Numbers of the lakes (from Table 1) where the species were found
Fridericia sp. 1			0.7 (0.0 – 11.1)	23
Fridericia sp. 2			4.4 (0.0 – 66.6)	23
Enchytraeidae gen. spp.	104.8 (0.0 – 313.4)	1, 2, 3, 4, 5, 6, 7	119.0 (0.0 – 614.0)	11, 12, 13, 17, 18, 19, 20, 21
Tubificidae				
Aulodrilus sp.	0.3 (0.0 – 3.7)	8		
A. limnobius Bretscher, 1899			0.7 (0.0 – 11.1)	23
A. pluriseta (Piguet, 1906)			0.9 (0.0 – 13.3)	20
Rhyacodrilus coccineus (Vejdovský, 1875)	0.3 (0.0 – 3.7)	6	10.8 (0.0 – 134.1)	15, 25
Limnodrilus sp.	1.2 (0.0 – 13.3)	6		
Alexandrovia ringulata (Sokolskaja, 1961)	0.6 (0.0 – 3.7)	7		
Spirosperma ferox Eisen, 1879	116.3 (0.0 – 311.8)	1, 2, 4, 6, 7, 8, 9, 10	132.7 (0.0 – 632.8)	11, 12, 15, 16, 20, 21, 22, 23, 24, 25
Lophochaeta ignota Štolc, 1886	2.5 (0.0 – 13.3)	1, 6, 7	30.9 (0.0 – 360.0)	11, 18, 19, 21
Tubifex tubifex (Müller, 1774)	63.4 (0.0 – 485.6)	2, 3, 7	31.5 (0.0 – 213.7)	11, 12, 16, 20, 21, 22, 24
Tubificidae gen. sp. juv. with hair chaetae	68.6 (0.0 – 241.6)	1, 2, 4, 5, 6, 7, 9	4.5 (0.0 – 55.3)	15, 20
Lumbriculidae				
Rhynchelmis sp. (*limosella*?)			0.3 (0.0 – 3.7)	21
Lumbriculus variegatus (Müller, 1774)	9.5 (0.0 – 52.9)	1, 2, 5, 6, 7, 8	15.6 (0.0 – 93.3)	11, 12, 15, 17, 22, 25
Tatriella slovenica Hrabě, 1939			20.6 (0.0 – 160.0)	14, 15
Stylodrilus heringianus Claparède, 1862			2.3 (0.0 – 34.4)	20
Lumbriculus sp.	11.5 (0.0 – 126.1)	9	3.3 (0.0 – 22.3)	19, 20, 25
? *Lamprodrilus* sp.	5.7 (0.0 – 63.5)	2		
? *Stylodrilus* sp.			4.2 (0.0 – 64.6)	18
Lumbricidae				
Eiseniella tetraedra (Savigny, 1826)			0.7 (0.0 – 11.1)	23

TABLE 3. The average abundance (N, ind. m^{-2}) and biomass (B, mg.m^{-2}) of oligochaetes, Pielou Index (E), dominant species (d>10).

Nº	Lake	N	B	E	Dominant species
1	Lake Nº 1-B.U.	851.0	367.7	0.52	*S. ferox* *V. macrochaeta*
2	Bol'shoe Kuz-ty	786.3	480.9	0.68	*S. ferox* *Ch. diaphanus*
3	Chan-ty	645.6	179.4	0.51	*T. tubifex*
4	Maloe Shuch`e	918.0	122.9	0.82	*S. ferox*
5	Usva-ty	143.7	111.5	0.89	*N. variabilis*
6	Gnet-ty	2973.8	386.4	0.80	*Ch. diaphanus*
7	Koma-ty	2113.9	508.0	0.74	*N. pseudobtusa* *N. barbata*
8	Plaun-ty	394.7	234.4	0.9	*S. ferox* *N. elinguis*
9	Bezymyannoe-U	1052.8	321.7	0.89	*S. ferox* *N. pardalis*
10	Protochnoe	144.3	79.9	0.68	*S. ferox*
11	Bol'shoe Balban-ty	2581.7	735.6	0.79	*N. simplex* *N. variabilis*
12	Maloe Balban-ty	1242.5	909.5	0.54	*S. ferox*
13	Verkhnee Balban-ty	120.0	12.0	0.91	*N. pseudobtusa*
14	Trubka	1080.0	340.0	0.59	*Cernosvitoviella* sp. *Tatriella* sp.
15	Padezha-ty	2509.8	1245.2	0.78	*S. ferox* *Cernosvitoviella* sp.
16	Forel`noe	486.8	176.7	0.83	*Ch. diaphanus* *N. pseudobtusa* *S. ferox*
17	Lake Nº 1-K	181.5	65.8	0.50	*L. variegatus*
18	Lake Nº 2-K	476.5	111.4	0.32	*L. variegatus*
19	Lake Nº 3-K	772.0	248.4	0.81	*L. ignotus*
20	Nom-ty	1281.4	368.3	0.76	*N. elinguis* *U. uncinata* *T. tubifex* *S. heringianus*
21	Patok	214.1	115.3	0.87	*P. hammoniensis* *S. ferox*
22	Losinoe	600.0	1120.0	0.92	*T. tubifex* *L. variegatus*
23	Lake Nº 1-V	3391.5	595.0	0.84	*N. pseudobtusa* *C. glandulosa* *Cernosvitoviella* sp. *Fridericia* sp. *S. ferox*
24	Lake Nº 2-V	2776.0	1526.0	0.65	*S. ferox* *T. tubifex*
25	Mezhgornoe	2342.1	2295.2	0.83	*S. ferox*

Average abundance and biomass of oligochaetes

Zoobenthos of the studied lakes consisted of 28 higher taxa of invertebrates, with 14–21 in each lake. The most widespread of these were Chironomidae, oligochaetes, Mollusca, Nematoda, Cladocera, Copepoda, Ostracoda, Hydracarina and Trichoptera. The total abundance of zoobenthos usually varied between 3,000–5,000 ind.m^{-2}, rarely over 10,000 ind.m^{-2}, and was lowest at the highest elevations. Biomass was low (1–5 g.m^{-2}).

Oligochaetes represented an important component of the zoobenthos, both in average abundance (11.1 and 16.5 % in the PU and SPU lakes respectively) and average biomass (12.5 and 21.9 %). However, this percentage varied in the individual lakes. In the PU lakes oligochaetes represented 0.6–58.9 % of abundance and 0.6–99.6 % of biomass. Their contribution to the benthic fauna in SPU lakes was 0.8–61.7 % of abundance and from 0.1–95.8 % of biomass. Their highest percentages were recorded in Lake Padezha-ty (SPU), with prevailing mud bottom. The average abundance and biomass of oligochaetes were both somewhat higher in the PU than in the SPU lakes (Table 4).

TABLE 4. Average abundance and biomass of oligochaetes in the samples from Polar (n=39) and Subpolar Ural Mountain lakes (n=49).

	Polar Urals		Subpolar Urals	
	ind.m^{-2}	mg.m^{-2}	ind.m^{-2}	mg.m^{-2}
average	1229.4	701.0	1059.3	490.8
± m	247.9	306.7	224.1	126.6

Proportional abundance of the separate families differed somewhat between regions (Table 5). In PU lakes the Naididae was the most abundant family, forming 53.7 % of all oligochaetes (from 23.1% in Lake Bol'shoe Kuz-ty to 60.2 % in the Lake № 1-B.U.). Among them, *Chaetogaster diaphanus, Nais barbata* and, less frequently, *N. pseudobtusa* were most abundant in the PU lakes, while *Uncinais uncinata* and *N. variabilis* were the most abundant species in the SPU lakes.

TABLE 5. Average abundance of different families of oligochaetes in the samples from Polar (n=39) and Subpolar Ural lakes (n=49).

	Polar Urals			Subpolar Urals		
	ind.m^{-2}	%	n	ind.m^{-2}	%	n
Naididae	495.3	53.7	17	186.3	26.0	10
Pristinidae	1.0	0.1	1	0.8	0.1	1
Enchytraeidae	137.3	14.9	3	253. 5	35.4	6
Tubificidae	258.6	28.0	8	230.7	32.2	7
Lumbriculidae	30.4	3.3	4	44.7	6.2	6
Lumbricidae				0.2	0.03	1

On the contrary, Tubificidae and Enchytraeidae were numerically dominant in the SPU lakes (more than 60 % of all oligochaetes). Enchytraeidae were dominant in some lakes (e.g. 93.3 % in the Lake № 2-V). The maximum share of Tubificidae in the abundance (60.8 % of all oligochaetes) was registered in Lake Maloe Balban-ty (the Kozhim River basin). In both PU and SPU lakes, *Spirosperma ferox* was the dominant tubificid. *Tubifex tubifex* and *Lophochaeta ignota* were abundant in SPU lakes only. Enchytraeidae were represented in most lakes mainly by immature individuals (more than 50 %) forming an important part of the oligochaete community. In some lakes juveniles of the genus *Cernosvitoviella* were the dominant taxa. Among Lumbriculidae, *Lumbriculus variegatus* was most abundant in both PU and SPU lakes. *Tatriella slovenica* was found in the SPU lakes only.
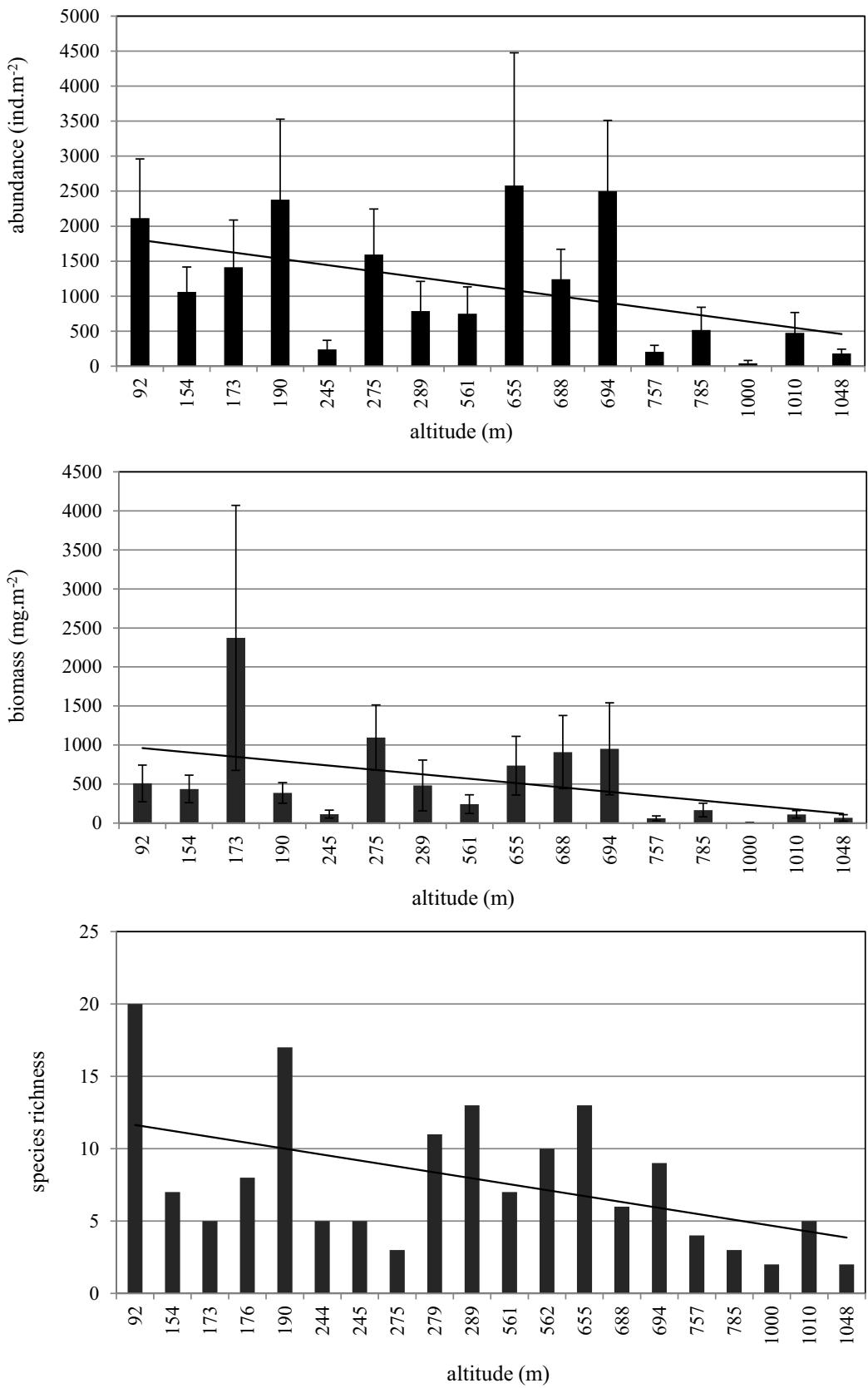
FIGURE 2. Average abundance (top), biomass (middle) and number of oligochaete species (bottom) at different elevations. The lakes located at similar elevations were combined into one group. The mean-square error was calculated from all samples collected from lakes at that elevation. " — " is the linear trend line.

Relationships with environmental variables

Elevation. We found that elevation influences the species composition, average abundance and biomass of oligochaetes in the Urals. All these parameters decrease with elevation (Fig. 2). At the highest elevations, number of oligochaete species was low and structure of communities was distinct. Although Naididae formed more than 50% of the abundance of oligochaetes at elevations up to 300 m a.s.l., this number decreased to less than 20 % in the higher lakes, up to 1000 m a.s.l. in elevation. The share of Tubificidae plus Enchytraeidae at these higher elevations was more than 60 %.

Water depth. Total biomass of zoobenthos and the number of species were significantly lower in mountain lakes where the bottom was formed by boulders, with small amount of mud. Lakes with mud bottoms at depths of 1.5–2.0 m were quantitatively the richest, here the biocenoses were dominated by mollusks and chironomids. The littoral zone in most of the lakes was less productive, yet the zoobenthos was more diverse due to variety of biotopes (e.g. different sediments and the presence of macrophytes). There were usually four dominant invertebrate groups here: mollusks, chironomids, small crustaceans and oligochaetes.

In an earlier investigation of lakes of the Bolshezemelskaya Tundra and foothill area of Urals, we found the most diverse and abundant oligochaete community in the littoral zone, at 0–3 m depth (Baturina & Loskutova 2010). In the present study we compared the distribution of oligochaetes at depths 0–3 m and 3–7 m in the Polar and Subpolar Urals (Figs 3 and 4).
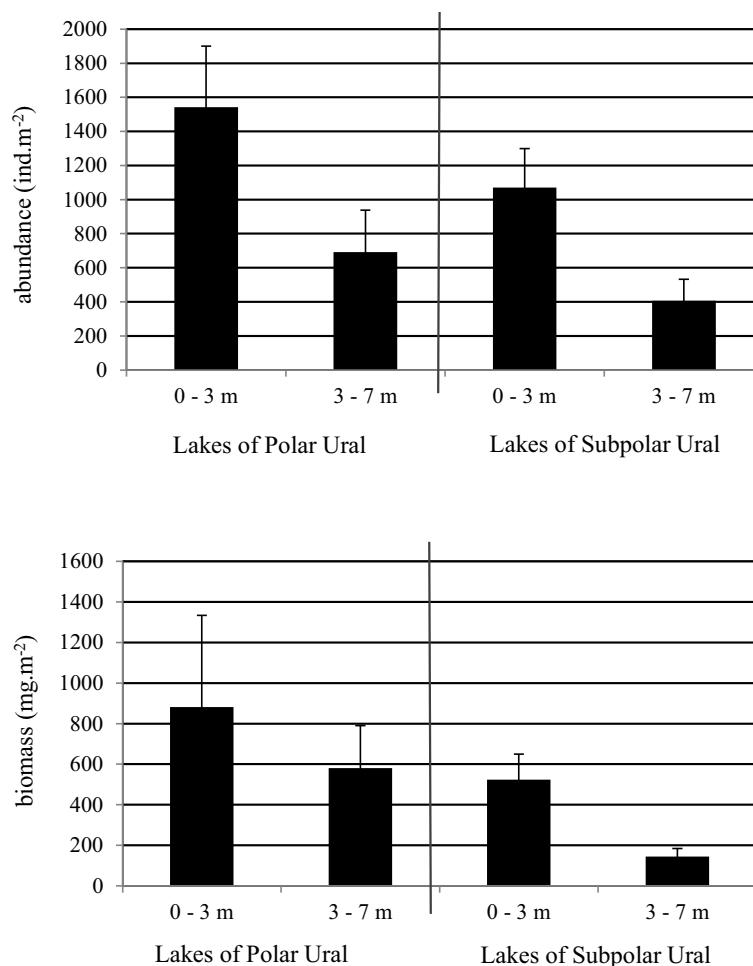

FIGURE 3. Average abundance (top) and biomass (bottom) of oligochaetes in the shallower (0–3 m) and deeper (3–7 m) zone of the Polar Ural and Subpolar Ural lakes.

The abundance and biomass of oligochaetes were also higher in the shallower zone of the lakes and decreased with increasing depth (Fig. 3). In the PU lakes, Naididae (mainly *Chaetogaster diaphanus, Nais barbata* and *N. pseudobtusa*) were abundant, representing more than 50 % of oligochaetes in the shallow zone (Fig. 4). The average abundance of oligochaetes decreased in the deeper zone where Tubificidae dominated (*Spirosperma ferox, Tubifex tubifex, Lophochaeta ignota* and unidentified immature Tubificidae, altogether 75 %).

In SPU lakes, the oligochaete fauna at the depths of 0–3 m consisted mainly of Enchytraeidae (37.0 % of abundance), Naididae (30.3%) and Tubificidae (25.4%) (Fig. 4). Among the Enchytraeidae, juveniles and the genus *Cernosvitoviella* dominated. *Nais variabilis* and *U. uncinata* were the most abundant naidids in the littoral zone of SPU lakes. As in the PU lakes, tubificids became dominant in the deeper zone (more than 80% of average abundance). *Spirosperma ferox* was the most common tubificid present, while *L. ignota* was nearly as common.
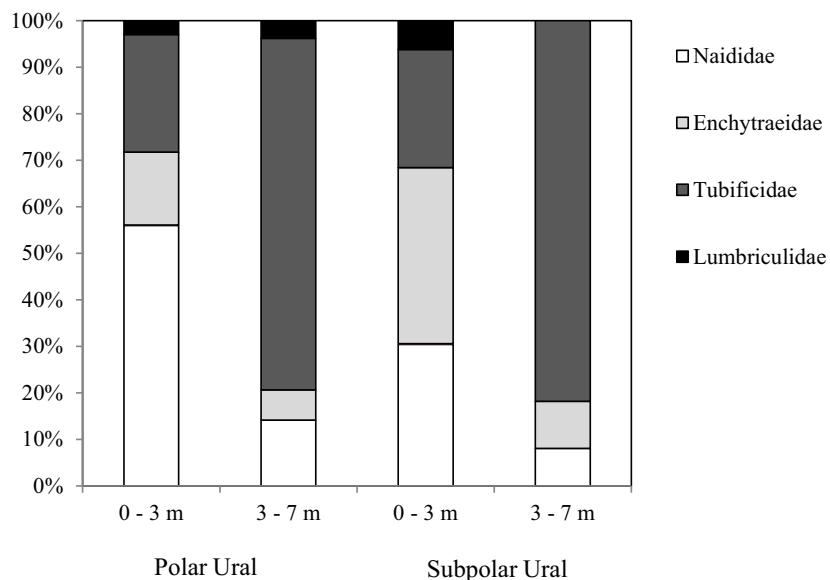
FIGURE 4. Proportional contribution of families to oligochaete abundance in the shallower (0–3 m) and deeper (3–7 m) zone of the Polar Ural (left) and Subpolar Ural lakes (right).

Bottom sediments. The most of studied lakes have soft sediments (mud (silt), and sand) in the deeper zones, but different sediment types in the littoral: either soft or hard (boulders, pebbles and gravel, often covered with algae, moss or silt).

In PU lakes the abundance and biomass of oligochaetes reached their maximum on hard substrata (stones and gravel) (Fig. 5A). Oligochaetes formed here 0.7–50 % of abundance and 0.1–64 % of biomass of the zoobenthos. Naididae, comprising up to 50 % of the total oligochaete abundance (Fig. 5B), were represented by 11 species (57 % of the fauna), of which *Chaetogaster diaphanus* and *Nais barbata* dominated. Enchytraeidae and Tubificidae (mainly *S. ferox* and *T. tubifex*) comprised on average 44% of oligochaete abundance on hard substrata. Mud bottoms both in littoral and deep-water zones were dominated by Tubificidae (62.5% of abundance; *S. ferox* forming more than 40 %). On the sandy bottom in the littoral, *N. barbata* prevailed among the Naididae.

In SPU lakes, average abundance of oligochaetes was similar on all bottom types, while biomass was highest on sand. The faunal composition of oligochaetes differed among the different sediment types (Fig. 5). On hard bottoms in the littoral, Enchytaeidae (mainly immatures and *Cernosvitoviella*) dominated the abundance (39.4%). Naididae (mainly *N. pseudobtusa* and *N. variabilis*) and Tubificidae (mainly *S. ferox*) were similarly abundant (respectively 26.7 and 26.8 %). On the mud bottom, generally in deeper water, Naididae and Tubificidae formed 81 % of total abundance of oligochaetes; with *S. ferox, T. tubifex, N. variabilis* and *U. uncinata* dominating. In contrast to PU lakes, Tubificidae (*S. ferox* and *L. ignota*) were important (more than 60% of the abundance of oligochaetes) on the sand bottom of littoral zone in SPU lakes.

Canonical Correspondence Analysis. For ordination plot of species (Fig. 6A), lakes (Fig. 6B) and environmental factors the eigenvalue for the first axis was 0.248, the second 0.156 and the third 0.134. The percent variance in species–environment relations was 18.3 for the first axis, 11.5 for the second and 9.9 for the third axis. For the ordination plot of species (Fig. 7A) and lakes (Fig. 7B) and geographical factors the eigenvalue for the first axis was 0.208, the second 0.160 and the third 0.009. The percent variance in species–environment relations was 15.3 for the first axis, 11.8 for the second and 6.8 for the third axis. The statistical significance of the relationships between all species, parameters and all variables was tested by a Monte Carlo permutation test.
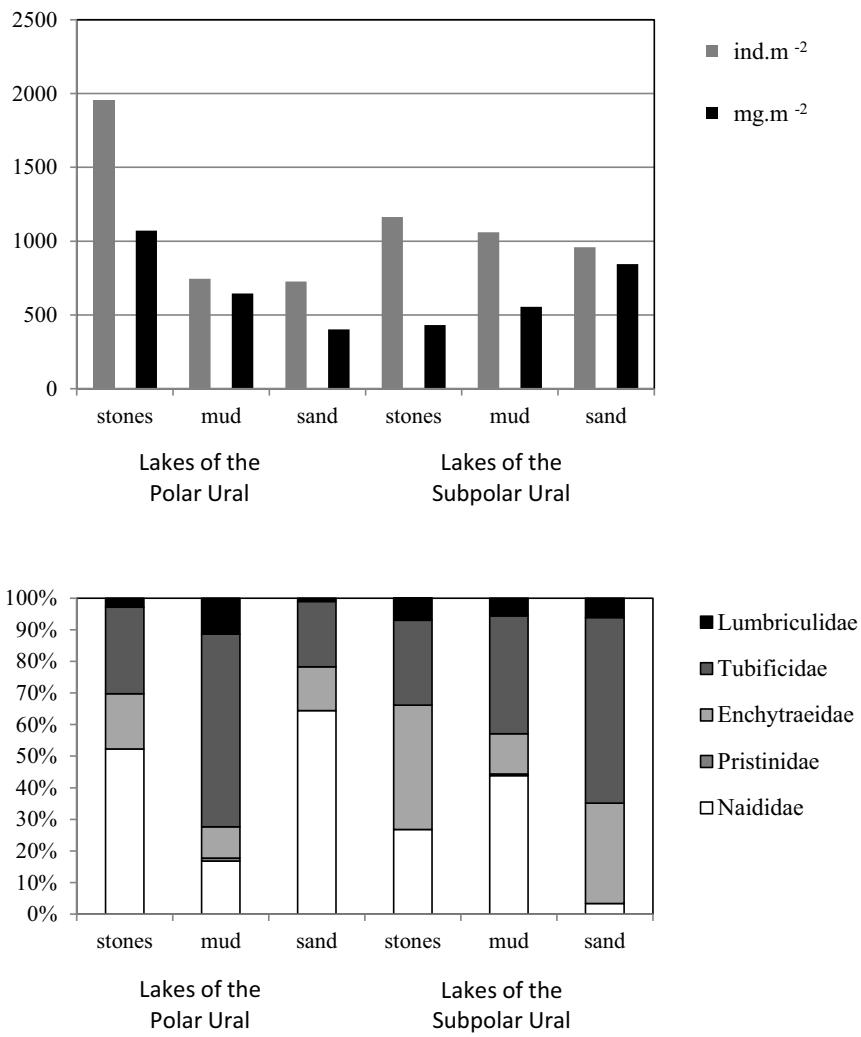
FIGURE 5. Average abundance and biomass of oligochaetes on the different bottom sediments (top) and proportional contribution of families to oligochaete abundance on the different bottom sediments (bottom).

Classification of the environmental conditions in the lakes showed that axis 1 is associated with detritus, substratum and silt (negatively) and macrophytes, moss, algae, sampling depth and maximum depth (positively). The following factors were correlated with axis 2: negatively with detritus, sampling depth and algae, and positively with substrate, macrophytes, moss and maximum depth. A group of lakes (10, 22, 24, 25; 12, 15, 23; 2, 8, 9; 14) was negatively correlated with the axis 1 in CCA (Fig. 6A). These lakes are characterized by hard bottom (boulders) with detritus or silt. The other groups of lakes (Pr. 3, 16, 17, 21; 13; 4, 11, 20 and Pr. 6, 7, 16) had positive relationships with this axis. In these lakes the bottom was often covered either with soft sediments (silt or sand) or boulders with algae or moss. Also, in these lakes the average depths were similar. As for the taxa, biomass, abundance and species number of oligochaetes, the environmental variables on plot (Fig. 6B) showed several groups. Some species (*Cognettia glandulosa, Lumbriculus variegatus, Spirosperma ferox, Nais pardalis, Cernosvitoviella* sp., *Tatriella slovenica* and Lumbriculidae spp.), as well as the biomass of all oligochaetes had negative relationship with axis 1. *Cernosvitoviella* sp. and *Tatriella slovenica* plotted in the upper left in Fig. 6B (negative correlation with axis 1 and positive with axis 2) revealed high abundance on the boulders in Lake Trubka (14). The distribution of the other species can be explained by the presence or absence detritus (negative correlation with axis 1 and axis 2). The lower right part of Fig. 6B unites the species depending on presence or absence of algae in the shallow zone of lakes. The groups of species and abundance of Tubificidae, Enchytraeidae, the number of species of Tubificidae, Lumbriculidae and Enchytraeidae on the upper right of Fig. 6B indicate that their distribution is probably influenced by the depth, as well as by presence of moss or macrophytes in the shallow zone of lakes.
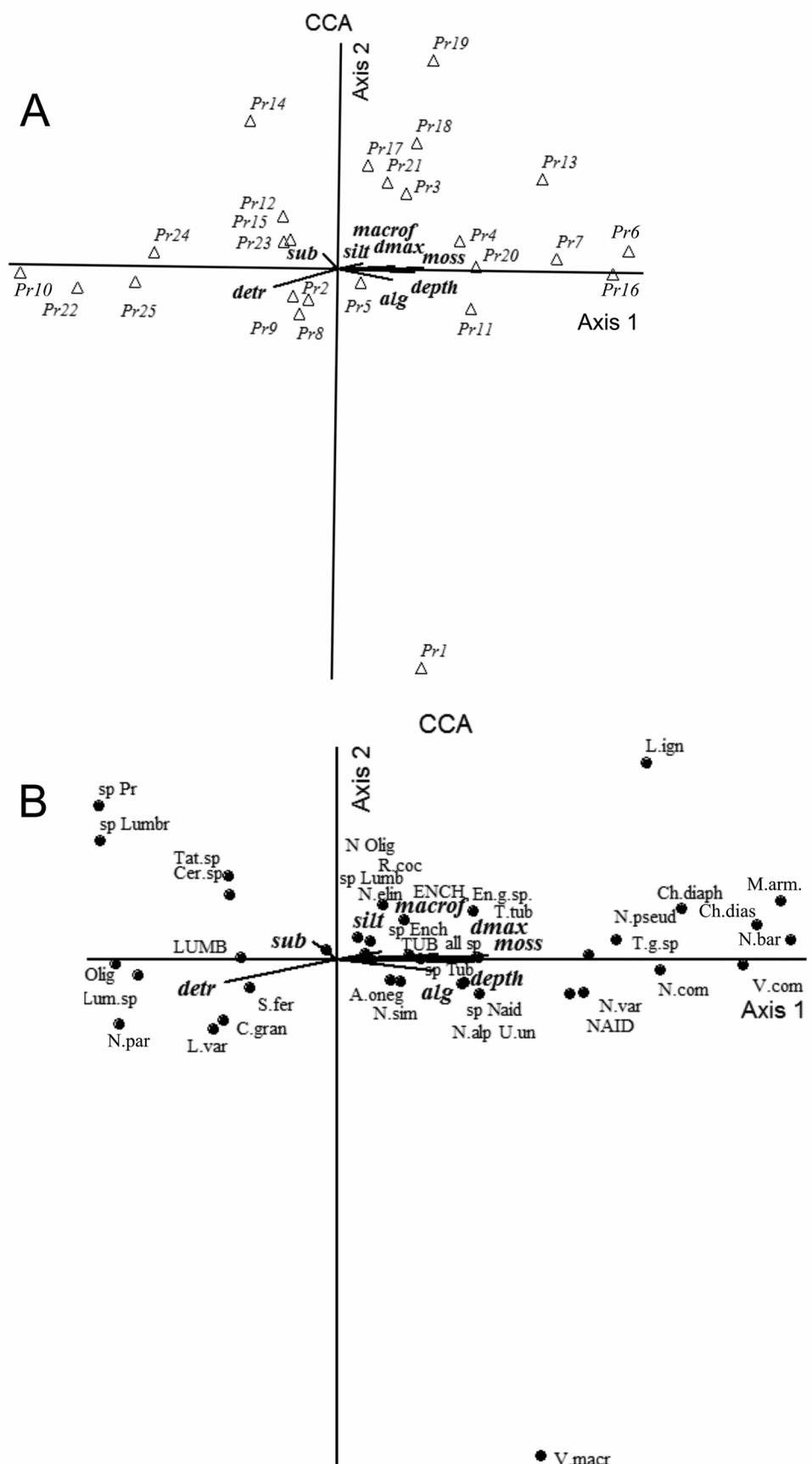
FIGURE 6. CCA diagrams of axes 1 and 2 of the lakes (A), species (B), and environmental factors. Pr. 1–25 are identical with Lakes 1–25 in Table 1. For abbreviations of species see Table 6.
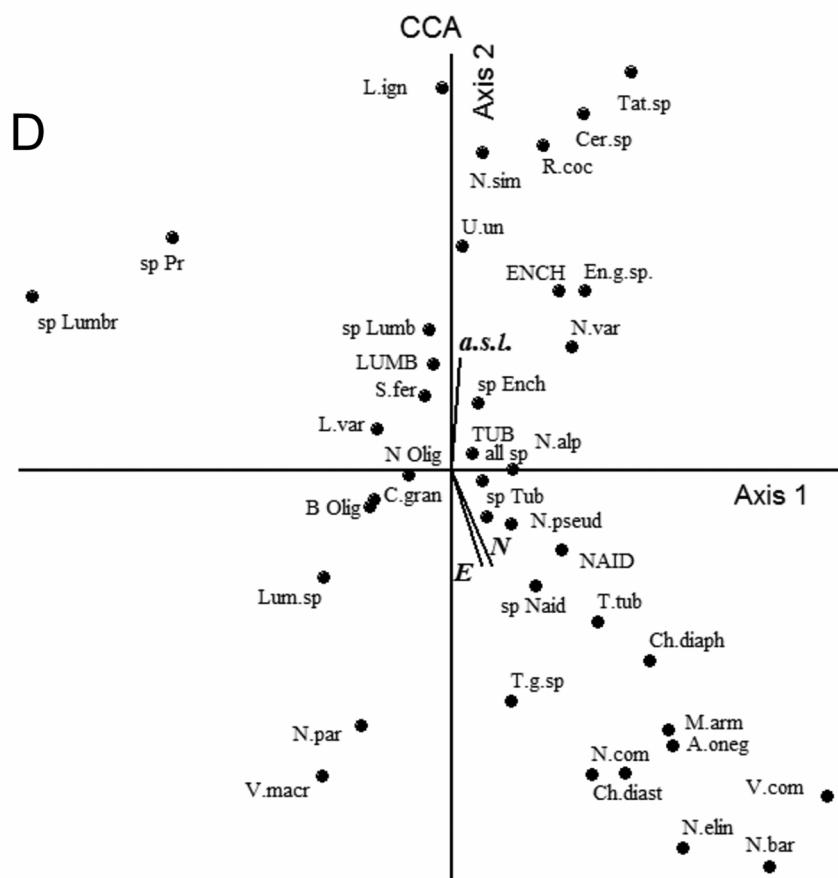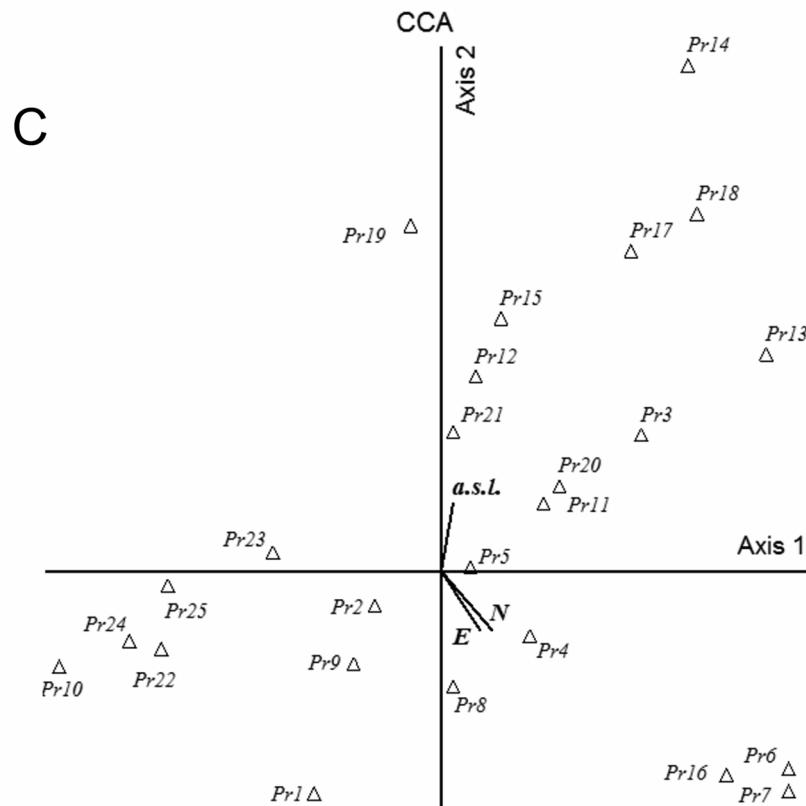
FIGURE 7. CCA diagrams of axes 1 and 2 of the lakes (C), species (D) and geographical coordinates. Pr. 1–25 are identical with Lakes 1–25 in Table 1. For abbreviations of species see Table 6.

The geographical factors were found to be statistically significant: the latitude (N), longitude (E), and elevation above sea level (a.s.l.). CCA indicated a positive relationship between all factors and the axis 1; a negative for the latitude and longitude, and a positive for a.s.l. with axis 2. In the upper right quadrant (Fig. 7A) are the lakes (7, 8, 11, 12, 13, 14) revealing high positive correlation with both axis 1 and 2. Some of these lakes are placed high in the mountains. The lakes 16, 6, 7 (low right quadrant in Fig. 7A) had a negative relationship with axis 1 and positive with axis 2. Among them, the PU lakes Gnet-ty (6) and Koma-ty (7) had very similar coordinates: N 68°08', E 65°21', and N 67°58', E 65°34', respectively. The Lake Forel`noe having negative correlation with a.s.l. CCA showed a negative correlation with both axis 1 and 2 for group of lakes 1, 2, 9, 10 (PU) and lakes 22, 24 (SPU). The elevation of each of these lakes is less than 300 m a.s.l. As for the abundance of oligochaetes and biomass, abundance and number of species, the geographic coordinate variables on plot (Fig. 7B) showed several groups, too. The distribution of *L. ignota, Cernosvitoviella* sp., *T. slovenica, N. alpina, N. simplex, N. variabilis, U. uncinata* and *R. coccineus* can be explained by the a.s.l. Other species (the lower right quadrant) and the species number of Naididae and Tubificidae, as well as the abundance of Naididae probably depend on the latitude (N) and longitude (E). The third group (lower left in Fig. 7B) was composed of species present in the lower elevation PU and SPU lakes.

TABLE 6. Abbreviations associated with Fig. 6, 7 (Canonical Correspondence Analyses in the Lakes 1–25)

Variable	Abbreviation
Coordinates: latitude	N
longitude	E
elevation, m	a.s.l.
substratum type	sub
silt (presence/ absence)	silt
detritus (presence/ absence)	detr
moss (presence/ absence)	moss
algae (presence/ absence)	alg
macrophytes (presence/ absence)	macrof
depth (average), m	depth
depth (maximum), m	dmax
biomass of oligochaetes	B Olig
Chaetogaster diaphanus	Ch. diap
C. diastrophus	Ch. dias
Nais alpina	N. alp
N. communis	N. com
N. elinguis	N. elin
N. pseudobtusa	N. pseud
N. variabilis	N. var
N. pardalis	N. par
N. barbata	N. bar
Vejdovskyella comata	V. com
abundance of Naididae	NAID
Enchytraeidae gen. spp.	Ench gen
Cognettia glandulosa	C. gran
Mesenchytraeus armatus	Mes. arm
Cernosvitoviella sp.	Cer. sp
abundance of Enchytraeidae	ENCH
number of species Enchytraeidae	sp ENCH
Spirosperma ferox	S. fer
Lophochaeta ignota	L. ign
Rhyacodrilus coccineus	R. coc
Lumbriculus variegatus	L. var
Tatriella slovenica	Tat. sl
abundance of Lumbriculidae	LUMB
number of species Lumbriculidae	sp LUMB

Discussion

Some authors (Lencioni et al. 2004) have observed that literature on the oligochaete fauna of high mountain habitats is scarce. There exist data on streams and lakes in the Scandinavian Mountains (Piguet 1919 a, b); Swiss Alps (Malard et al. 2001); Italian Alps (Dumnicka & Boggero 2007); Carpathians (Hrabě 1939; Dumnicka 1976, 2000); Pyrénées (Juget & Giani 1974); Šar Planina massif (Živić et al. 2010) and Balkan Range (Uzunov & Varadinova 2000) on the Balkan Peninsula; and Eastern Black Sea Mountains in Turkey (Yıldız et al. 2012).

Many authors have regarded elevation as the most important factor influencing the distribution of oligochaetes in the remote alpine lakes across Europe (Dumnicka & Galas 2002; Kownacki et al. 2006; Schenková et al. 2001 and others). A significant correlation was also found between their abundance and the elevation in Turkish lakes (Yıldız et al. 2012). Our study identified several factors (latitude and longitude, elevation, depth, presence of algae or moss) being in significant correlation with the distribution of oligochaetes. In the lakes of Ural situated at up to 500 m a.s.l. (mainly PU lakes), the dominant group by average abundance included Naididae (*Nais barbata, N. pseudobtusa, Chaetogaster diaphanus*, and others), Enchytraeidae (Enchytraeidae gen. sp.) and Tubificidae (*Spirosperma ferox*). In the higher elevation lakes (mainly in SPU), a community comprised less the dominating Naididae (*Uncinais uncinata, N. pseudobtusa*) but more Enchytraeidae (*Cernosvitoviella* sp., Enchytraeidae gen. spp.), Tubificidae (*Spirosperma ferox*) and Lumbriculidae.

The oligochaete fauna found in the Ural lakes, with a high number of species, particularly in the family Naididae, is distinguished from that of the other, previously studied European high-mountain lakes that are less diverse, and lower numbers of naidid taxa. Most naidid species are grazers, positively correlated with periphyton (Schenková & Helešic 2006); thus abundance of the Naididae depends on the amount of periphyton. The algae may be particularly lush and productive during the long polar days, supporting summer development of naidids. The number of species and abundance of Naididae decreased considerably in the higher elevation lakes, up to 1000 m a.s.l., suggesting that a complete bottom freezing also may limit the number of naidids because their hibernating individuals and cocoons are sensitive to long-term freezing (Dumnicka & Galas 2002).

The littoral zone of most PU lakes was characterized by variable bottom types (frequently with moss or algal cover) and macrophytes. These conditions support the development of Naididae, particularly *Chaetogaster diaphanus, Nais pseudobtusa* and *N. barbata*, which have been found elsewhere in North Europe in similar habitats. The results from CCA showed that distribution of these species, as well as general abundance of Naididae was related to elevation, algae, moss and latitude. In the more stony, shallow littoral areas of the SPU lakes, *N. variabilis* prevailed. However, on the mud bottom in deeper water, *N. variabilis* was also dominant, together with *Uncinais uncinata*. Dominance of *N. variabilis* has been also shown in other high-mountain lakes of Europe (Piguet 1919; Hrabě 1939; Dumnicka & Boggero 2007).

Enchytraeidae was the most frequently encountered family in the European alpine water bodies. In particular, the genus *Cernosvitoviella* has been found both in mountain streams and standing waters; some authors have described increasing abundance of *Cernosvitoviella* with increasing elevation (Giani 1979; Dumnicka & Galas 2002; Dumnicka & Boggiero 2007).On the contrary, this genus was not found in the high-mountain lakes of East Siberia studied by Kaygorodova et al. (2012). In our investigation, *Cernosvitoviella* was the most frequently encountered genus of Enchytraeidae in the SPU but not in the PU lakes. Abundance of *Cernosvitoviella* sp. as well as the species number of Enchytraeidae depends on several parameters of environment (for example, substratum and elevation).

Some authors relate the distribution of Tubificidae to their preference for substrata with high organic content and fine particle size (Schenková et al. 2001). Among tubificids, *Spirosperma ferox* prevailed both in PU and SPU lakes, mainly on soft bottom. This species, as well as other tubificids, have been recorded as most abundant in sediment with medium silt content in Germany (Sauter & Güde 1996), but other authors have described *S. ferox* as an opportunistic species in high mountain ecosystems, having wide adaptive abilities (Dumnicka & Galas 2002). The distribution of *S. ferox* has been positively correlated with elevation and negatively with water depth and dissolved oxygen in Turkish alpine lakes (Yıldız et al. 2012). According to our data, abundance of *S. ferox* was positively associated with elevation and presence of detritus, and negatively responded to presence of moss and algae. The tubificids *S. ferox, Tubifex tubifex* and *Lophochaeta ignota* prevailed in different biotopes, especially in the SPU lakes. These species are represented in all studied mountain massifs of Europe.

Lumbriculidae is a thermophobe family of the northern temperate zone (Timm 1980; Popchenko 1988). *Lumbriculus variegatus* has been found as negatively correlated with temperature and positively with water depth in Turkish lakes (Yıldız et al. 2012). In our study, *L. variegatus* as well as the species number of Lumbriculidae were negatively correlated with some unknown environmental factors. Another lumbriculid, *Tatriella slovenica*, was positively correlated with elevation. *T. slovenica* is known in Europe from a few localities and in small number only (Dumnicka & Galas 2002).

Acknowledgements

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