

HELMINTH COMMUNITIES OF *COREGONUS LAVARETUS* (SALMONIDAE: COREGONINAE) FROM LAKE KAMENNOYE (KOSTOMUKSHA STATE NATURE RESERVE, RUSSIA)

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Macroecological models are useful for assessing trends in variability for developing monitoring strategies of successional changes and anthropogenic transformation of aquatic ecosystems. Modelling of the relationships of the generalised population indices also makes possible to reveal qualitative differences in the structure of parasite component communities. We analysed helminth communities of *Coregonus lavaretus* from a natural water body, Lake Kamennoye (Kostomuksha State Nature Reserve, Russia). The component community of metazoan parasites of *C. lavaretus* was represented by nine helminth species. Infection with cestodes (two species), nematodes (three species), and trematodes (one species) reflects the presence of zooplankton, aquatic insects and molluscs in the diet of fish, while infection with trematode larvae (three species) occurs by percutaneous penetration. The complete ITS1-5.8S-ITS2 cluster of the rRNA gene was sequenced in order to identify trematode larvae. Metacercariae of *Diplostomum* sp. LIN 5 were the most abundant among them. Using populational approaches, we described the species richness and the diversity of infra- and component communities of the parasites. We also described the species composition and the structure of the component community, the distribution and the accumulation rate of species richness, and the relationships between the infection intensity and the prevalence. Five species (*Diplostomum* sp. LIN5, *Tylodelphys immer*, *Crepidostomum farionis*, *Proteocephalus longicollis*, and *Raphidascaris acus*) were considered as the core species of the component community, while other helminths were considered as satellite species. We conclude that infra-communities play a key role in the formation of species richness, structure and abundance of the parasitic component community of *C. lavaretus*. Infra-communities in younger age groups of *C. lavaretus* are characterised by the paucity and a relatively high diversity of the species composition of parasites, which is probably a consequence of their diverse diet. In older fish, the species richness of infra-communities increases but the species diversity of the parasites declines, indicating a pronounced dietary specialisation. An analysis of species richness and population characteristics indicates that in Lake Kamennoye, the parasite communities of *C. lavaretus* are fairly stable, which reflects the stability of the entire lake ecosystem.

Key words: abundance, parasites, population, prevalence, species richness, trophic webs, whitefish

Introduction

Lake Kamennoye is situated in the Kostomuksha State Nature Reserve, which is a part of the Green Belt of Fennoscandia stretching along the Russian-Finnish-Norwegian border. Lake Kamennoye, which has preserved its natural state, is considered as a key object in the system of environmental monitoring in the border areas (Ilmast et al., 2014). Many aspects of the aquatic ecosystems of the Kostomuksha State Nature Reserve have been extensively studied, but the composition and the structure of the parasitic communities of the fish are poorly known (Ieshko et al., 1983, 1997, 2015; Barskaya et al., 2008; Nemova et al., 2012; Vysockaya et al., 2015, 2021).

Coregonus lavaretus (Linnaeus, 1758) is one of the most numerous fish species in the Kostomuksha State Nature Reserve. It is represented there by three (lesser sparsely-rakered, blue, and densely-rakered) forms, which differ from each other morphologically and ecologically (Pervozvansky, 1986; Ilmast et al., 2016; Vainikka et al., 2017). *Coregonus lavaretus* harbours a fairly rich parasitic fauna due to the differences in the biotopic distribution, diet and food priorities of its different forms (Ieshko et al., 1983). A study of the composition and structure of parasitic communities in Lake Kamennoye, taking into account their life cycles strategies, offers possibilities of a quantitative assessment of the ecological niche of *C. lavaretus* in an undisturbed water body.

Modelling of the relationships of the generalised population indices is still seldom used for revealing the specificity of relationships between species in the host-parasite system. At the same time, macroecological models such as accumulation curves of species richness of the component communities of parasites, abundance-occupancy relationships (AORs) and abundance-variance relationships (AVRs) are becoming increasingly more popular in ecological studies of both free-living (Hanski, 1982; Hanski & Gyllenberg, 1993; Gaston, 1996; Gaston et al., 2000, 2006; Guégan, 2000; Heino, 2005; Verberk et al., 2010) and parasitic organisms (Poulin, 1998; Morand & Krasnov, 2008; Matthee & Krasnov, 2009; Pérez-del-Olmo et al., 2011). These models have been shown to be suitable not only for individual species but also for communities (Gaston et al., 2006). For instance, the AORs model faithfully reflects the restructuring of parasitic communities under the influence of host introduction (Sarabeev et al., 2018). An analysis of relationships of integrated population indices makes it possible to reveal qualitative changes in the structure of parasite component communities, while AORs and AVRs models can be useful for assessing trends in their variability under conditions of biological invasions and for developing the monitoring strategies of successional changes and anthropogenic transformation of aquatic ecosystems.

In this study we have investigated the composition and the structure of infra- and component communities of metazoan parasites of *C. lavaretus* in Lake Kamennoye in order to model the rate of accumulation of the parasite species richness, to study the dynamics of population indices and the associated variability of prevalence, mean abundance and variance of mean abundance of the parasites in the community. We showed how mathematical models can be applied to quantitative characterisation of parasitological data for the purpose of forecasting and monitoring the ecological conformity of *C. lavaretus* to the environment.

Material and Methods

Lake Kamennoye is located in the Kos-tomuksha State Nature Reserve (North Karelia, 64.466667° N, 30.216667° E). The River Kamennaya flowing out of Lake Kamennoye connects the lakes Lovozero, Kimas and Nyuk and flows into the River Chirka-Kem (Kem River

Basin). The surface area of Lake Kamennoye is 105.5 km²; the water surface area is 95.5 km². The length of Lake Kamennoye is 24.4 km; its maximum width is 12.1 km. Its average depth is 8 m, while the maximum depth is 26 m. The water of Lake Kamennoye has a high natural quality corresponding to the oligohumic oligotrophic type. The fish fauna is represented by 15 species, the most abundant being *Perca fluviatilis* Linnaeus, 1758, *Esox lucius* Linnaeus, 1758, *Coregonus albula* (Linnaeus, 1758), and *C. lavaretus*. In Lake Kamennoye, *C. lavaretus* is mostly represented by the small lesser sparsely-rakered form (Pervozvansky, 1986). The studies were conducted in June 2009 and June 2010. The fish individuals were caught by gill nets with mesh size 40 mm and 50 mm. In total, five gill nets (height 1.8 m, length 30 m, mesh size 40–50 mm) were used under the licences issued by the Karelian branch of the Federal Agency for Fishery of the Russian Federation for research aims (№1814 in 2009, and №1905 in 2010). In total, 32 fish individuals were caught (16 individuals in each year). The age of *C. lavaretus* was determined according to Chugunova (1959) and Pravdin (1966). In 2009, the sample mainly consisted of young individuals (2+ – 3+ years), with only three older individuals (4+ – 6+ years). In 2010, the sample consisted of older individuals (4+ – 10+ years).

A standard parasitological method of necropsy and processing of various parasite groups was conducted according to Bykhovskaya-Pavlovskaya (1985) and Shigin (1986). All fish organs were visually examined for infection, and all found macroparasites were registered. Microscopic examination of organs and tissues for protozoan and myxosporidian invasion was not conducted. The parasites were identified using various keys (Bauer, 1987; Khalil et al., 1994; Moravec, 1994). A taxonomic list of the parasites is given according to the World Register of Marine Species (<http://www.marinespecies.org/>).

The metacercariae of the genera *Tylodelphys* Diesing, 1850 and *Diplostomum* von Nordmann, 1832 were collected for an integrative study (Faltýnková et al., 2014; Pérez-del-Olmo et al., 2014; Locke et al., 2018). Some metacercariae were stained with acetic acid carmine, then mounted in Canadian balsam for morphological investigation (Shigin, 1986). Some other specimens were used for molecular studies. The total genomic DNA was isolated from individual

parasites fixed in 96% ethanol using DNA-Extran kits (Synthol, Moscow) following the manufacturer's instructions. A complete ITS1-5.8S-ITS2 cluster of the rRNA gene was amplified using primers designed by Galazzo et al. (2002): D1F (5'-AGGAA TTCCT GGTAA GTGCA AG-3') and D2R (5'-CGTTA CTGAG GGAAT CCTGG-3'). PCR products were obtained on a BioRad T100 thermocycler (Bio-Rad Laboratories Inc., USA). PCR was carried out in the reaction mixture of 25 µl volume containing 10 ng of total DNA, 75 mM Tris-HCl (pH 8.8), 20 mM (NH₄)₂SO₄, 0.01% Tween 20, 5 mM MgCl₂, 0.25 mM of each dNTPs, 1.5 pmol of each primer, and 0.6-0.7 u of Taq DNA polymerase. Specific PCR conditions were as follows: denaturation at 94°C for 2 min. followed by 35 cycles (94°C for 1 min, 55°C for 1 min., 72°C for 2 min.) and a final extension at 72°C for 10 min.

The amplified products were purified with Omnix Purification Kits («Omnix», St. Petersburg, Russia) following the manufacturer's instructions, sequenced using the same primers of PCR reactions with MegaBACE 1000 DNA Analysis System («Beagle», St. Petersburg, Russia). Consensus sequences were assembled within MEGA v.10 (Kumar et al., 2018) and deposited in GenBank with accession numbers MT951902–MT951907 and MZ262515–MZ262516. The newly obtained and the previously published sequences were aligned with those of closely related species of the Diplostomoidea in GenBank using Clustal W implemented in MEGA v.10 (Kumar et al., 2018). The alignment was trimmed to the 984 bp length. *Posthodiplostomum centrarchi* (Hoffman, 1958) and *Parastrigea diodavena* Dubois & Macko, 1972 were selected as the outgroup as members of the same superfamily Diplostomoidea Poirier, 1886.

The general time-reversible model GTR+G was estimated as the best nucleotide substitution model for the dataset using the jModelTest v.1.1 (Posada, 2008). A phylogeny was reconstructed with Maximum Likelihood using MEGA v.10 and with Bayesian Inference using MrBayes 3.2 (Ronquist & Huelsenbeck, 2003; Kumar et al., 2018). Branch support was estimated by bootstrap analyses with 1000 replicates, and BI was conducted with 1 000 000 generations. The tree was visualised in FigTree v.1.4 software (Rambaut, 2016).

In accordance with the established approaches to the description of parasitic commu-

nities (Bush & Holmes, 1986; Holmes & Price, 1986), we used the concepts of the infra-community (all parasites in a host individual) and the component community (all infra-communities in the host population). Prevalence and generalised abundance indices were used as integral characteristics of the communities. Prevalence (P) was the proportion of fish individuals in a sample infected with a given parasite species, while the arithmetic mean (M) and standard deviation (S) characterised the magnitude and the variability of the infection intensity of the host, that is, the number of individuals of a parasite species in the sample, with uninfected fish individuals also taken into account. The parasites composing the component community in the studied fish population were divided into two groups with the help of the infra-community clustering using *k*-mean clustering. Logarithmically transformed values of species abundance were used as the baseline data. The first group consisted of frequently occurring core species, while the second group consisted of sporadically occurring satellite species (Hanski, 1982).

Species richness was described by accumulation curves $s = an^b$, in which parameter «a» predicts the average number of species in the infra-community of parasites of the first fish individual studied, and parameter «b» characterises the growth rate of the number of parasite species «s» with the increasing number of fish individuals examined «n» (Ieshko et al., 2019). The dependence of prevalence, P, and dispersion $D = S^2$ on mean abundance of parasites (M) was described with the help of models $P = aM^b$ (Morand & Krasnov, 2008) and $D = aM^b$ (Taylor, 1961). The linear growth rates measured by parameter «b» were compared by taking the logarithms of the baseline values and using the free term «a» as a constant. The variation ranges of the parameters were estimated by a simple nonparametric bootstrap test with the number of iterations $B = 1000$. Confidence intervals were determined by the percentile method. The indices were compared with the help of Monte Carlo Randomization (MCR) with the same number of iterations B. The significance of differences (*p*) in this approach is the adjusted proportion of null-model combinations (empirical difference not greater than the randomised one, $|d_{obs}| \leq |d_{ran}|$) from the total number of iterations B. The distribution of parasites across hosts was compared using the Kolmogorov-Smirnov formula with

the null-model $\lambda_{\text{obs}} \leq \lambda_{\text{ran}}$. The standard value of $\alpha = 0.05$ was taken as the critical value for p (Shitikov & Rosenberg, 2013). The data were processed in MS Excel, PAST 4.06 (Hammer et al., 2001), and R 4.0.1 (R Core Team, 2020) using basic functions.

Results

The component community of metazoan parasites of *Coregonus lavaretus* from Lake Kamennoye consisted of nine helminth species of different systematic groups (Table 1). The class Cestoda was represented by two species: *Triephanophorus crassus* Forel, 1868 and *Proteocephalus longicollis* (Zeder, 1800) Benedict, 1900. The class Enoplea was represented by three species: *Pseudocapillaria* (*Ichthyocapillaria*) *salvelini* (Polyanski, 1952) Moravec, 1982, *Raphidascaris* (*Raphidascaris*) *acus* (Bloch, 1779) Railliet & Henry, 1915, and *Camallanus lacustris* (Zoega in Müller, 1776) Railliet & Henry, 1915. The class Trematoda was represented by four species: *Crepidostomum farionis* (Muller, 1780) Lühe, 1909, *Diplostomum spathaceum* (Rudolphi, 1819) Olsson, 1876, *Diplostomum* sp. LIN 5 of Blasco-Costa et al. (2014), and *Tylodelphys immer* Dubois, 1961.

Diplostomid metacercariae found in the retina of the *C. lavaretus* belonged to *Diplostomum* sp. LIN 5 described by Blasco-Costa et al. (2014) and by Faltýnková et al. (2014) from salmonid fish in Iceland (Fig. 1). Metacercariae from the eye lens morphologically and molecularly matched *D. spathaceum* (Fig. 1). Based on the nuclear DNA sequences, metacercariae of the genus *Tylodelphys* found in the vitreous humour were closest to *T. immer* described from North America (Locke et al., 2018; Achatz et al., 2022) (Fig. 1). The p -distance difference between *T. immer* specimens from Canada and Karelia was 0.2% (the level of intraspecific divergence), whereas the p -distance difference between *T. immer* specimens and specimens of congeneric species ranged from 2% to 5%. The low differentiation of sequences probably reflects variability of the interpopulation level, and besides, the nuclear genome sequences of the ITS1-5.8S-ITS2 cluster of the rRNA gene are always more variable than mitochondrial gene sequences (Locke et al., 2018). Since in Canada the salmonid fish *Salvelinus fontinalis* (Mitchill, 1814) is also an intermediate host of *T. immer*, it is possible that the diplostomid

could disperse together with the freshwater pearl mussel *Margaritifera margaritifera* (Linnaeus, 1758) (Vikhrev et al., 2022). Vikhrev et al. (2022) reconstructed the post-glacial expansion routes of *M. margaritifera* based on FST genetic distances and the fact that the distribution of *M. margaritifera* is directly associated with the salmonid expansion (Vikhrev et al., 2022). They also documented that freshwater-pearl-mussel populations from North America and North-eastern Europe were the closest groups, judging by FST distances, supporting the opinion that the Barents Sea and White Sea basins were colonised by the North Atlantic form of *Salmo salar* Linnaeus, 1758.

Prevalence and generalised indices of the parasite abundance in two samples of the *Coregonus lavaretus* surveyed in two subsequent years were calculated (Table 1). The population indices of most of the helminth species (frequency distribution, prevalence, mean abundance and its variance) in the studied samples of *C. lavaretus* did not differ significantly (Table 1, MCR-test: $p > 0.094$). For three species (the nematode *R. acus* and trematodes *C. farionis* and *Tylodelphys immer*), the values of frequency distribution, prevalence, mean abundance and its variance were significantly higher in 2010 (MCR-test: $p < 0.033$). Based on the results of the analysis of the structure of infra-communities by k -mean clustering, five species were considered as the core species of the component community: *Diplostomum* sp. LIN5, *T. immer*, *C. farionis*, *P. longicollis*, and *R. acus*. Other helminth species were considered as satellite species.

Species accumulation curves modelling of the increase in species richness of the component parasite communities in the studied *C. lavaretus* samples demonstrated differences with the increasing number of individuals examined (Table 2, Fig. 2). The expected number of parasite species forming the infra-community of the first *C. lavaretus* individual in the sample of 2010 (coefficient a) was statistically significantly higher, and the rate of species accumulation (coefficient b) was lower than in *C. lavaretus* in 2009 (Table 2, MCR-test: $p < 0.001$). The exclusion of the three older *C. lavaretus* individuals (4+ and 6+) from the 2009 sample enhanced the differences between the years but did not lead to any considerable changes in the parameters of the model (MCR-test: $p > 0.097$).

Table 1. Parasites of *Coregonus lavaretus* from Lake Kamennoye: species composition, abundance, prevalence, and structure of component communities

Parasite species	2009 (2+ – 6+, n = 16)				2010 (4+ – 10+, n = 16)			
	max	P, %	M, ind.	S, ind.	max	P, %	M, ind.	S, ind.
Number of parasite species per fish specimen								
Total	5	100	2.49	1.79	7	100	2.88	1.31
Number of parasite individuals per fish specimen								
<i>Pseudocapillaria (Ichthyocapillaria) salvelini</i> (Polyanski, 1952) Moravec, 1982	–	–	–	–	4	25.0 6.3–50.0	0.25 0.06–0.50	0.45 0.25–0.52
<i>Raphidascaris (Raphidascaris) acus</i> (Bloch, 1779) Railliet & Henry, 1915, l.	2	12.5 0.0–30.1	0.19 0.00–0.50	0.54 0.00–0.82	9	56.3 31.3–81.3	2.94 0.94–5.38	4.73 1.50–6.66
<i>Camallanus lacustris</i> (Zoega in Müller, 1776) Railliet & Henry, 1915	–	–	–	–	1	6.3 0.00–18.8	0.06 0.00–0.16	0.25 0.00–0.40
<i>Proteocephalus longicollis</i> (Zeder, 1800) Benedict, 1900	9	56.3 31.3–81.3	2.56 0.63–4.88	4.86 0.89–6.87	12	75.0 50.0–93.8	2.13 1.00–0.50	3.14 1.02–4.92
<i>Triaenophorus crassus</i> Forel, 1868, pl.	3	18.8 0.00–37.5	0.19 0.00–0.38	0.40 0.00–0.50	1	6.3 0.00–18.8	0.06 0.00–0.19	0.25 0.00–0.40
<i>Crepidostomum farionis</i> (Muller, 1780) Lühe, 1909	4	25.0 6.3–43.9	1.38 0.06–3.56	4.00 0.25–6.42	11	68.8 50.0–93.8	6.19 3.00–9.56	7.30 5.31–9.06
<i>Diplostomum spathaceum</i> (Rudolphi, 1819) Olsson, 1876, mtc.	5	31.3 12.5–56.3	0.88 0.13–1.94	1.93 0.34–2.84	4	25.0 6.3–43.8	0.44 0.06–1.00	1.03 0.25–1.59
<i>Diplostomum</i> sp. LIN5 (Blasco-Costa et al., 2014), mtc.	14	87.5 68.8–100.0	11.75 7.44–17.13	9.67 5.24–0.50	13	81.3 62.5–100.0	7.50 4.00–10.69	6.49 4.40–9.06
<i>Tylodelphys immer</i> Dubois, 1961, mtc.	6	37.5 12.5–62.5	0.50 0.19–0.88	0.73 0.40–0.91	14	87.5 68.8–100.0	6.31 3.50–10.06	7.19 2.24–10.42

Note: n – sample size (number of fish examined), max – maximum number of parasite individuals per fish; the minimum number is zero everywhere, P – prevalence (proportion of infected fish individuals), M – mean number of parasite individuals per fish, S – standard deviation; confidence intervals for the parameters constructed by bootstrapping; l – larva; pl – plerocercoid; mtc – metacercaria.

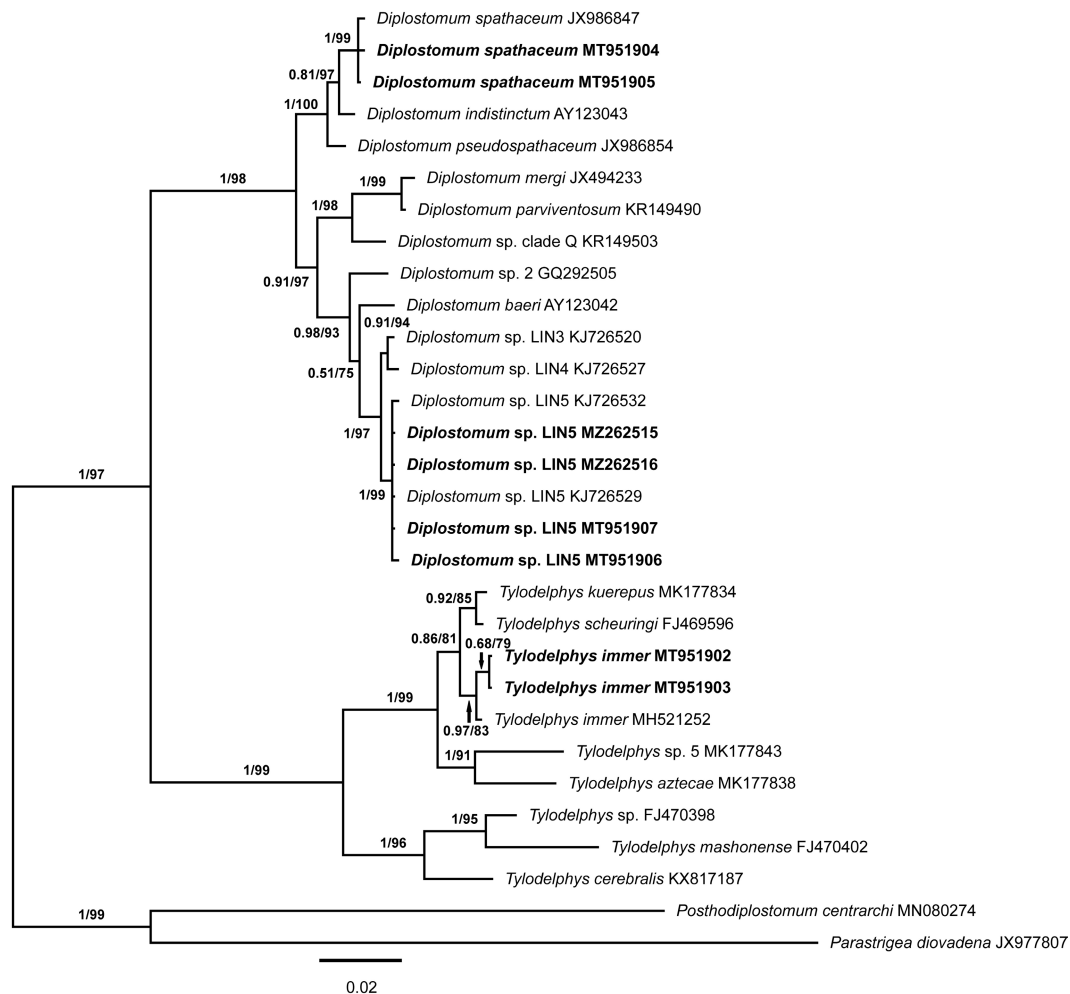


Fig. 1. Phylogenetic position of diplostomid species from the eyes of *Coregonus lavaretus* in Lake Kamennoye based on the analysis of ITS1+5.8S+ITS2 partial gene sequences performed with the use of Maximum Likelihood and Bayesian Inference algorithms. Numbers at nodes indicate Bayesian posterior probabilities / bootstrap values (only values > 0.5/50 are shown). New sequences are in bold.

Table 2. Parameters of regression model $s = an^b$ for accumulation of parasite species in *Coregonus lavaretus* from Lake Kamennoye in various years

Parameters	Value	<i>t</i>	<i>p</i>	<i>R</i> ²	<i>lim</i>
2009 (2+ – 6+), <i>n</i> = 16					
<i>a</i>	3.59	82.94	< 0.001	0.680	3.47–3.71
<i>b</i>	0.27	49.96	< 0.001		0.26–0.30
2009 (2+ – 3+), <i>n</i> = 13					
<i>a</i>	3.50	74.07	< 0.001	0.680	3.37–3.73
<i>b</i>	0.30	45.41	< 0.001		0.28–0.33
2010 (4+ – 10+), <i>n</i> = 16					
<i>a</i>	4.78	101.94	< 0.001	0.690	4.64–5.05
<i>b</i>	0.23	53.06	< 0.001		0.22–0.25

Note: *n* – number of examined fishes, *t* – Student’s test value of difference of coefficients from zero, *p* – significance level of *t*; *R*² – coefficient of determination; *lim* – confidence intervals of the coefficients.

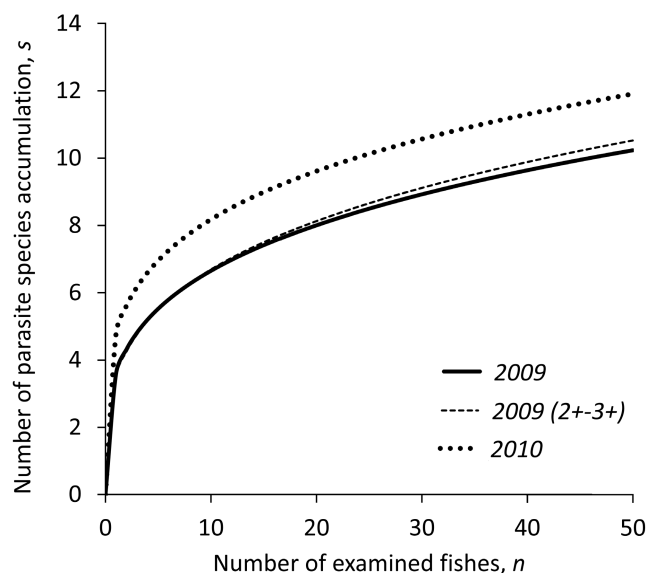


Fig 2. Accumulation curves of parasite species in *Coregonus lavaretus* from Lake Kamennoye sampled in various years. The parameters of the models and their statistical significance are given in Table 2.

The parameters of the models describing the relationship between the mean abundance and other population indices (Fig. 3) indicate a higher linear growth rate for prevalence and a lower one for variance of abundance in 2010 (Table 3), but the observed differences were not statistically significant (MCR-test: $p > 0.230$). A greater variation in the model growth rate (coefficient *a*) in 2009 was not associated with the age differences in the fish since the exclusion of older individuals did not lead to any significant reduction of the variability.

Discussion

The influence of biotic and abiotic factors on the circulation of parasites in terrestrial and

aquatic communities has been demonstrated in numerous publications (e.g. Dobson & May, 1987; Marcogliese & Cone, 1997; Lafferty et al., 2006). The composition and structure of parasite communities formed in a water body depend on the diversity of hosts and the general organisation of the ecosystem. The transmission success of the parasites in populations is determined, first of all, by their incorporation in the existing trophic chains and the specificity of their interactions with the host populations. Host specificity allows a more rational use of resources, reducing pressure on host populations and competitive tension between the parasites. A stable equilibrium between populations in the host-parasite system is established at a certain level of aggregation in the distribution of parasite individuals. Studies of fish parasites of protected water bodies allow us to assess the impact of a new long-term factor such as anthropogenic pollution, eutrophication, and commercial fishing which may shift this balance to a new level (e.g. Allan et al., 2003; Keesing et al., 2006; Sonnenholzner et al., 2011).

The component community of parasites of *Coregonus lavaretus* in Lake Kamennoye is represented by species typical for oligotrophic water bodies (Anikieva et al., 1983). The helminths found in our study are common across the range of *C. lavaretus*. They belong to various faunal complexes and differ in the degree of their specificity. The nematode *P. salvelini*, the cestodes *P. longicollis* and *T. crassus*, and the trematode *C. farionis* parasitise in a broad range of salmonids. Like their hosts, these helminths are adapted to the life in oligotrophic water bodies with low temperatures and limited diversi-

ty of plankton and benthos. The nematodes *R. acus* and *C. lacustris* and the metacercariae of trematodes from the genera *Diplostomum* and *Tylodelphys* occur in various hosts from various

taxonomic and ecological groups, and are eurythermal and eurybiontic (Anikieva et al., 1983; Pugachev, 2003; Barskaya et al., 2008; Anikieva & Ieshko, 2019).

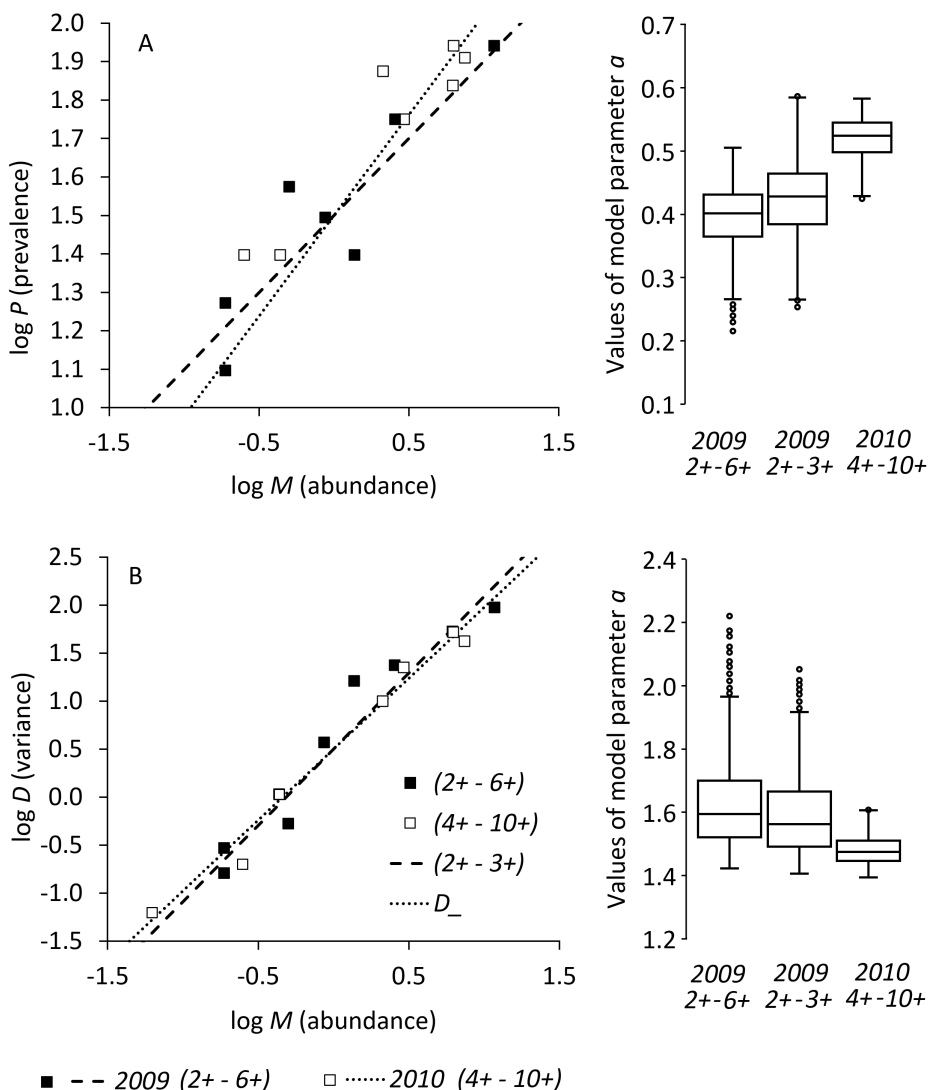


Fig 3. Models of relationships between mean abundance and prevalence (A) and variance of abundance (B) of parasites of *Coregonus lavaretus* from Lake Kamennoye in various years. The parameters of the models and their statistical significance are given in Table 3.

Table 3. Rates of linear growth of prevalence and abundance variance with the increasing mean abundance of parasites: regression model parameters

Samples	<i>a</i>	<i>t</i>	<i>p</i>	<i>R</i> ²	<i>lim a</i>
Prevalence, $\log P = a \cdot \log M + 1.5$					
2009 (2+ - 6+), <i>n</i> = 16	0.40	5.36	0.002	0.830	0.22–0.50
2009 (2+ - 3+), <i>n</i> = 13	0.43	4.37	0.004	0.809	0.25–0.59
2010 (4+ - 10+), <i>n</i> = 16	0.52	10.43	< 0.001	0.936	0.42–0.58
Variance, $\log D = a \cdot \log M + 0.5$					
2009 (2+ - 6+), <i>n</i> = 16	1.59	8.81	< 0.001	0.931	1.42–2.22
2009 (2+ - 3+), <i>n</i> = 13	1.55	10.43	< 0.001	0.950	1.41–2.05
2010 (4+ - 10+), <i>n</i> = 16	1.48	24.44	< 0.001	0.987	1.39–1.62

Note: *n* – number of examined fishes, *P* – prevalence, *M* – mean and *D* – variance of the number of parasite individuals per fish, *t* – Student’s test value of coefficient *a* difference from zero, *df* – degrees of freedom, *p* – significance level of *t*; *R*² – coefficient of determination; *lim b* – confidence intervals of coefficient *b*.

The helminths registered in *C. lavaretus* from Lake Kamennoye have a complex life cycle and complex transmission pathways. *Coregonus lavaretus* can serve their intermediate or definitive host. The most common variant of parasite transmission is its integration into the predator-prey relationships. For instance, *C. lavaretus* gets infected with the cestodes *P. longicollis* and *T. crassus* and the nematode *C. lacustris* when feeding on plankton. Intermediate hosts of *P. longicollis* and *T. crassus* are copepod crustaceans such as *Tritia* Risso, 1826, *Mesocyclops* G.O. Sars, 1914, and *Eudiaptomus* Kiefer, 1932 (Kuperman, 1974; Anikieva et al., 1983), while the life cycle of *C. lacustris* involves crustaceans from the order Cyclopoida (Moravec, 1994). Infection of *C. lavaretus* with *R. acus* is apparently associated with benthos feeding, since the paratenic hosts of this nematode are molluscs, oligochaetes, amphipods, water lice and insect larvae developing in water (Moravec, 1994). Feeding on the amphipods *Gammarus pulex* (Linnaeus, 1758) and the larvae of mayflies, *C. lavaretus* becomes the definitive hosts of the trematode *C. farionis* (Moravec, 1982; Soldánová et al., 2017; Petkevičiūtė et al., 2018). The life cycle of the nematode *P. salvelini* has not been elucidated, but is probably similar to that of *P. tomentosa*, whose intermediate hosts are oligochaetes (Moravec, 1994).

Infection with some trematodes is not associated with feeding. Their larvae penetrate the host through the skin. The percutaneous penetration is characteristic of the species *D. spathaceum*, *Diplostomum* sp. LIN5, and *Tylodelphys immer*. In this case, the spatial proximity of *C. lavaretus* and the first intermediate hosts, the gastropods *Ampullaceana balthica* (Linnaeus, 1758), is important for effective transmission (Faltynkova et al., 2014; Soldánová et al., 2017).

The presence of the nematode *P. salvelini* in the infra-communities and a significant increase in the prevalence and abundance of core species, the trematode *C. farionis* and the nematode *R. acus*, indicate an increasing proportion of benthos in the diet of older individuals of *C. lavaretus*. The population characteristics of the third core species, the cestode *P. longicollis*, whose infection is associated with planktonic crustaceans, did not change significantly with the increasing age of *C. lavaretus*. Out of the parasites with percutaneous penetration, the most successful are the trematodes *Diplosto-*

mum sp. LIN5 and *Tylodelphys immer*. The main factor determining the infection intensity of *C. lavaretus* is their association with shallow-water habitats, where snails, the intermediate hosts of trematodes, are abundant.

The curves showing the accumulation of species with the increasing numbers of samples have been studied for parasite communities of various fish species (Walther et al., 1995; Dove & Cribb, 2006; Sarabeev, 2015; Sellers et al., 2015). The parameters of the models are usually regarded as generalised characteristics of the specificity of parasite infra-communities in specific host populations. In our case, infra-communities were poorer and more variable in younger *C. lavaretus* individuals. Only the trematode *Diplostomum* sp. LIN5 and the cestode *P. longicollis* were their relatively constant components. The leading role of the latter is due to the limited diet of young specimens of *C. lavaretus*, which mostly feed on planktonic crustaceans (Pervozvansky, 1986). The variability appears to be associated with the adaptive food-selection behaviour of young fish, which start feeding on larger invertebrates as they grow.

Adults of *C. lavaretus* typically have a mixed diet, where the zooplankton plays a considerable role alongside with benthos. The dominant benthic organisms making up about 50% in the diet of *C. lavaretus* are the larvae of chironomids (*Procladius* spp., *Prodiamesa* spp., *Cryptochironomus* spp., *Pentapedilum* spp.), caddisflies *Neureclipsis* spp., and *Ephemera* spp., as well as the molluscs *Pisidium* spp. Zooplankton is mainly represented by diplostracan crustaceans (*Limnospira frontosa* G.O. Sars, 1862, *Holopedium gibberum* Zaddach, 1855, *Bosmina (Eubosmina) coregoni* Baird, 1857, *Eudiaptomus gracilis gracilis* (Sars G.O., 1863)), and the proportion of copepods (e.g. *Megacyclops viridis viridis* (Jurine, 1820), *Mesocyclops leuckarti leuckarti* (Claus, 1857), *Eucyclops macruroides macruroides* (Lilljeborg, 1901)) is about 10% (Pervozvansky, 1986; Ilmast et al., 2014). Accordingly, the number of core species in the parasite infra-communities of adult *C. lavaretus* increases to five. When the formation of trophic relationships is completed, the infra-communities become relatively stable, so the rate of increase in species richness of the parasitic community in older age groups of *C. lavaretus* is lower than in juveniles. This result supports the idea that the rate of accumulation is determined not by the taxonomic composition

of parasites but by the species richness of infra-communities forming the component community (Dove & Cribb, 2006; Ieshko et al., 2019).

The participation of the parasites with percutaneous penetration in the formation of the helminth community structure seems to be a matter of chance. However, it cannot be ruled out that *C. lavaretus* individuals feeding predominantly on benthic organisms and spending more time near the bottom are more likely to be infected with these parasites than the individuals feeding on plankton.

Macroecological models, AORs and AVR, are used for generalised quantitative description of organism communities. The central paradigm of AOR in parasitology assumes that abundant species occur frequently, while species with low abundance are rare. However, the diversity of relationships in the host-parasite system cannot be meaningfully generalised on such a simplified basis, since the character of parasite distribution across hosts can vary broadly. Only the general principle of spatial structure organisation remains unchanged: in a host population, uninfected and weakly infected individuals constitute most of it, while heavily infected individuals are relatively rare. Therefore, the parasite distribution across hosts in component communities is best described by left-asymmetric curves (Ieshko et al., 2019). The AVR model aims to summarise this specificity of spatial relationships. According to the model, as the mean abundance grows, its variance also grows due to an increasingly uneven distribution of the parasite individuals across hosts. In stable component communities, one would expect a more rapid increase of the prevalence of species and a slower increase of the variance of mean abundance. These trends, revealed for a number of parasitic systems based on the extensive material (Ieshko et al., 2019, 2020), are also manifested to some extent for *C. lavaretus* in Lake Kamennoye: the species richness of parasitic infra-communities is lower in the younger age group of *C. lavaretus*, and under these conditions the prevalence is growing slower, while the variance is growing faster.

Thus, we observed the absence of significant differences between the model parameters considering the transformation of the species composition and changes in the dominance structure in various age groups of the fish. These data and, perhaps, the seasonal component of

the dynamics of the parasite species indicate that the component community of *C. lavaretus* in Lake Kamennoye in general is fairly stable and the host-parasite relationships in this lake are well-established. This balance is likely to change only if a significant transformation of the environmental conditions occurs. Since the new factor must be powerful enough to lead to a significant shift in model parameters, AORs and AVR models can serve as reliable indicators of the macro-ecological state of the ecosystem as a whole.

Conclusions

Our study has demonstrated that the component communities of parasites of *C. lavaretus* in undisturbed northern lakes are unsaturated and consist of species with various prevalence trends. There is no established structure of dominant species. We found that species that have a high prevalence and infection intensity in some years may have very low values of these parameters in other years. The results suggest that helminths of *C. lavaretus* possess all the key attributes of indicator species for the state of protected aquatic communities in the North of Europe: they portray the host's ecological affiliations and represent the diversity of the host's trophic and biotopic relationships with plankton and benthos. Modelling of species accumulation curves is important for assessing the species diversity of parasites as a tool for choosing a sufficient sample size and predicting the species richness. Coefficients of the power-law equations are meaningful measures of the structure and diversity of parasite infra-communities.

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СООБЩЕСТВА ГЕЛЬМИНТОВ *COREGONUS LAVARETUS* (SALMONIDAE: COREGONINAE) В ОЗЕРЕ КАМЕННОЕ (КОСТОМУКШСКИЙ ЗАПОВЕДНИК, РОССИЯ)

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Макроэкологические модели применимы для оценки трендов их изменчивости для разработки стратегии мониторинга сукцессионных изменений и антропогенной трансформации водных экосистем. Моделирование взаимодействия популяционных индексов также делает возможным выявлять качественные различия в структуре компонентных сообществ паразитов. Нами проанализированы сообщества гельминтов *Coregonus lavaretus* из природного водоема, оз. Каменное (Костомукшский заповедник, Россия). Компонентное сообщество многоклеточных паразитов *C. lavaretus* включает девять видов гельминтов. Заражение цестодами (два вида) и нематодами (три вида) отражает наличие зоопланктона и водных насекомых в рационе рыб, в то время как заражение трематодами (четыре вида) происходит перкутанно. Полный кластер ITS1-5.8S-ITS2 гена рРНК был секвенирован для идентификации личинок трематод. Наиболее многочисленным и широко распространенным видом были метацеркарии *Diplostomum* sp. LIN5. Используя популяционный подход, нами определено видовое богатство и разнообразие инфра- и компонентных сообществ паразитов *C. lavaretus* оз. Каменное. Также описаны видовой состав и структура компонентного сообщества паразитов *C. lavaretus* оз. Каменное, распределение и скорость накопления видового богатства, а также взаимосвязь между интенсивностью заражения и распространенностью. Пять видов (*Diplostomum* sp. LIN5, *Tylodelphys immer*, *Crepidostomum farionis*, *Proteocephalus longicollis* и *Raphidascaris acus*) рассматриваются как основные виды компонентного сообщества *C. lavaretus*, а другие виды гельминтов – как виды-сателлиты. Сделан вывод, что инфрасообщества играют ведущую роль в формировании видового богатства, структуры и численности паразитарного компонентного сообщества *C. lavaretus* в оз. Каменное. Показано, что инфрасообщества в младших возрастных группах *C. lavaretus* характеризуются скудностью и относительно высоким разнообразием видового состава паразитов, что, вероятно, является следствием разнообразия их рациона. У рыб старшего возраста видовое богатство инфрасообществ увеличивается, но видовое разнообразие паразитов снижается, что свидетельствует о выраженной диетической специализации *C. lavaretus*. Анализ видового богатства и популяционных характеристик свидетельствует о стабильности сообществ паразитов *C. lavaretus* в оз. Каменном, что указывает на стабильность экосистемы оз. Каменное и территории Костомукшского заповедника в целом.

Ключевые слова: видовое богатство, паразиты, популяция, сиг обыкновенный, трофические сети, численность