Feeding habits shape infection levels by plerocercoids of the tapeworm *Triaenophorus crassus* in muscle of a sympatric pair of whitefish in an oligotrophic lake

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DOI: https://doi.org/10.1017/S0022149X20000991

Key words: coregonids, whitefish parasites, COI gene, *Triaenophorus crassus*

Word count: 3801

Abstract

Teletskoye Lake (West Siberia, Russia) is inhabited by a sympatric pair of whitefish, with each member of the pair being characterized by different feeding habits. *Coregonus lavaretus pidschian* (Gmelin, 1789) is a large "benthivorous" form, while *C. l. pravdinellus* (Dulkeit, 1949) is a small "planktivorous" form. Fish were collected from the end of August to the middle of September in 2017 and 2019 – 2020 in the north part of Lake Teletskoye. For the "benthivorous" form the prevalence, intensity, and abundance of *T. crassus* ranged from 22.4–51.9%, 1.9–2.8, 0.4–1.3, correspondingly, whereas the same indices for the "planktivorous" form ranged from 94.7 to 97.5%, 4.2 – 4.8, and 4.0 – 4.7, correspondingly. The level of prevalence of infection and abundance of *T. crassus* in muscle was relatively stable among studied years for both forms. The level of prevalence was higher in the years 2019 and 2020 than in 2017 for the "benthivorous" form, whereas for the "planktivorous" form this index did not change during the studied years. For the first time, a partial sequencing of the COI gene (593 bp) for *T. crassus* was sequenced. All 15 plerocercoids of *T. crassus* were represented by four haplotypes.

Introduction

Sympatric pairs of whitefish belonging to the *Coregonus lavaretus* complex inhabit many oligotrophic lakes in the Palearctic region of the northern hemisphere. These lacustrine sympatric pairs serve as an intriguing model for investigating different aspects of fish evolutionary biology (e.g., Østbye *et al.,* 2006, Solovyev *et al.,* 2019). Within such pairs, a very important feature is the demonstration of different feeding habits for each within the same lake. The relatively low level of productivity of oligotrophic lakes enforces whitefish to use food items from different taxonomical groups in order to assimilate the available food supply of such lakes efficiently. As a result, it leads to trophic diversification of whitefish into planktivorous "dwarf" and benthivorous "normal" forms that, consequently, decrease the competition for the food resources of the lake (e.g., Bernatchez, 2004).

Teletskoye Lake (West Siberia, Russia) is inhabited by one such sympatric whitefish pair (Bochkarev & Zuikova, 2006). *Coregonus lavaretus pravdinellus* (Dulkeit, 1949) is a small form that may reach only around 17 cm Smith's fork length and 40 g of total body weight in its maximum age (seven years old), while *C. l. pidschian* (Gmelin, 1789) is a larger form (20–25 cm Smith's fork length, 150 g total body weight,at the age of seven years) with age exceeding 14 years (Bochkarev & Zuykova, 2006; Bochkarev, 2009).The first mention of whitefish from Teletskoye Lake can be found in the year 1865, in the article entitled "About herrings from Teletskoye Lake" in the newspaper "The news of Tomsk Province /Tomskie gubernskie novosti/" written by Gulyaev (1865). At the present time, their origin, phylogenetic relationships and taxonomic position are still disputed (Politov, Gordon & Baldina, 2010). According to the analysis of mtDNA they are genetically very closely related to each other and share the same haplotypes (Bochkarev, Zuykova & Katokhin, 2011). Although the purpose of this work is not to rectify taxonomical issues, due to the intricate taxonomical position of these fish, we will consider these fish as ''forms'' and obviate any discussion of subspecies, etc... These two forms will be hereafter referred to as ''benthivorous'' for *C. l. pidschian* and ''planktivorous'' for *C. l. pravdinellus*.

Generally, the occurrence of a parasite species in a host population depends on the host's genetic factors and feeding preferences (Pulkkinen *et al.*, 1999; Francová *et al.*, 2011). It has been shown that parasites provide information on various aspects of their host's biology and can serve as a specific indicator of the host's habitat selection and feeding behavior (Bertrand *et al.*, 2008). Members of the genus *Triaenophorus* are widely distributed in fish in the northern hemisphere (Valtonen *et al.,* 1989). and have a complex life cycle, with two intermediate hosts and one definitive host. It is well known that plerocercoids of this parasite invade the muscle tissue of coregonid and salmonid fishes and negatively affects the growth of this intermediate host (Kuperman, 1981; Schähle *et al.,* 2016). Copepods, as the first intermediate host, are infected by procercoids of *T. crassus* and then transmitted to the second intermediate host (coregonid and salmonid fishes). At the end, pike *Esox* *lucius* feeds on infected fish and the life cycle of *T. crassus* is completed (Kuperman, 1981; Rosen & Dick, 1984; Pulkkinen *et al.,* 1999). In Teletskoye Lake *T. crassus* was found in muscles of both forms of whitefish, as the second intermediate host, and in *E. lucius* as a definitive host (Titova, 1954). From this point of view, the sympatric pair of whitefish in Teletskoye Lake is an applicable model for the estimation of differences in feeding habits via assessment of their parasite community.

We hypothesized that trophic diversification of whitefish into "planktivorous" and "benthivorous" forms is likely to affect the transmission of *T. crassus* via food webs (higher in "planktivorous" form than in "benthivorous" one).

The main aim of the present study was to estimate the relation between different feeding habits of the "benthivorous" and "planktivorous" forms and the infection level of *T. crassus* plerocercoids in their muscles. Additionally, as cestodes are a species-rich taxa and can seriously impact fisheries, aqua- and agriculture, and wildlife conservation, this study includes work to augment existing DNA databases on these species to advance DNA barcode studies. For this, the mitochondrial COI region was amplified for analysis to partially sequence the COI gene of *T. crassus* in order to provide improved resolution to future phylogenetic analyses for this species of cestode.

Materials and methods

Study area and sampling

Fish were collected from the end of August to the middle of September in 2017 and 2019 – 2020 in the north part of Lake Teletskoye (51.79 N; 87.30E). Teletskoye Lake is a large (223 km^2) and deep (maximum 325 m) oligotrophic lake (basin of Ob River) in the Altai Mountains (Altai Republic, Russia). The water temperature of the upper 1 m of the water column ranged from 17.1 to 18.3 ^{o}C. All fish were captured using gill-nets (mesh sizes 18 and 22 mm) at depths from 2 to 15 m and transported to the laboratory in the Teletskoye Lake field station of the Institute of Systematic and Ecology of Animals SB RAS. The fish were anesthetized on ice prior to sacrifice. Afterwards, the fish were identified, measured (Standard length, SL), and weighed (total body weight, BW) with accuracy until 0.1 mm and 0.1 g respectively. In order to analyze the prevalence of infection of *T. crassus* in fish muscle, we collected 67 (SL = 214.5±4.3, BW = 134.8±7.6), 25 (SL = 211.4±3.9, BW = 146.6±8.6), and 54 (SL = 186.4±4.7, BW = 89.0±9.2) individuals of the "benthivorous" form and 38 (SL = 136.4±0.8, BW = 28.2±0.5), 30 (SL = 136.1±1.9, BW = 31.3±1.0), and 33 (SL = 133.1±1.5, BW = 26.8±0.9) individuals of the ''planktivorous'' form in the years 2017, 2019, and 2020 respectively. The fish age was estimated using scales sampled from the left side of the body between the dorsal fin and lateral line (only for 2017 year of sampling, table 2).

The parasitological analysis of fish muscle was performed as described by Schähle *et al*. (2016). The prevalence and mean intensity of parasite infestation were calculated according to the definitions by Bush *et al*. (1997). The prevalence (P) of parasite infestation (in %) was calculated as:

$$P=I*100/N,$$

Where I is number of host infected, and N is total number of host examined. The error of prevalence index (E) was calculated by the following formula:

$$E=\sqrt{[P\times(100-P)/N]},$$

where P is prevalence, and N is total number of host examined.

Mean intensity of invasion (I) was assessed as the average of number of individuals of a particular parasite species (K) in a single infected host (n):

$$I=K/n,$$

Mean abundance of invasion (A) was assessed as the average of number of individuals of a particular parasite species (K) in all studied host (n):

$$A=K/n,$$

Error of intensity and abundance indices (SE) was calculated according to:

$$SE=SD/\sqrt{n},$$

Where SD is standard deviation of row of number of individuals of a particular parasite species in a single infected host, and n is total number of infected hosts (intensity) or all hosts (abundance).

One hundred thirteen individuals of *T. crassus* were mounted in Berlese's medium and used to measure the morphological parameters of the scolex hooks (fig. 1). All measurements of scolex hooks were done as described in Kuchta *et al.* (2007) using an Axiolab microscope (Carl Zeiss, Germany) with software Toup View vx86, 3.7.2608 (ToupTekPhotonics, China). All measurements for scolex hooks are given in micrometres (μm).

All data are presented as a mean ± standard error (SE). To estimate the differences between parasite intensity (only for the "planktivorous" form) and abundance across different age groups (2017) and sampling years (2017 and 2019 – 2020), as well as in terms of fish standard length among different sampling years (2017, 2019, and 2020), the Mann–Whitney test was applied using PAST v. 3.16 (Hammer *et al.*, 2001). In the same program, to explore the correlation between parasite abundance and fish standard length, a Spearman rank correlation test (ρ) was used. The effect of "whitefish form" as a factor on the parasite abundance and intensity was tested using one-way ANOVA at $p \leq 0.05$. The effect of "age" as a factor on the parasite abundance and intensity was tested using one-way ANOVA at $p \leq 0.05$ only for age groups where there were infected individuals.

DNA extraction, amplification and sequencing

Total DNA was extracted from fifteen ethanol preserved individuals of *T. crassus* using the DNA-sorb B kit (Central Research Institute of Epidemiology, Russia) according to the manufacturer's protocol. To obtain a barcode sequence for *T. crassus*, we amplified a 593 bp portion of the mitochondrial cytochrome c oxidase subunit 1 gene (COI). Amplification was performed using the primers and PCR conditions as described in Van Steenkiste *et al*. (2015). The PCR products were purified by adsorption on Agencourt Ampure XP (Beckman Coulter, Indianapolis, IN, USA) columns and subjected to Sanger sequencing using the BigDye Terminator V.3.1 Cycle Sequencing Kit (Applied Biosystems, Waltham, MA, USA) with subsequent unincorporated dye removal by the Sephadex G-50 gel filtration (GE Healthcare, Chicago, IL, USA). The Sanger products were analyzed on an ABI

3130XL Genetic Analyzer (Applied Biosystems). The purification and sequencing of PCR products were performed in the SB RAS Genomics Core Facility (Novosibirsk, Russia). The manual editing and alignment of sequences were performed with MEGA 7 (Kumar, Stecher & Tamura, 2016). The number of haplotypes and levels of DNA polymorphism were calculated using the program DNASP 6 (Rozas *et al.* 2017). Sequences were deposited into GenBank (NCBI) under the following accession numbers: MT951570 – MT951584.

Results

Fish

All results of ANOVA (Mann-Whitney test) comparisons among different years for the "benthivorous" and "planktivorous" forms are given in table 1. The SL and BW of the "benthivorous" form were significantly lower in 2020 (SL = 186.4±4.7, BW = 89.0±9.2) year than in 2017 (SL = 214.5±4.3, BW = 134.8±7.6) and 2019 (SL = 211.4±3.9, BW = 146.6±8.6) years. We have found similar trends for the "planktivorous" form: lower SL and BW in the year 2020 (SL = 133.1±1.5, BW = 26.8±0.9) than in 2017 (SL = 136.4±0.8, BW = 28.2±0.5) and 2019 (SL = 136.1±1.9, BW = 31.3±1.0). Positive significant correlation was found between SL and BW for the "benthivorous" (Spearman ρ = 0.97, p = 6.16×10^{-43}, n = 67, 2017 year; ρ = 0.80, p = 0.0000021, n = 25, 2019 year; ρ = 0.96, p = 2.90×10^{-30}, n = 54, 2020 year) and "planktivorous" (Spearman ρ = 0.77, p = 0.0000013, n = 38, 2017 year; ρ = 0.76, p = 0.0000013, n = 30, 2019 year; ρ = 0.65, p = 0.000037, n = 33, 2020 year) forms for all studied years. Thus, further comparisons between parasitological indices were done with SL only.

Infection rate of T. crassus in muscle of the "planktivorous" and "benthivorous" forms

The relationship between number of cysts and fish SL for the "planktivorous" form is shown in figure 2a. The average of intensity and abundance of parasite infection in fish muscle ranged from 4.2±0.6 to 4.8±0.5 and from 4.0±0.6 to 4.7±0.5, respectively. In the muscle of the ''planktivorous'' forms, the prevalence of *T. crassus* infestation ranged from 94.7±3.6% (2017) and 97.5±2.5% (2019) to

97.0±3.0% (2020) (fig. 2a). A positive correlation was found between SL of the ‘‘planktivorous’’ form and the number of cysts in muscle tissue in 2017 (Spearman ρ = 0.26, p = 0.12, n = 38) and 2019 (Spearman ρ = 0.30, p = 0.11, n = 30), whereas in 2020 the correlation was significantly negative (Spearman ρ = -0.39, p=0.02, n = 33). Fish gender (“sex”) was not a factor affecting the abundance in fish muscle in 2017 and 2019 (ANOVA, F = 1.36, p = 0.26, df = 37, 2017 year and F = 1.52, p = 0.20, df = 30, year 2019).

The relationship between abundance of *T. crassus* in muscle and fish SL for the “benthivorous” form is shown in figure 2b. The average of intensity and abundance of parasite infection in fish muscle ranged from 1.9±0.4 to 2.8±0.3 and from 0.4±0.1 to 1.3±0.3, correspondingly. The prevalence of *T. crassus* infestation ranged from 22.4±5.1 (2017) and 46.7±9.3 (2019) to 51.9±6.8 (2020) (fig. 2b). Negative correlation between SL of the “benthivorous” form and abundance was found in 2017 (Spearman ρ = -0.13, p = 0.29, n = 67), 2019 (Spearman ρ = -0.19, p = 0.38, n = 25), and 2020 (Spearman ρ = -0.44, p=0.0009, n=54). The factor “sex” had no affect on the abundance in fish muscle (ANOVA, F = 0.26, p = 0.44, df = 64, 2017 year).

The abundance of *T. crassus* in muscle of the “planktivorous” form was significantly higher (Mann-Whitney test) than that in the muscle of the “benthivorous” form for all age groups in 2017 year (where these calculations could be performed): age 3+ (U = 3, p = 0.041), age 4+ (U = 5.5, p = 0.0031), and age 5+ (U = 0, p = 0.0015) (table 2). The effect of “whitefish form” as a factor on the level of intensity (ANOVA, F = 5.62, p = 0.022, df = 50, 2017 year; F = 2.36, p = 0.13, df = 40, 2019 year; F = 16.40, p = 0.00015, df = 59, 2020 year) and abundance (ANOVA, F = 56.24, p = 2.33×10^{-11}, df = 104, 2017 year; F = 15.97, p = 0.0002, df = 54, 2019 year; F = 47.78, p = 8.26×10^{-10}, df = 86, 2020 year) of *T. crassus* in muscle was significant.

No significant effects of “age” as a factor on the levels of intensity (only for the “planktivorous” form: ANOVA, F = 1.38, df = 31, p = 0.27) and abundance (ANOVA, F = 1.92, df = 35, p = 0.15 for the “planktivorous” form and ANOVA, F

= 1.20, df = 60, p = 0.32) for both forms were found. But the significant differences (Mann-Whitney test) for level of abundance between ages 6+ and 8+ ($U = 49.5$, $p = 0.042$) for the "benthivorous" form and between ages 4+ and 5+ ($U = 10.5$, $p = 0.031$) for the "planktivorous" form were found (table 2). For the "planktivorous" form the significant difference (Mann-Whitney test) for level of intensity were found only between ages 4+ and 5+ ($U = 10.5$, $p = 0.037$) (table 2), whereas for the "benthivorous" form it was impossible to estimate these differences due to the low number of infected whitefish in most of the age groups.

The level of intensity and abundance of *T. crassus* in muscle was relatively stable among studied years for both forms (fig. 3a). The level of prevalence was higher in the years 2019 and 2020 than in 2017 for the "benthivorous" form, whereas for the "planktivorous" form this index did not change during the studied years (fig. 3b).

Scolex hook measurements and DNA sequencing

Measurements of scolex hooks are summarized in table 3. All scolex hook measurements fit within the ranges described by previous studies. Partial sequences of the mitochondrial COI gene (593 bp) were obtained. Among 15 sequences, four haplotypes with five polymorphic sites were found. The haplotype diversity was 0.467 with variance and standard deviation of 0.02184 and 0.148, correspondingly. Nucleotide diversity was 0.00286.

Discussion

In the present study, we have analyzed the infection level of *T. crassus* in muscle of two sympatric forms of whitefish that inhabit Teletskoye Lake. We have collected fish groups similar in terms of size, as those described in previous studies (Titova, 1954; Bochkarev & Gafina, 1993; Bochkarev & Zuikova, 2006). Apparently, fish with such a range of body weight and standard length represent the dominant cohort of individuals within populations in Teletskoye Lake.

In order to confirm the taxonomic position of *T. crassus* in whitefish in Teletskoye Lake we have conducted a morphological analysis of 113 specimens according to Kuperman (1968, 1973) and Kuchta *et al.* (2007). According to our morphological results, the studied plerocercoids belong to the species *T. crassus*. Moreover, we provide the first data for barcode analysis based on part of the COI mitochondrial gene for this species.

The first mention of *T. crassus* infection of whitefish from Teletskoye Lake was registered in 1954 with the range of prevalence of infection registered as from 20 to 60% (Titova, 1954). Unfortunately, due to that fact that the young "benthivorous" form is morphologically very similar to the "planktivorous" form of the same size, in the afore-mentioned study no information was provided about which form of whitefish exactly was investigated. In a later study it was shown that the levels of *T. crassus* infection for the "benthivorous" form was relatively low (prevalence – 52%, intensity 2.1, and abundance 1.1) compared to the "planktivorous" form (prevalence – 100%, intensity and abundance – 3.9) (Bochkarev & Gafina, 1993).

Parasitological analysis of the ''planktivorous'' form performed during three years in Teletskoye Lake has revealed that the prevalence of *T. crassus* infestation ranged from 94.7% to 97.5%. The average of intensity and abundance of parasite infection was 4.2 – 4.8 and 4.0 – 4.7, correspondingly. We have found a positive significant correlation between standard length of the ''planktivorous'' form of whitefish and number of cysts in its muscle in the years 2017 and 2019, whereas in 2020 the correlation was negative. Similar results were obtained by Schähle *et al.* (2016) when the infection level of *T. crassus* was studied in muscle of whitefish from Lake Achensee (Austria). It could be explained by an accumulation of cysts in fish muscle with age, because it is known that the plerocercoids of *T. crassus* may exist in fish muscle for more than one year. The negative correlation we explain by the generally smaller size of the fish collected in 2020 and the small number of fish with standard length more than 150 mm (only one individual). Parasitological analysis of the "benthivorous" forms observed in the same years has revealed that a significantly lower range of prevalence (22.4–51.9%), intensity (1.9–2.8), and abundance (0.4–1.3) of *T. crassus* infestation compared to the "planktivorous" form. We have found the negative correlations between standard length of the "benthivorous" form and number of cysts in its muscle during sampling years. Such differences in infection level of this fish are explained by the different feeding habits of the studied whitefish forms. Indeed, it has been shown that the ''planktivorous'' form has a narrow trophic specialization and feeds on zooplankton (different copepods and cladoceras) in both summer and winter periods, whereas the diet of the "benthivorous" form is more taxonomically diverse (larvae of insects, mollusks, gammarids, etc.) (for more details see Bochkarev & Zuikova, (2006)). Significantly higher levels of plerocercoid infection in the muscle of the ''planktivorous'' form is explained by a diet heavily biased on zooplankton, at least during periods of high levels of infection within this first intermediate host. Moreover, the ''planktivorous'' form continues to feed on zooplanktonic items during seasons where vegetation persists (from May to October) (Bochkarev & Zuykova, 2006). According to the present study, the plerocercoid of *T. crassus* was found in almost all age groups of the "benthivorous" and "planktovorous" forms. But the relatively low level of plerocercoid infection in the muscle of the "benthivorous" form is explained by a lower level of zooplanktonic organisms in its diet (Bochkarev & Zuykova, 2006). A higher level of diversity of the cladoceran *Eurycercus lamellatus* (14.2%) in the diet of the "benthivorous" form has been documented previously (Bochkarev & Zuykova, 2006). Moreover, the infected cladoceran *E. lamellatus* can also be a potential intermediate host for the *Triaenophorus* parasite. Another possible way for the "benthivorous" fish to be infected by this cestode (for which the first intermediate host is zooplankton) is to consume a reservoir host (e.g. invertebrate benthic organisms). Indeed, many invertebrates may feed on zooplankton organisms thereby becoming reservoir hosts for cestodes. For example, the occurrence of *Proteocephalus* larvae was shown in alder-fly larvae (Megaloptera), which are predators and feed on copepods infected with *Proteocephalus* procercoids (Scholz *et al.*, 1999).

Our findings regarding the relation of trophic specialization and different levels of *T. crassus* infection are also confirmed by a recent study (Pulkkinen *et al.*, 1999; Schähle *et al.*, 2016). It was shown that prevalence of *T. crassus* in whitefish

(*Coregonus lavaretus*) from three different sampled areas in Lake Saimaa (Finland) ranged from 20 to 100%, whereas *T. crassus* were rarely recorded in *C. albula*; only two fish were infected of the 901 studied (Pulkkinen *et al.*, 1999). In another study the infection level of *T. crassus* in *C. lavaretus* from Lake Achensee was 100% and for *C. albula* – less than 16% (Schähle *et al.,* 2016). These differences in prevalence values are also explained by the different habitat and trophic position of the studied fish.

In conclusion, in this study we investigated the relationships between feeding habits and different levels of *T. crassus* infection in sympatric pairs of whitefish from Lake Teletskoye. Our study showed that the trophic specialization of whitefish into "planktivorous" and "benthivorous" forms affected the transmission of *Triaenophorus* parasites through food webs with different levels of infection. Based on the results regarding different infection levels of *T. crassus* in these two forms of whitefish, we can conclude that parasites can be an indicator of trophic niche specialization and reflect changes in habitat selection by fish. Further, as both forms are capable of being infected though at distinctly different levels, this difference may ultimately be a driver of the evolution of *T. crassus*, however confirmation of such nascent speciation will require additional more detailed genetic analyses.

This research was supported by the Russian Foundation for Basic Research (grant number 19-34-60028).

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Figure 1. Measured morphological parameters of the scolex hooks of *T. crassus*.

Figure 2a. Abundance of *T. crassus* in muscle of the "planktivorous" form in Teletskoye Lake in studied years; ▲ – 2017, □ – 2019, ◆ – 2020.

Figure 2b. Abundance of *T. crassus* in muscle of the "benthivorous" form in Teletskoye Lake in studied years; ▲ – 2017, □ – 2019, ◆ – 2020.

Figure 3a. The average levels of intensity (□ - "planktivorous" form; ■ - "benthivorous" form) and prevalence (○ - "planktivorous" form; ● - "benthivorous" form) of *T. crassus* in muscle of both forms in Teletskoye Lake during studied years.

Figure 3b. The average levels of abundance (□ - "planktivorous" form; ■ - "benthivorous" form) of *T. crassus* in muscle of both forms in Teletskoye Lake during studied years.

Table 1. The results of ANOVA and Mann-Whitney test comparisons among different years for the “benthivorous” and “planktivorous” forms.

Tests	Years	Tests	Forms of whitefish	
			Benthivorous	Planktivorous
SL, ANOVA (Mann-Whitney test)	2017 vs. 2019	F / (U)	11.63/731.0	1.70/530.0
		Df.	145	100
		P / (p)	$2.1x10^{-5}$/0.35	0.19/0.63
	2017 vs. 2020	F / (U)	11.63/884.5	1.70/483.0
		Df.	145	100
		P / (p)	$2.1x10^{-5}$/$1.5x10^{-6}$	0.19/0.098
	2019 vs. 2020	F / (U)	11.63/275.5	1.70/441.5
		Df.	145	100
		P / (p)	2.1 $x10^{-5}$/$2.6x10^{-5}$	0.19/0.47
BW, ANOVA (Mann-Whitney test)	2017 vs. 2019	F / (U)	11.22/766.0	7.18/392.0
		Df.	145	100
		P / (p)	3.0 $x10^{-5}$/0.53	0.0012/0.028
	2017 vs. 2020	F / (U)	11.22/878.5	7.18/471.0
		Df.	145	100
		P / (p)	3.0 $x10^{-5}$/1.5 $x10^{-6}$	0.0012/0.073
	2019 vs. 2020	F / (U)	11.22/169.0	7.18/269.0
		Df.	145	100
		P / (p)	$3.0x10^{-5}$/9.9 $x10^{-8}$	0.0012/0.0019

BW – body weight; SL – standard length; F – F values, Df. – degrees of freedom, and p – p values are from ANOVA; (U) – U values and (p) – p values are for pair wise comparisons calculated by Mann-Whitney test from ANOVA.

Table 2. Prevalence, intensity, and abundance of *T. crassus* in muscle of the “benthivorous” and “planktivorous” forms in Teletskoye Lake in 2017.

Age	N	Forms of whitefish										
		Benthivorous					Planktivorous					
		SL (mm)	BW (g)	Prevalence	Intensity	Abundance	N	SL (mm)	BW (g)	Prevalence	Intensity	Abundance
2+	ND	ND	ND	ND	ND	ND	3	129.5±0.5	24.1±1.0	66.7±27.2	2.0±1.0[ab]	1.3±0.9[ab]
3+	3	135.9±3.3	30.6±1.7	33.3±27.2	2.0±0.0	0.7±0.7[ab]	10	132.2±1.1	26.6±0.6	100.0±0.0	11.3±1.1[ab]	4.9±1.1[ab]
4+	5	153.4±5.1	42.1±5.4	20.0±17.9	1.0±0.0	0.2±0.2[ab]	18	137.7±0.5	28.8±0.6	94.4±5.4	3.3±0.7[a]	3.1±0.7[a]
5+	11	188.6±3.8	83.1±5.6	18.2±11.6	1.0±0.0	0.2±0.1[ab]	4	141.9±1.5	30.5±1.1	100.0±0.0	5.5±0.6[b]	5.5±0.6[b]
6+	10	212.0±2.6	118.8±4.4	50.0±15.8	2.4±1.0	1.2±0.6[a]	2	147.5±3.2	34.3±2.4	100.0±0.0	8.5±7.5[ab]	8.5±7.5[ab]
7+	10	220.5±2.4	143.3±5.0	20.0±12.6	3.5±1.5	0.7±0.5[ab]	ND	ND	ND	ND	ND	ND
8+	16	228.5±2.7	156.4±5.6	12.5±8.3	1.5±0.5	0.2±0.1[b]	ND	ND	ND	ND	ND	ND
9+	6	251.2±6.0	194.8±16.8	16.7±15.2	1.0±0.0	0.2±0.2[ab]	ND	ND	ND	ND	ND	ND
10+	4	258.8±5.1	238.3±15.0	0.0±0.0	0.0±0.0	0.0±0.0[nd]	ND	ND	ND	ND	ND	ND
11+	1	273.9±0.0	270.6±0.0	1.0±1.0	1.0±1.0	1.0±1.0[nd]	ND	ND	ND	ND	ND	ND
12+	1	272.0±0.0	301.6±0.0	0.0±0.0	0.0±0.0	0.0±0.0[nd]	ND	ND	ND	ND	ND	ND

ND – no data; N – number of individuals; nd – not determined (see the Materials and methods); the lowercase letters denote significant differences among the age groups for each whitefish forms (ANOVA, Mann-Whitney test).

Table 3. Measurements (in µm) of scolex hooks of *Triaenophorus crassus* presented by Kuperman (1968, 1973), Kuchta *et al.* (2007) and present study.

Measurements	Kuperman (n = 280)	Kuchta *et al.* (n = 177)	This study (n = 113)
1	253–341 (300.9 ± 1.2)	103–428 (305.8 ± 6.9)	288–411 (364.9 ± 2,1)
2	121–176 (148.6 ± 0.6)	110–254 (157.1 ± 2.1)	150–207 (182.8± 1,1)
3	187–275 (238.5 ± 1.4)	104–342 (257.3 ± 3.3)	224–310 (265.7± 1.6)
4	154–231 (189.7 ± 1.5)	117–327 (210.3 ± 3.7)	183–266 (218.1± 1.3)
5	ND	82–309 (149.9 ± 2.5)	88–187 (143.9± 1.6)
6	ND	87–302 (146.3 ± 3.3)	65–168 (128.1± 1.5)
7	ND	134–364 (257.0 ± 3.4)	196–319 (267.7± 2.4)

1 – width of basal plate; 2 – height of basal plate; 3 –length of longer lateral prong; 4 – length of shorter lateral prong; 5 – distance between longer lateral and median prongs; 6 – distance between shorter lateral and median prongs; 7 – distance between both lateral prongs; ND – no data; n – the number of studied specimens. All measurements are given in µm and presented as a range, followed by a mean ± standard error in parentheses.