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Morphoecological characteristics and feeding of wild rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) inhabiting the Krasnoyarsk Reservoir

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Abstract. The paper provides information on the biological parameters and feeding of rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) that has entered the Krasnoyarsk Reservoir by escaping from fish farm cages. In the diet of the studied individuals, eleven groups of food components are found; imagoes of terrestrial insects and chironomid larvae dominate in ration. At the same time, studied individuals are characterized by slow linear and weight growth, low condition factor and stomach fullness, as well as a significant presence of non-food components in food boluses, indicating an insufficient supply of wild population with food resources. In addition, studied fish are characterized by a high degree of morphological malformations of the axial skeleton, which could affect their locomotor functions and ability to reproduce. Therefore, emergence of a self-reproducing population of rainbow trout in the Krasnoyarsk Reservoir is currently assessed as unlikely.

Keywords: biological invasions, rainbow trout, reservoirs, fish growth, fish feeding, morphological malformations

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Introduction

Rainbow trout *Oncorhynchus mykiss* (Walbaum, 1792) is one of the most popular cold-water species for aquaculture and recreational fishing. Since 1888, rainbow trout has been acclimatized in water bodies all over the world, except Antarctica (Alimov and Bogutskaya, 2004). Rainbow trout is now recognized as one of the most widespread and dangerous invasive species in the world (Lowe et al., 2000). Trout are able to form self-reproducing populations when escaping from fish farms to natural water bodies (Welcomme, 1988). They may cause a decline in the abundance of a number of fish species (mainly native salmonids), competing with them for habitats and food resources (Shelton et al., 2015; Thibault and Dobson, 2013).

In the Russian Federation, cage breeding of rainbow trout is carried out in almost all large natural freshwater systems (Mamontov, 2021). However, despite regular catching of rainbow trout specimens of different ages in the water bodies associated with cage fish farms, reliable cases of natural reproduction of introduced rainbow trout are known only in Lake Ezhlyu-kol (Altai Republic) (Sobanskii, 1982) and Lake Imandra (Murmansk Oblast) (Kitaev et al., 2005). Rainbow trout has not been included in the list of the most dangerous invasive species in Russia (Dgebuadze et al., 2018); nevertheless, monitoring studies to predict its naturalization in the water bodies are being conducted in many regions of Russia (Reshetnikov and Popova, 2012; Rostovtsev et al., 2021; Shirobokov, 1993; Sobanskii, 2017; Zakharov and Boznak, 2021).

In the water bodies of the fishery region of the Yenisei River, cage breeding of rainbow trout has launched in the 1980s (Zuev et al., 2016). During this period, trout farms were established in the Mainskoe, Nazarovskoe and Bereshskoe reservoirs, as well as at the non-freezing section of the Yenisei River downstream the dam of the Krasnoyarsk hydroelectric power station. There are documented cases of unauthorized release of this species into the high-mountain lakes of the Sayan Range (Zuev et al., 2016). In recent years, the commercial rearing of rainbow trout has increased significantly at the Krasnoyarsk hydroelectric power station (within the city of Krasnoyarsk and its environs) and in the Krasnoyarsk Reservoir.

Perennial commercial rearing of rainbow trout in cage fish farms causes its regular escaping to the host water body (reservoir), as well as downstream to the Yenisei River and its tributaries. Since the late 2000s, rainbow trout, which escapes from cages, are recorded regularly in control catches in the Mainskoe Reservoir (Evgrafov, 2006). In the downstream of the Krasnoyarsk HPP and in the Krasnoyarsk Reservoir (Karaulny Bay, Tochilny Bay, Biryusa Bay, etc.), the abundance of wild individuals of this species has also increased significantly in recent years.

Despite no reliable information is known so far about the reproduction of rainbow trout in the water bodies of the Yenisei River basin, monitoring of biological indicators of accidentally introduced individuals is of great importance for determining the invasive potential of this fish species. As the abundance of rainbow trout increases, it may become a serious competitor for food with other salmonids in the Yenisei River basin (grayling, lenok, as well as Siberian taimen, included in the Appendix to the Red Book of the Krasnoyarsk Krai[1]).

[1] Decree of the Government of the Krasnoyarsk Krai dated July 30, 2021 No. 529-p "On Amendments to the Decree of the Administration of the Krasnoyarsk Krai dated April 6, 2000 No. 254-p 'On Rare and Endangered Species of Wild Animals' and the Decree of the Council of Administration of the Krasnoyarsk Krai dated May 3, 2005 No. 127-p "On rare and endangered species of wild plants and mushrooms".

The study aims to assess the invasive potential of rainbow trout accidentally introduced into the Krasnoyarsk Reservoir considering the biological parameters of wild-caught fish.

Materials and methods

Ichthyological material was sampled in June 2021 in the Karaulny Bay of the Krasnoyarsk Reservoir (N 55°11′31″ E 91°49′19″) at 4-km distance from the nearest trout farm. Fish were caught by fixed gillnets (mesh size of 22–50 mm), installed at a 0.5–2.0-m depth close by to the nameless stream flowing into the bay. In total, data on 10 captured individuals was considered.

Processing of ichthyological material was carried out in accordance with generally accepted methods (Pravdin, 1966; Zinoviev and Mandritsa, 2003). The age and linear weight indicators of the caught fish were determined: (1) absolute body length and Smith's body length, with 1-mm accuracy with a ruler, (2) total body weight and weight without intestines, with 1-g accuracy at the platform scales.

The material on feeding was sampled and processed in accordance with the guidance by E.N. Pavlovsky (1961). The mass of entire food bolus and food components separately were measured with 0.01-g accuracy on a torsion balance. Animal components were identified to large taxonomic groups (Kutikova and Skorobogatov, 1977; Opredelitel..., 1997, 1999, 2001). Data on feeding are presented as weight proportions (%) and as occurrence in the total number of stomachs examined. The index of relative importance of food components (IR), stomach fullness ($^{o}/_{ooo}$), and Fulton-Clark condition factor were determined (Popova and Reshetnikov, 2011; Pravdin, 1966; Zinoviev and Mandritsa, 2003). Separately, the amount and mass of non-food components in the intestines were recorded. Calculations were made for seven gastrointestinal tracts containing food bolus.

The analysis of morphological malformations of the skeleton was carried out on digested macropreparations, clarified with an aqueous solution of hydrogen peroxide. The bones of the skull, axial skeleton, paired and unpaired fins were examined. The axial skeleton was differentiated into three sections: trunk (A), transitional (I), and caudal (C). Alphanumeric designations are used in the work to describe the location and malformation type of the spine: the location of the malformation is encoded by a letter, its type, by a number. The nomenclature of morphological malformations of the skeleton is given in accordance with the work of Yu.V. Chebotareva (2009). The quantitative indicators of skeletal morphological malformations were evaluated: (1) frequency of occurrence of abnormal individuals (the

Table 1. Size and age characteristics of rainbow trout of the Krasnoyarsk reservoir. TL – absolute length, SL – Smith length, Q – body weight, n – sample size. Values above the line are the arithmetic mean ± error of the mean (*SE*), below the line, limits of variation (min–max).

Age, years	TL, mm	SL, mm	Q, g	N, ind.
2+	251	244	156	1
3+	302 ± 4 / 282–323	295 ± 5 / 273–319	268 ± 20 / 204–356	8
4+	333	325	389	1

proportion of abnormal individuals in the sample), (2) total number of malformations (a set of different types of malformations found in all individuals in the sample), (3) relative occurrence of malformations (the ratio of the total number of malformations of a certain type to the sum of all registered malformations in the sample), and (4) number of malformations per individual (the number of malformations noted in one anomalous individual) (Borkin et al., 2012).

Results and discussion

Size and age composition

Rainbow trout in the catches were represented by immature individuals aged 2+–4+ years. The absolute body length of the fish ranged from 251 to 333 mm, weight, from 135 to 361 g. The average length and weight of the caught individuals were 300 mm and 269 g. Four-year-old fish dominated in the catches. Detailed information about the size and age characteristics of the wild-caught rainbow trout of the Krasnoyarsk Reservoir is presented in Table 1.

Low rates of linear and weight growth were characteristics of rainbow trout individuals inhabiting the Krasnoyarsk Reservoir (Fig. 1). Considering the data on the growth of rainbow trout in the study area, length and weight of rainbow trout inhabiting the Krasnoyarsk Reservoir were larger only when comparing with individuals from the Mainskoe Reservoir characterized by colder temperature conditions (Evgrafov, 2006). The growth rate of rainbow trout of natural populations inhabiting lakes was significantly higher than in the reservoirs of the Yenisei River basin. Apparently, this was due to both better feeding conditions and more favorable temperature regime (Lukin, 1998; Sobanskii, 1982). The period of fish maturation under unfavorable temperature and trophic conditions was also extended significantly. In particular, in wild populations of rainbow trout inhabiting the Krasnoyarsk Reservoir, gonads were at the II stage of development at the age of 3+–4+, while the individuals of the corresponding age groups were already spawning in lakes Imandra and Ezhlyu-kol (Lukin, 1998; Sobanskii, 1982).

It should be noted that the resident forms of rainbow trout living within the natural range were also characterized by significant differences in growth rates under the influence of the temperature factor. In particular, populations of rainbow trout inhabiting the cold-water rivers of the Shantar Islands were significantly smaller by body length (by 15–20%) and body weight comparing to the Kamchatka populations of this species (Gruzdeva et al., 2015, Yarzhombek, 2000).

In studied specimens, condition factor ranged 0.97–1.77 (on average, 1.38) according to Fulton, and 0.88–1.52 (on average, 1.14), according to Clark. The average value of Fulton's condition factor corresponded to the normal values accepted for some species of salmonids (Barnham and Baxter, 2003). According to the same classification, the values of condition factor for individual fish ranged from extremely low to good, which indicated an uneven supply of fish with food.

At the same time, there were natural and naturalized populations of rainbow trout characterized by lower condition factor. For example, average condition factor by Fulton was 1.1, by Clark, 0.9, in a resident rainbow trout inhabiting Bolshaya Vorovskaya River at Kamchatka (Polin, 2017). In introduced populations of rainbow trout inhabiting oligotrophic Kolsai lakes (Kazakhstan), average values of condition factor according to Fulton ranged as 1.2–1.6 (Kozhabaeva et al., 2019).

Food

Eleven groups of food components were found in the gastrointestinal tracts of rainbow trout (Table 2). Pupae and larvae of chironomids, including *Stictochironomus crassiforceps* (Kieffer, 1922), *Stenochironomus* sp., and *Diamesa* sp., prevailed by frequency of occurrence in the food bolus. Pupae of caddisflies and imagoes of terrestrial Coleoptera and Hemiptera were subdominants. Imagoes of terrestrial Coleoptera and Hemiptera, as well as chironomid larvae, prevailed by the share by weight in the food bolus. Juvenile fish (European perch), water striders (Gerridae), and pupae of caddisflies made a significant contribution to the food bolus mass.

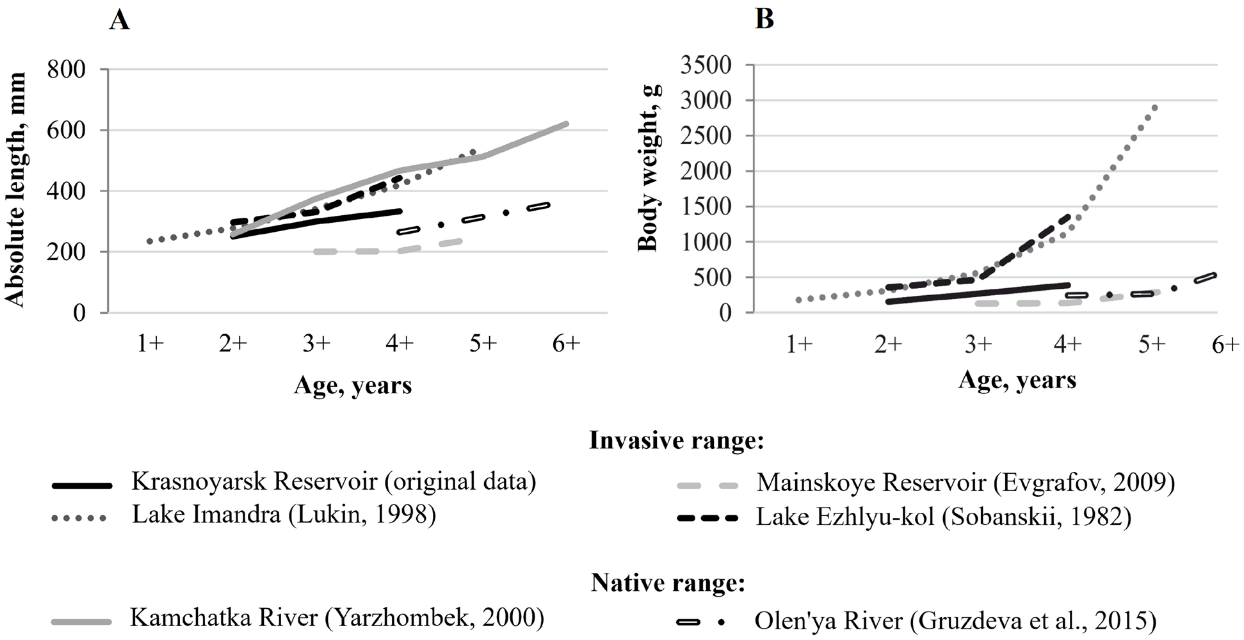

Fig. 1. Rates of linear (**A**) and weight (**B**) growth of rainbow trout in some water bodies of native and colonized areas.

Other groups of organisms did not play a significant role in the trout feeding. The highest index of the relative importance of food components was noted for adults of terrestrial beetles and hemipterans, and chironomid larvae. Gut filling index varied from 8.4 to $148.6^{o}/_{ooo}$, averaging $72.1^{o}/_{ooo.}$ Detailed information on the frequency of occurrence and food object share by weight in the food boluses of rainbow trout of the Krasnoyarsk Reservoir is presented in Table 2.

In the studied individuals, a wide range of non-food components were registered in the food bolus, such as fish scales, wood, mammalian hair, fragments of plastic braiding of wires, and silicone fishing lures ("shads"). Non-food components were found in six out of seven stomachs examined. At the same time, in each stomach containing non-food components, scales of large specimens of bream and roach were found, their size exceeded significantly the scale size of the studied fish. Share of non-food components by weight ranged from 1 to 97% (53% on average) of the total mass of the food bolus.

Therefore, according to the data collected in 2021, terrestrial insects fallen into the water and chironomid larvae (the most common group of organisms in the zoobenthic community of the coastal zone of the reservoir) formed the basis of the diet of 2+–4+-year-old fish in summer (Krasnoyarsk Reservoir..., 2008). According to the parameters of bottom biocenoses, the Krasnoyarsk Reservoir belonged to low-feeding water bodies (Vyshegorodtsev and Zadelenov, 2013). The zoobenthos biomass at the depths inhabited by fish did not exceed 1.4 g/m^2 on average; low growth rate of rainbow trout was largely due to these conditions in the Krasnoyarsk Reservoir (Krasnoyarsk Reservoir..., 2008). When comparing growth rates (by weight) of wild rainbow trout using only natural food resources and cage-reared trout in the Karaulny Bay, the first were growing slower by an order of magnitude. In less than two years of rearing, the weight of cage-reared trout reached 1.50 kg, while that of wild individuals did not exceed 0.16 kg (Chetvertakova et al., 2021). In addition, low provision of wild rainbow trout with food resources was evidenced by low gut filling indices (Molchanova and Khrustalev, 2017), as well as a significant amount of non-food components in the food bolus.

Morphological malformations

Indicators of diversity and occurrence of morphological malformations are a kind of response to the action of genetic factors (inbreeding, polyploidy, and mutations) and environmental factors. They traditionally serve as criteria for assessing the ecological and physiological well-being of mature individuals and juvenile fish (Boglione et al., 2014; Eissa et al., 2021; Pulcini et al., 2010). The presence of such malformations affects the physiological processes of fish and thus may affect locomotor functions, growth, reproductive success, disease resistance, etc. (Eissa et al., 2021). Since there is currently no evidence of natural reproduction of rainbow trout in the Krasnoyarsk Reservoir, the occurrence of morphological malformations characterizes mainly the conditions for egg incubation and juvenile rearing in fish farms, which are the source of penetration of this species into the reservoir. However, given the genetic causes of

Table 2. Frequency of occurrence and share of organisms by weight in food boluses of rainbow trout from the Krasnoyarsk Reservoir. F is the frequency of occurrence, P, share by weight, IR, index of relative importance of food components. The most significant components are highlighted in bold.

Food component	Index		
	F, %	P, %	IR, %
Terrestrial Coleoptera and Heteroptera (imago)	**57.14**	**37.4**	**42.7**
Aquatic Heteroptera (*Limnoporus*)	28.57	12.5	7.14
Aquatic Coleoptera (*Haliplus*)	14.29	0.3	0.09
Chironomidae (pupa and larva)	**71.43**	**27.2**	**38.9**
Simuliidae (larva)	14.29	0.04	0.01
Hydracarina	28.57	0.1	0.06
Aranei	14.29	0.1	0.03
Trichoptera (pupa)	**42.86**	8.2	7.03
Ephemeroptera (larva)	14.29	0.01	< 0.01
Juvenile fish (European perch)	14.29	14.2	4.06
Plants' seeds	14.29	0.01	< 0.01

many types of morphological disorders and their impact on key life processes in fish (Eissa et al., 2021), the occurrence of such malformations may be used as one of the criteria characterizing the physiological state of wild trout individuals as potential spawners.

Morphological malformations of the skeleton were found in 50% of individuals of ten studied specimens of rainbow trout caught in the Krasnoyarsk Reservoir. A total of fourteen malformations belonging to eight types were noted. All diagnosed types of malformations were localized in the spinal column, including five types in the caudal region: C1 (open neural arch), C2 (fusion of the vertebral bodies), C3 (fusion of the branch of the neural arch of one vertebra with the neural branch of the next vertebra), C4 (fusion of the haemal arches of two vertebrae), C5 (underdevelopment of the branch of the neural arch). Two types of malformations were found in the trunk region: A1 (open neural arch) and A6 (presence of an additional branch of the neural arch); in the transitional region, one type, I1 (open neural arch). The most common were open neural arches and fusion of the vertebral bodies. Details of the number and distribution of skeletal malformations are presented in Table 3. The average number of malformations per individual was 1.4. Regard must paid to the individual characterized by presence of seven malformations in the spinal column at once (Fig. 2).

The revealed structural abnormalities of the vertebral bodies and rays of the caudal axial skeleton are one of the most common types of morphological malformations in trout, which juveniles develop in aquaculture (Boglione et al., 2014; Jagiełło et al., 2020; Pulcini et al., 2010).

The share of skeletal morphological malformations in rainbow trout inhabiting the Krasnoyarsk Reservoir significantly exceeds this indicator for water bodies that are not affected by intense technogenic pollution (Yablokov, 2013). Therefore, the physiological state of wild rainbow trout in the Krasnoyarsk Reservoir may be characterized as unfavorable. High ratio of skeletal malformations in wild fish of "cage" origin may indicate a lack of genetic and ecological homogeneity of broodstock in cage fish farms (Jagiełło et al., 2020), which also reduces the reproduction success of "cage" trout in natural water bodies (Artamonova et al., 2016). Significant fluctuations in the water regime of the reservoir, as well as the high abundance of ichthyophagous fish (primarily European perch, exceeding 50% by abundance and biomass in local ichthyocenosis) are other factors hindering the distribution and natural reproduction of rainbow trout in the Krasnoyarsk Reservoir (Krasnoyarsk Reservoir..., 2008; Vyshegorodtsev and Zadelenov, 2013). In addition, a stable ice cover forms in the reservoir and its large tributaries in winter, which is critical for the survival of physostomous fish (Mikheev, 1982).

Conclusions

According to the data obtained, rainbow trout, which has entered the Krasnoyarsk Reservoir as a result of escaping the fish cages, has a low invasive potential. Its population is currently represented by individuals experiencing ecological pessimism. The number of wild rainbow trout in the reservoir is small; obviously, wild population is supported solely by the accidental escaping of fish from cage fish farms.

The unfavorable ecological state of rainbow trout in the Krasnoyarsk Reservoir is evidenced by the low rates of food supply and growth of fish, as well as late maturation. In addition, the studied fish specimens

Table 3. Parameters of skeletal malformations in rainbow trout of the Krasnoyarsk Reservoir.

Type of malformation	Index	
	Number of malformations	Relative occurrence, %
A1	1	7.1
A6	1	7.1
I1	5	35.7
C1	1	7.1
C2	3	21.4
C3	1	7.1
C4	1	7.1
C5	1	7.1
Total number of malformations	**14**	
Share of individuals with malformations, %	**50.0**	
Number of malformations per individual ± error of the mean (*SE*)	**1.4 ± 0.7**	

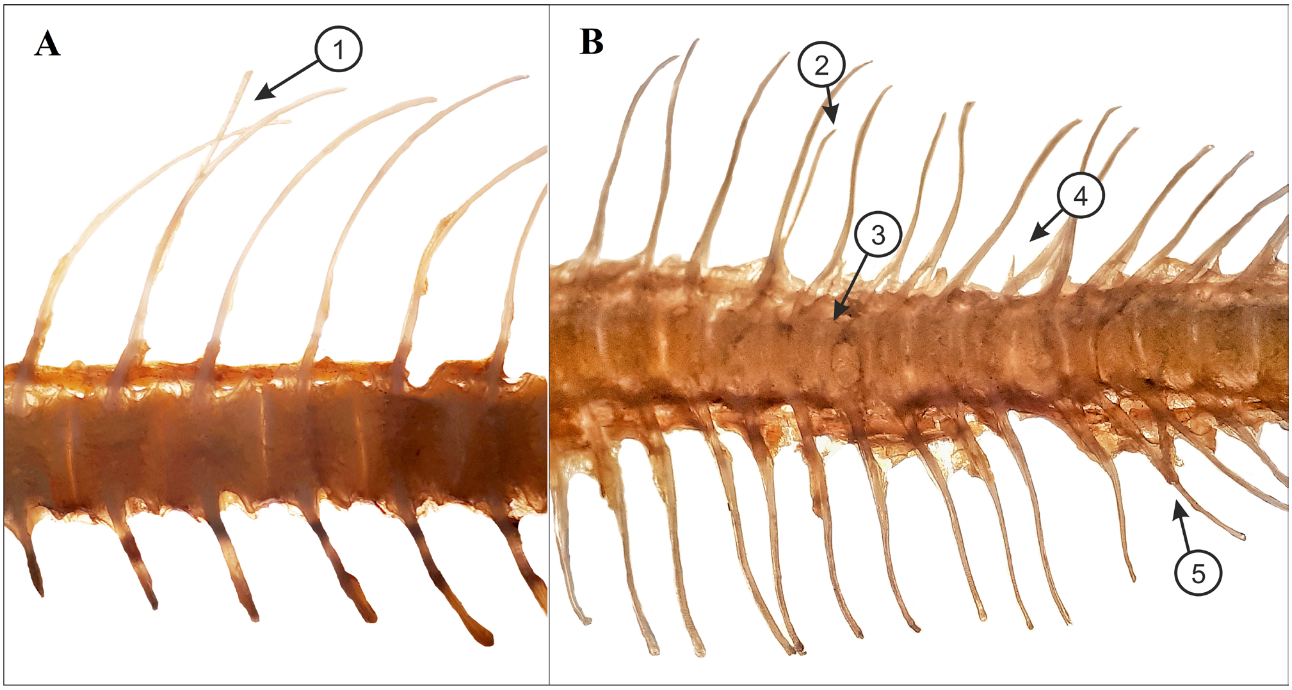

Fig. 2. Malformations of the transitional (**A**) and caudal (**B**) sections of the spinal column in rainbow trout of the Krasnoyarsk Reservoir: 1 – open neural arch (I1), 2 – open neural arch (C1), 3 – fusion of the vertebral bodies (C2), 4 – underdevelopment of the branch of the neural arch (C5), 5 – fusion of the haemal arches of two vertebrae (C4).

are characterized by a high occurrence of morphological malformations of the axial skeleton, which may affect their physiological parameters. The emergence of a self-maintaining population of rainbow trout in the Krasnoyarsk Reservoir is assessed as unlikely under the conditions of unstable hydrological regime, low food resources, and high pressure from ichthyophagous fish.

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