DYNAMICS OF ABUNDANCE AND BIOLOGICAL PARAMETERS OF THE EUROPEAN GRAYLING *THYMALLUS THYMALLUS* (SALMONIDAE: THYMALLINAE) OF THE TIMAN WATERCOURSE ACCORDING TO LONG-TERM OBSERVATIONS

E.I. Boznak[1,]*, A.B. Zakharov[1]

[1]*Institute of Biology, Komi Research Center, Ural Branch, Russian Academy of Sciences, Syktyvkar, Russia*

**E-mail: boznak@ib.komisc.ru*

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An analysis of long-term data on the relative abundance, sexual maturation, linear growth and age structure of the European grayling *Thymallus thymallus* (Linnaeus, 1758) living in one of the watercourses of the middle Timan in the area of bauxite mining and transportation, is presented. It is shown that in the absence of significant disturbances to habitats, the dynamics of abundance and structural and functional parameters of the grayling aggregations are determined to a greater extent by the intensity of non-commercial fishing than by climatic conditions. If the exploitation load is reduced and the quality of the aquatic environment is maintained, the grayling population in the Vym River can be expected to restore to the level characteristic of undisturbed aggregations of this fish species.

Keywords: European grayling, dynamics of abundance, age structure, linear growth, sexual maturation.

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INTRODUCTION

The economic development of new territories is accompanied by an increase in the load on aquatic ecosystems (Arctic biodiversity …, 2013; Schinegger et al., 2013), the state of which, in addition to natural factors, is affected by human activities. The resulting restructuring of the fish population of water bodies is closely linked to changes in numbers, age structure, fertility, growth rate and speed of sexual maturation its constituent populations (Reshetnikov et al., 1982;Gerasimov et al., 2013; Amundsenet al., 2019).

On the territory of the Vym River catchment (a large Timan watercourse, a second-order tributary of the Northern Dvina River), the largest bauxite deposit in Eurasia has been under development for almost three decades (since 1997). In this area, from 1982-2002, we conducted reconnaissance studies, and since 2005, we have been monitoring the state of invertebrate communities and fish in watercourses within the zone of influence of the Middle Timan bauxite mine.

In the rivers of the Urals and the Middle Timan, the European grayling *Thymallus thymallus* (Linnaeus, 1758) is the dominant species, defining the character of the entire fish population (Zakharov, Boznak, 2019; Ponomarev, Zakharov, 2021). This species also experiences the main impact from fishermen. Long-term observations provide an excellent opportunity to study the processes occurring in the grayling population under changing habitat conditions.

The aim of this work is to analyze, based on long-term observations, the population dynamics and changes in the main biological indicators of the European grayling population inhabiting a typical watercourse of the Middle Timan in the area of bauxite mining and transportation.

MATERIALS AND METHODS

Grayling samples were collected during reconnaissance studies (1982-2002) and subsequent monitoring (2005-2022) of the fish population at the control site in the upper reaches of the Vym River (64°13′56″N, 51°32′19″E). The Vym River is the largest right tributary of the Vychegda River (a first-order tributary of the Northern Dvina River) (Fig. 1), with a length of 499 km and a catchment area of 25,600 km ^{2} (Atlas ..., 1997). In its upper course, it is a typical Timan semi-mountainous watercourse with sandy-pebble (sometimes boulder-pebble) substrate. The riverbed width does not exceed 60 m (usually 30-40 m), and the depth varies within 0.2-1.5 m (Shubina, 2006). The current velocity in the reaches is 0.6 m/s, and on the riffles up to 1 m/s or more. In the summer-autumn period, the water temperature in the upper reaches of the Vym River does not exceed 15°C, and the dissolved oxygen content is usually 6-11 mg/dm ^{3} (on average about 9 mg/dm ^{3}).

Fish catches were conducted annually from August 17 to September 05 for 5-7 days. Such materials allow characterizing the relative abundance and biological indicators of grayling at the end of summer feeding before the beginning of its seasonal movements from tributaries to the main river channel. For fishing, stationary gill nets (made of monofilament fishing line) with a total length of 100-200 (average 160) m were used, with mesh sizes of 20, 30, and 40 mm, constituting 10, 50, and 40% of the total length of fishing gear, respectively. Nets were set in the coastal zone at sections of reaches with slow current and in holes along the current or at a slight angle to it. The depth at the net setting locations was 1.2-1.5 m. The design, locations, and checking schedule of the nets remained constant throughout the work. In shallow, fast-flowing sections of the river, fish were caught by spinning. To assess the biological indicators of grayling for 1982-2002, data from spinning catches were used.

For the captured specimens (2959 individuals), body length was measured to the end of the middle rays of the caudal fin (FL) with an accuracy of 1 mm and body weight with an accuracy of 1 g; during dissection, sex and stage of gonad maturity were noted. The age of fish was determined by scales collected from the first two scale rows above the lateral line under the dorsal fin (Pravdin, 1966). Linear growth of fish was evaluated by the method of back-calculation using Lea's direct proportionality formula (Chugunova, 1959; Dgebuadze, 2001). To reduce errors, all scale samples were processed by a single operator. Based on the age structure of catches, the coefficient of total mortality was calculated (Ricker, 1979) and the relative abundance of grayling generations (Tereshchenko, Zuyanova , 2006) .

The relative abundance of fish was determined as the catch per unit fishing effort (individuals/effort per day), i.e., the number of individuals caught in 30 m of nets during 24 hours. Changes in abundance dynamics were analyzed by constructing a dynamic phase portrait (Tereshchenko, Verbitsky, 1997) , which has shown its effectiveness in studying both individual fish populations (Tereshchenko et al., 2015, 2016) and their communities (Reshetnikov et al., 2011; Reshetnikov, Tereshchenko, 2018; Boznak et al., 2019) .

RESULTS

The relative abundance of grayling in the upper reaches of the Vym River during 2005-2017 gradually decreased from 5.1 to 2.8 specimens/effort, with fluctuations having a period of 3-4 years. The amplitude of such fluctuations also decreased from 2.4 (in 2005-2007) to 0.6-0.8 (in 2010-2017) specimens/effort. After 2017, the grayling population began to increase, reaching a maximum in 2022 (Fig. 2a).

Analysis of the dynamic phase portrait allowed us to identify three different periods in the functioning of the upper Vym grayling population. In 2005, this group was in the process of transitioning to a new state with a lower abundance level, and the rate of abundance decline at that time was the highest for the entire observation period (−2.4 (specimens/effort)/year). Further, the rate of change of this indicator decreased, and from 2007, the trajectory began to take the form of a tightening spiral, characteristic of systems in a stationary state. During this time, only cyclical fluctuations in abundance around the value of ~ 3.5-3.8 specimens/effort were observed in the grayling population. After 2018, the system trajectory changes again. The curve on the graph takes the form of a convex arc, typical for systems in the process of transitioning to a new state with a higher value of the analyzed parameter (Fig. 2b). Indeed, by 2022, the relative abundance of grayling (based on smoothed data) increased by more than 1.6 times compared to the data from 2005.

Thus, for further analysis, the entire data series can be divided into four stages: 1) relatively high abundance (until 2005); 2) declining abundance (2005-2006); 3) periodic fluctuations in abundance at a low level – a state of dynamic equilibrium (2007-2018) and 4) increasing abundance – transition to a new state (2019-2022).

The age structure of grayling caught at different times did not remain constant. In collections made before 2005 (before the decrease in abundance), fish at the age of 5+ predominated, with a maximum age reaching 12+. During the period of low abundance (2007-2018), the modal age of captured fish was usually 4+, and the maximum, as a rule, did not exceed 9+ years.

It should be noted that spinning catches were usually characterized by a higher proportion of individuals from younger age groups (3+ and 4+). However, when comparing the age structure of samples collected using gill net orders and spinning in 2007-2015 and 2020-2022, significant differences ($p < 0.05$ according to Pearson's χ^2 test) were observed in only five out of 12 cases. In two of these cases, the volume of collected material was small (in 2007, 23 specimens were caught by spinning and 37 by nets; in 2008, 35 and 33 specimens respectively). Thus, despite the unequal selectivity, collections made with these gear types provided qualitatively similar representations of the grayling age structure (both the number of age classes and the modal age group usually coincided).

At the beginning of the population increase phase (2019 and 2020), catches maintained a high occurrence of the 4+ age group; later, the modal age increased to 5+ (2021) and 6+ (2022), while the maximum did not exceed 8+ (table).

The total mortality coefficient of grayling also increased significantly during the observation period. Thus, in 1982-2005, its average value was 0.63; in 2007-2018 (the period of consistently low abundance), it increased by almost 1.5 times (0.99), and in 2019-2022 - to 1.33. The variability of this indicator also changed. While at the beginning of observations, the difference between the minimum and maximum values of the mortality coefficient did not exceed 2.2 times (0.35-0.78), during the period of low abundance, the minimum and maximum differed by almost 4.4 times (0.47-2.06), and at the stage of increasing abundance - by 6.7 times (0.35-2.35).

Age structure of European grayling *Thymallus thymallus* catches in the upper reaches of the Vym River, %

Year	Number of fish, specimens	Age Group											
		1+	2+	3+	4+	5+	6+	7+	8+	9+	10+	11+	12+
1982	71		1.4	16.9	1.4	55.0	14.1	4.2	4.2	1.4	1.4		
1989	19	52.5	5.3	26.3	5.3	5.3	5.3						
1996	90			1.1	2.3	6.8	23.9	52.2	8.0	2.3		2.3	1.1
1998	41		2.4	2.4	2.4	36.7	9.8	17.1	7.3	12.2	4.9	2.4	2.4
2000	37			7.5	20.0	37.5	17.5	15.0		2.5			
2002	80			6.3	31.3	27.4	25.0	7.5	2.5				
2005	190		0.5	3.7	22.2	60.4	10.1	1.6	0.5	0.5		0.5	
2006	16			8.0	14.0	32.0	26.0	2.0		18.0			
2007	60	3.3		10.0	43.4	3.3	25.0	13.3	1.7				
2008	68			7.4	42.6	38.2	7.4	2.9	1.5				
2009	212			6.6	32.6	44.7	15.6	0.5					
2010	170		2.1	29.2	18.1	23.5	20.8	5.6		0.7			
2011	215		0.9	7.0	40.5	16.7	20.0	9.8	5.1				
2012	252		1.6	50.6	25.8	12.4	4.8	2.4	1.6	0.4	0.4		
2013	201			10.4	65.2	10.9	10.0	1.5	1.0	0.5	0.5		
2014	189		0.5	11.1	65.1	22.2	1.1						
2015	235			4.7	43.0	40.4	10.6	0.9	0.4				
2016	125		0.8	27.2	35.2	24.8	10.4	1.6					
2017	26			11.5	61.6	19.2	7.7	0.0					
2018	123		0.8	49.6	29.3	17.9	1.6	0.8					
2019	61			11.5	42.6	24.6	21.3						
2020	151		0.7	2.7	52.0	37.3	5.3	2.0					
2021	164			8.0	10.4	68.1	12.9	0.6					
2022	231		0.9	1.7	31.1	19.0	39.0	6.1	2.2				

Note. In 1982-2002, materials were collected by spinning, in subsequent years - by fixed nets and spinning.

Data on the relative abundance and age structure of control catches of grayling (table) made it possible to assess the contribution of individuals belonging to different generations to the total population during the monitoring period (Fig. 3).

In net catches, which depend on a certain size selectivity of fishing gear, grayling began to appear from the age of 2+ and 3+. The largest number of captured individuals occurred in age groups 4+ and 5+. Further, their proportion naturally decreased, and in most cases, the generation left the composition of catches when fish reached the age of 7+ and 8+. As a result, the abundance of the commercial part of the population depended on the abundance of individuals of age classes belonging to different generations. Thus, the high abundance of grayling in 2005 was associated with the presence in the samples of a large number of fish born in 2000 (age 5+), and a significant number of individuals belonging to the 2001 generation (4+). The increase in catches in 2009 was caused by peaks in the occurrence of generations born in 2004 (5+) and 2005 (4+), overlapping each other against the background of a noticeable number of fish belonging to the 2003 generation (6+). The local rise in grayling abundance observed in 2013 is associated with the predominance in catches of fish from the 2009 generation (4+). The high occurrence of grayling from the 2015-2016 generations led to an increase in the abundance of the species in the Vym River, observed (with some fluctuations) after 2018 (Fig. 3).

Analysis of data on the proportion of different generations in control catches based on a modified biostatistical method allows us to assess the grayling generations born in 2004, 2009, 2010, 2013, 2015, and 2016 as numerous. Within these generations, the total proportion of fish aged 3+... 6+ significantly exceeded that in the generalized age structure of Vym grayling catches (relative abundance significantly exceeds 100%). The generations born in 2003, 2005, 2007, and 2011 are characterized by average abundance, while the generations of 2006, 2008, 2012, 2014, and 2017 are classified as small in number. There is a statistically significant positive correlation (Spearman: $\rho_s = 0.75$, $p = 0.03$) between the relative abundance of a generation and the water level during the warm period (May-October) of the year preceding its emergence (Fig. 4).

Linear growth of individuals from generations that formed the grayling population at different stages of its functioning had its own characteristics. Until the age of 6+ inclusive, fish growth was generally quite similar, and differences in average length (5-13 mm) and body weight (5-12 g) were insignificant and, as a rule, statistically non-significant. Subsequently, fish caught after 2007 (generations 2003-2018) showed a noticeable decrease in the rate of linear growth. As a result, individuals aged 7+ and older from generations formed after 2003, during the period of low abundance, were notably inferior in average length to fish caught before 2000 (during the period of high abundance). For example, in the 9+ age group, this lag exceeded 40 mm (Fig. 5).

The first cases of sexual maturation in the Vym River grayling from generations formed during the period when the upper reaches of the river were difficult to access for fishermen (1972-1993) were noted at the age of 3+. The proportion of mature fish in this age group did not exceed 6%. The majority of individuals during this period matured in the sixth (5+) year of life. In the generations of 2003-2018, during the period of low abundance, maturation significantly accelerated: in the 3+ age group, maturity was observed on average in more than half of the individuals (56%), and in the 4+ group in almost 85% of fish. Moreover, the rate of sexual maturation of fish from the 2015-2018 generations, which provided an increase in numbers in 2018-2022, generally corresponds to that of fish living during the period of consistently low abundance (Fig. 6).

DISCUSSION

The data presented above allow us to characterize the changes that occurred at different stages of the functioning of the grayling population in the Vym River. The process of population decline (2005-2006) and the transition of this group to a new state of dynamic equilibrium (2007-2018) was accompanied by changes in a number of population indicators: the proportion of fish in younger age groups increased, catches were dominated by first-maturing and immature individuals, and specimens aged 10+ and older completely disappeared from the collections. At the same time, the Vym River grayling showed accelerated sexual maturation.

The increase in grayling numbers that began after 2019 occurred without significant changes in population parameters. During this period, there was an increase in the proportion of fish that had already participated in spawning (5+ and 6+), however, catches still contained a significant number of immature and first-maturing individuals, the maximum age did not exceed 8+, and the total mortality coefficient even increased. The growth pattern and rate of sexual maturation of fish remained the same. Thus, the population increase observed since 2019 occurred due to the overlap of abundance peaks of two numerous grayling generations (born in 2015 and 2016) and the presence in catches of a significant number of individuals born in 2017 and 2018.

Apparently, natural factors do not have a direct impact on the observed changes in the abundance and structural and functional indicators of the Vym grayling groups. A previous analysis showed the absence of a statistically significant correlation (according to Spearman) between the abundance of grayling in the Vym River and the average annual air temperature, which determines the duration of the feeding period, and precipitation (Boznak et al., 2019), as well as between average annual temperatures and the sizes of same-age fish caught at different times (Boznak, Zakharov, 2021). The main indicators characterizing water quality in the Vym River also remained stable. The water temperature in August throughout the entire monitoring period (depending on weather conditions) was 7-12°C, the amount of suspended solids averaged 7.7 mg/l, and water transparency typically exceeded 3.5 m. Only in high-water years, due to the influx of large amounts of bog runoff into the river, the amount of suspended particles in the water increased to 29.0 mg/l, and water transparency decreased to 1.5 m.

Technogenic disturbances and erosion pollution zones (seasonal runoff from the road) in the upper reaches of the Vym River, identified at the locations where transport communications cross it, are localized (Afanasenko et al., 2010; Zakharov, Boznak, 2019) and apparently do not have a noticeable impact on the condition of the main fish feeding areas. Indeed, during the observation period, the concentration of suspended solids in the water of the main river channel varied from <0.5 (in 2022) to 29.0 mg/dm^3 (in 2009), which corresponds to their content (19.5 mg/dm^3) in a conditionally background section of the river located 16 km upstream, with no notable sediment accumulation or siltation observed. The content of major ions in the water (mg/dm^3): HCO_3^- (170.0), SO_4^{2-} (27.0), Cl^- (1.5), Ca^{2+} (41.0), Mg^{2+} (14.0), $Na^+ + K^+$ (4.0) – is close to that observed in the upper Vym River in June 1979 (Shubina, 2006).

The average zoobenthos biomass at the control section of the Vym River in different years (2000-2022) varied widely (from 1 to 52 g/m^2), with no systematic decrease observed (M.A. Baturina, IB Komi SC UB RAS, personal communication). There is also no apparent relationship between benthos biomass and the abundance of the grayling generation formed during this period. For example, in August 2007 and 2008, the average benthos biomass at the control site of the Vym River was 0.8 and 3.5 g/m^2 respectively (Zakharov, Boznak, 2019). At the same time, the grayling generation formed in 2007 was characterized by average abundance (107%), while in 2008 it was low (52%).

Apparently, the main anthropogenic factor affecting the fish population in the upper reaches of the Vym River is intensive non-commercial (recreational) fishing. The industrial development of the Middle-Timan bauxite deposit (1997) was accompanied by the construction of a road that made the upper reaches of the Vym River accessible to anglers, which sharply increased the pressure on the ichthyofauna from uncontrolled fishing. In the early 2000s, the first hunting and fishing base was built here. Today, there are six fishing sites with a total length of 85 km in the upper reaches of the river, used for organizing recreational fishing. It is quite difficult to assess the increased fishing pressure. However, according to our observations at the control section of the Vym River channel with a length of 10 km, there may be simultaneously from two to five fishermen whose activities are not controlled. Control fishing with spinning and float fishing rods conducted in August 2007-2022 showed that one fisherman's catch per day, depending on weather conditions, can range from 0.4 to 15.6 kg of grayling (4.3 kg on average). Assuming that such fishing is carried out for 10 days per month, fish removal from 1 km of the river during the warm season (June-September) can amount to 34-86 kg, which significantly exceeds the average annual fish productivity of Timan rivers (5-8 kg/ha or 15-24 kg/km of river channel) (Solovkina, 1975).

It is indicative that since the early 2000s, the grayling population has noticeably decreased, and the rejuvenation of the age structure and reduction in the number of age classes indicated a restructuring of its population from a long-cycle to a medium-cycle type (Zinoviev, 2005).

Despite numerous examples of declining populations of salmoniform (Salmoniformes) fish species (Martynov, 2007; Popov, 2007; Sidorov, Reshetnikov, 2014), there are known cases when populations in favorable conditions quickly restored their numbers through recolonization from neighboring areas (Kennedy et al., 2012) , effective reproduction in years with optimal water levels (Lobón-Cerviá, 2009) or due to reduced fishing pressure (Sarvala et al., 2020; Boznak et al., 2023) .

The above-noted relationship between the water level in the Vym River and the abundance of the grayling generation formed the following year (Fig. 4) can be explained by the decrease in fishing pressure during high-water years. The increase in the river water level from May to October reduces the efficiency of grayling catch, which in turn positively affects the number of reproductive part of the population and contributes to the emergence of a numerous generation in the current year.

The impact of fishing can also be considered as the main factor influencing the change in the character of growth (Fig. 5) and the acceleration of sexual maturation (Fig. 6) of the Vym grayling. It is believed that under conditions of intensive fishing, rapidly maturing fish gain a selective advantage (Borisov, 1978; Enberg et al., 2012), with a higher probability of participating in reproduction (Naish, Hard, 2008) . The acceleration of maturation can also be contributed to by the increase in food availability that occurs when the fished population is thinned (Nikolsky, 1974; Kotenev et al., 2009).

After the onset of sexual maturity, the growth of rapidly maturing individuals usually slows down (Dgebuadze, 2001). In addition, as a result of the removal of fast-growing fish from the population, which reach commercial sizes earlier, older age groups may be dominated by individuals with relatively low growth rates.

CONCLUSION

To date, the development of the Middle Timan bauxite deposit has not led to significant technogenic disturbances of the Vym River. The hydrological and hydrochemical regimes of this watercourse have remained in a condition close to natural. The main influence on the abundance of commercial fish species in the Vym River is exerted by intensive non-commercial (recreational) fishing, which has sharply increased due to the development of the transport communication system and increased accessibility of the area. Under the influence of uncontrolled recreational fishing, the grayling population by the early 2010s transitioned to a relatively stable state with a low level of abundance and altered age structure. At the same time, an acceleration of sexual maturation and a change in the pattern of linear growth of fish were observed.

Despite the occurred changes, the grayling population of the Vym River has maintained its reproductive potential. When favorable conditions arise and/or fishing intensity decreases, this group demonstrates the ability to quickly increase its numbers. With continued low fishing pressure, we can expect restoration of structural and functional indicators characteristic of undisturbed grayling populations.

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COMPLIANCE WITH ETHICAL STANDARDS

All manipulations with research objects complied with ethical standards approved by legal acts of the Russian Federation, principles of the Basel Declaration, and were approved by the decision of the Commission on Compliance with Standards for Responsible Treatment of Animals (compliance with bioethical standards) of the Institute of Biology of the Komi Scientific Center of the Ural Branch of the Russian Academy of Sciences (conclusion No. 7/2024 dated 23.04.2024).

CONFLICT OF INTEREST

The authors of this work declare that they have no conflict of interest.

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FIGURE CAPTIONS

Fig. 1. Schematic map of the work area location: *1* – material collection site, *2* – Middle Timan bauxite mine, *3* – railway and road, (→) – flow direction.

Fig. 2. Dynamics of the relative abundance of European grayling *Thymallus thymallus* (a) and dynamic phase portrait of its change (b) according to control net catch data in the upper reaches of the Vym River: data: (---) – original, (—) – smoothed by cubic spline method; (■) – state in the year indicated nearby.

Fig. 3. Relative abundance of European grayling *Thymallus thymallus* in the Vym River of different birth year cohorts: *1* – 1996–1999, *2* – 2000, *3* – 2001, *4* – 2002, *5* – 2003, *6* – 2004, *7* – 2005, *8* – 2006, *9* – 2007, *10* – 2008, *11* – 2009, *12* – 2010, *13* – 2011, *14* – 2012, *15* – 2013, *16* – 2013, *17* – 2014, *18* – 2015, *19* – 2016, *20* – 2017, *21* – 2018.

Fig. 4. Relative abundance of European grayling *Thymallus thymallus* cohorts born in 2008 – 2017 (■) and the average water level from May to October of the previous year (—■—) in the Vym River. Water level data are provided from the gauging station at Veslyana village (https://allrivers.info/gauge/vym-veslyana. Version 03/2024).

Fig. 5. Linear growth (*FL* – Smith's fork length) of European grayling *Thymallus thymallus* in the Vym River of cohorts formed during different functional stages of the population: *1* – 1972–1993, *2* – 2008–2012, *3* – 2015–2018.

Fig. 6. Proportion of sexually mature fish in age groups of European grayling *Thymallus thymallus* in the Vym River from cohorts formed during different functional stages of the population: *1* – 1972–1993, *2* – 2008–2012, *3* – 2015–2018.