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ICHTHYOLOGY

Population Growth and Age Structure of the Pikeperch *Sander Lucioperca* (Percidae) from Lake Necheritsa (Sebezhsky National Park, Pskov Oblast, Sebezhsky District)

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Abstract—The size, age, and sex structures of pikeperch *Sander* (L.) from Lake Necheritsa (Sebezhsky National Park) have been studied, as has the linear growth using back-calculation according to the Leo direct dependence function. The growth of pikeperch is described formally by linear equation $L(t) = 5.4x + 0.2$ (cm). The length frequencies of individual age groups are normally distributed, which corresponds to ideas about linear fish growth. The population is represented by 13 age classes; the maximum length of an individual in the sample is 872 cm. The analysis of the diet showed the presence of 6 mass fish species observed in the catch, including the young pikeperch; the ratios of individual species in the diet and the sample indicates an absence of electivity of nutrition. According to the estimates, the proportion of pikeperch in the ichthyocenosis in the period 1989–2022 in Lake Necheritsa has increased ~8 times. A comparative analysis of the linear growth of pikeperch from populations of different regions under environmental conditions, differing in a number of values of key parameters, is carried out. Growth rates of pikeperch from southern populations are generally higher and more consistent with asymptotic growth, while the size limits and life expectancy are generally higher in northern populations. A hypothesis has been tested about the causes of differences in the nature of linear growth.

Keywords: Sebezhsky, age, linear growth, temperature, latitude

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INTRODUCTION

Zander *Sander lucioperca* (L.) is a species with a high degree of variability of the intraspecific structure in its range, which is due to its species characteristics and habitat in reservoirs and watercourses of different types and different climatic zones (Tanasiychuk, 1974; Strelnikov, 1996; Kushnarenko et al., 2004). Spatial heterogeneity of the pikeperch habitat in individual areas of the range has led to the formation of a mosaic system of local populations with a pronounced set of adaptations associated with unique growth parameters, age composition, time of sexual maturity, and spawning frequency, as well as with morphological and reproductive features (Krpo-Ćetković and Stamenković, 1996; Ložys, 2003; Akbarzadeh et al., 2009; Kovalenko et al., 2014; Parés-Casanova and Cano, 2014). The complex population structure of the species, formed in addition to natural causes by anthropogenic transformations of the habitat (fragmentation of river basins by hydroelectric dams and changes in the hydrological regime and pollution), makes the pikeperch an informative model object for studying the processes of divergence and adaptation under the influence of natural and anthropogenic factors. In this regard, it is important to note the role of the species as a test object and bioindicator of pollution in the context of steadily increasing anthropogenic load on natural ecosystems (Gladyshev et al., 2001). At the same time, to analyze the spatiotemporal variability of a species, quantitative characteristics of the parameters of populations from natural reservoirs and watercourses that have not undergone significant anthropogenic restructuring and which could be considered natural standards are required. Pikeperch populations from the system of reservoirs and watercourses of the Pskov Lake District, belonging to the Western Dvina River basin, can be considered standards of this kind. Some of the water bodies are located on the territory of the Sebezhsky National Park, a federal institution of nature conservation, scientific research, and environmental education. One of its tasks is to preserve the natural biodiversity of terrestrial and aquatic ecosystems (Aleksandrov and Kuryanovich, 2001).

Size and age indicators are one of the key indicators of the state of a species population (Jůza et al., 2023; Tesfaye et al., 2023), since they represent an integrated response of the organism to the complex impact of the values of various environmental parameters (Mina and Klevezal, 1976; Dgebuadze, 2001). The contributions of a number of factors to the formation of the age structure of the population and the nature of growth cannot always be separated due to the nonlinear response of the biological system to their combined effect (Bigon et al., 1989). Nevertheless, it seems possible to identify a number of key environmental parameters against which specific population indicators are formed. One of the most common approaches to indirectly assessing the influence of the environment on population structure and growth functions is a comparative analysis of size and age indicators of this species from regions with different climatic conditions and water bodies of different types (Lappalainen et al., 2003; Zykov and Ivanov, 2008; Kuzishchin, 2016).

The aim of this work is to study the size–age and sex structure of the pikeperch population of Lake Necheritsa, provide an analysis of growth rates based on the reverse calculation of length, estimate the relative abundance of the species in the ecosystem, and conduct a comparative analysis of the nature of the linear growth of pikeperch in populations from regions with different climatic conditions.

MATERIAL AND METHODS

The material was collected in September 22–October 2, 2022, in Lake Necheritsa (56°13′ N, 28°44′ E), located in the Sebezhsky National Park. The lake is the last in a system of lakes connected by channels: Sebezhskoe–Orano–Glybochno–Beloe–Ozeryavki–Necheritsa, and the second largest lake in the national park, with a surface area of 12.8 km^2 and an average depth of ~4 m. The length of Lake Necheritsa is 8.6 km, and the maximum width is 3.2 km; the lake consists of three parts with an area of 2.3 km^2, 2.1 km^2, and 7.7 km^2. It is connected via the Svolna and Drissa rivers with the Northern Dvina River. The lake is almost completely surrounded by forest; on the eastern shore there is only the village of Volotsnya (around eight houses). Fish were caught at all depths of the northern part of the lake, covering an area of 2.3 km^2 gill nets with mesh sizes of 18, 25, 27, 30, 35, 40, 50, 60, 70, and 80 mm. A total of 17 net installations were carried out along various transects of the water area to cover the entire biotopic heterogeneity of the reservoir; nets of all mesh sizes were set at different distances from the shore and over the entire range of depths (Fig. 1). The nets were set in the evening and checked in the morning; the fishing lasted on average 10 h. The bottom of this section of the lake is flat, with a depth of ~5 m observed over 80% of the entire water area.

Biological analysis was carried out according to standard methods (Pravdin, 1966). The primary analysis of the material included measuring the weight and length of each individual—commercial, according to Smith, and zoological—as well as determining sex. Twenty-four males, 34 females, and 12 juveniles were taken for bioanalysis. Scales were collected in bulk for estimating age and recalculating length; scales were taken from the same area bodies—under the lateral line within the projection of the first dorsal fin (Pravdin, 1966). All fish are photographed. Immediately after the catch was collected, the stomachs of the pikeperch were opened to analyze the food bolus.

For inverse calculation, the formulas of Li (Chugunova, 1959; Mina, 1976) and Lea's direct proportionality (Kovtun, 1981; Lea, 1910) are widely used. In the first case, it is necessary to estimate the length of the fish body at the time of the formation of the first scale plate (Vovk, 1956; Chugunova, 1959), calculated by approximating the linear or power function of the distribution of fish lengths depending on the size of the scales, as a result of which the curve of the function cuts off a segment on the ordinate axis equal to the desired length. For certain reasons (see Research Results), the formula of direct proportionality of Lea was used to reverse calculate the length of the pikeperch:

$$l_i = \frac{l_n S_i}{S_n}, \tag{1}$$

where l_i and l_n are the length of the fish in the ith age and at the age of capture, respectively; S_i and S_n are the radius of the scales in the ith age and at the age of capture.

The scales were measured using an MBS-1 binocular microscope (Soviet Union) with an eyepiece micrometer; based on the results, a graph was constructed of the dependence of the pikeperch length on the longitudinal diameter of the scales (Fig. 2). Annual increments on scales were also determined in ocular micrometer units at the same magnification. The calculation was carried out in Excel; statistical data processing was carried out in Statistica v. 10.

The growth rates were calculated using the formula for estimating the specific growth rate of Schmalhausen–Brody, taking into account the increase in length by compound interest; that is, the increase in shares of each subsequent year was estimated taking into account the shares of the increase for the previous year (Schmalhausen, 1935; Mina and Klevezal, 1976; Dgebuadze, 2001):

$$C_l = \frac{\log l_1 - \log l_2}{0.4343 \times (t_1 - t_2)}, \tag{2}$$

where C_l is specific growth, l_1 and l_2 are the average length of fish of a given species at certain points in time t_1 and t_2, and 0.4343 is the coefficient for converting

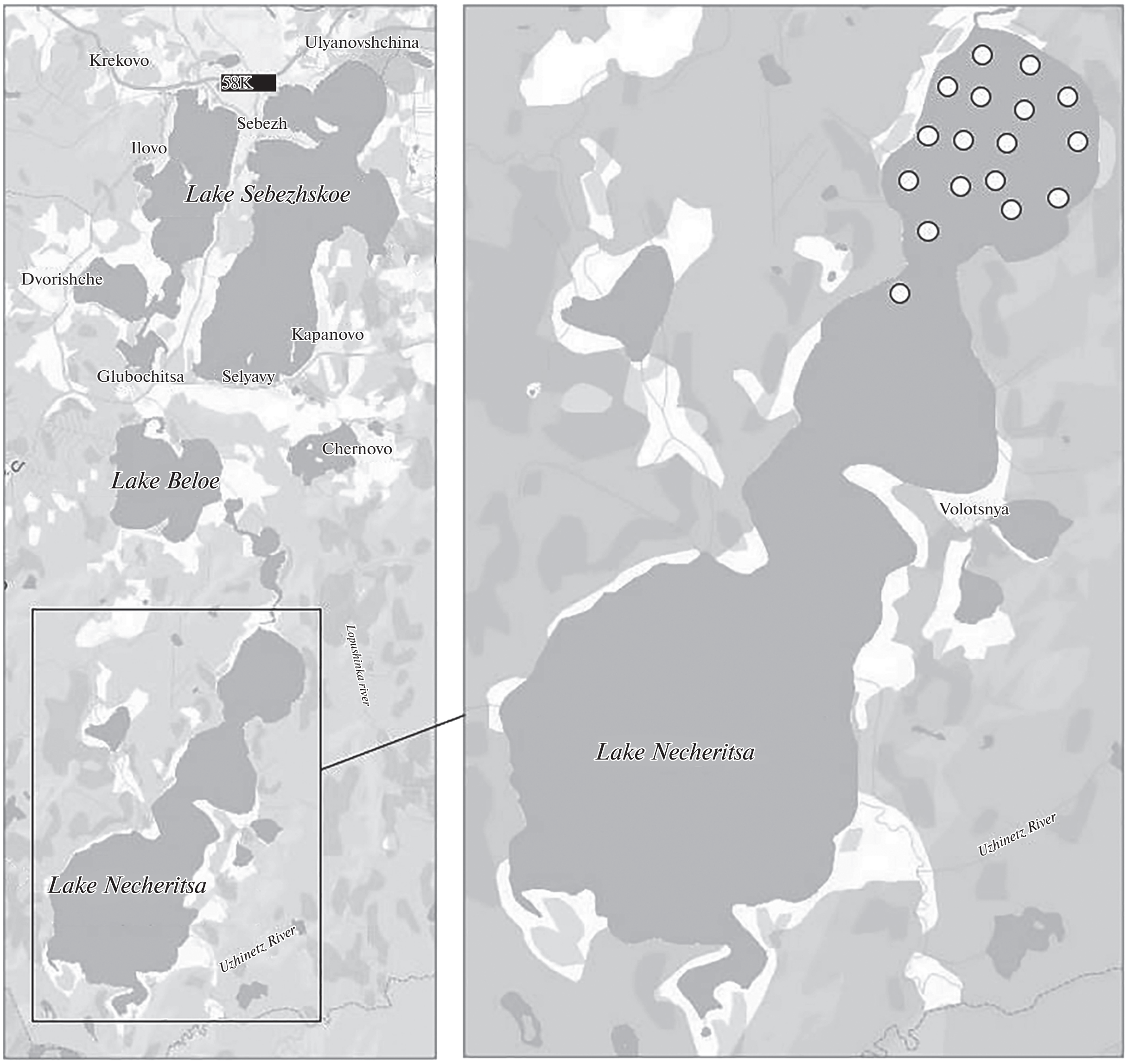

Fig. 1. Map of the study area: Lake Sebezhskoye (Sebezhsky district, Pskov oblast); sampling stations are marked with circles.

natural logarithms to decimal ones. Since the time scale step is equal to 1 year (the difference in brackets is equal to 1), formula (2) takes the following form:

$$C_l = \ln l_1 - \ln l_2. \quad (3)$$

The composition of the pikeperch diet was assessed based on the composition of the food bolus, which was studied using the counting method (Shorygin, 1952; Manual ..., 1961).

RESULTS

The following species were noted in the catches: roach *Rutilus rutilus* (L.) 932 individuals (~56% of the fish in the catch), perch *Perca fluviatilis* (L.) 265 individuals (~16% of the population), white bream *Blicca bjoerkna* (L.) 218 individuals (~13%), bream *Abramis brama* (L.) 165 individuals (~10%), pike *Esox lucius* (L.) 5 individuals (<1%), tench *Tinca tinca* (L.) 4 individuals (<1%), rudd *Scardinius erythrophthalmus* (L.) 5 individuals (<1%), ide *Leuciscus idus* (L.) 3 individuals (<1%), and ruff *Gymnocephalus cernuus* (L.) 2 individuals (<1%); all in all, there was a total of 1599 individuals. The number of pikeperch *Sander lucioperca* in the catch amounted to 70 specimens, or ~4% of the entire fish sample (1669 specimens).

The pikeperch sample included 11 age classes (Table 1); the proportions of males and females were ~41% (24 specimens) and ~59% (34 specimens), respectively. The hypothesis of equality of the sample proportions of males and females was tested using the chi-square test: the value $\chi^2 = 3.24$ is less than the threshold 3.84 at one degree of freedom for the level

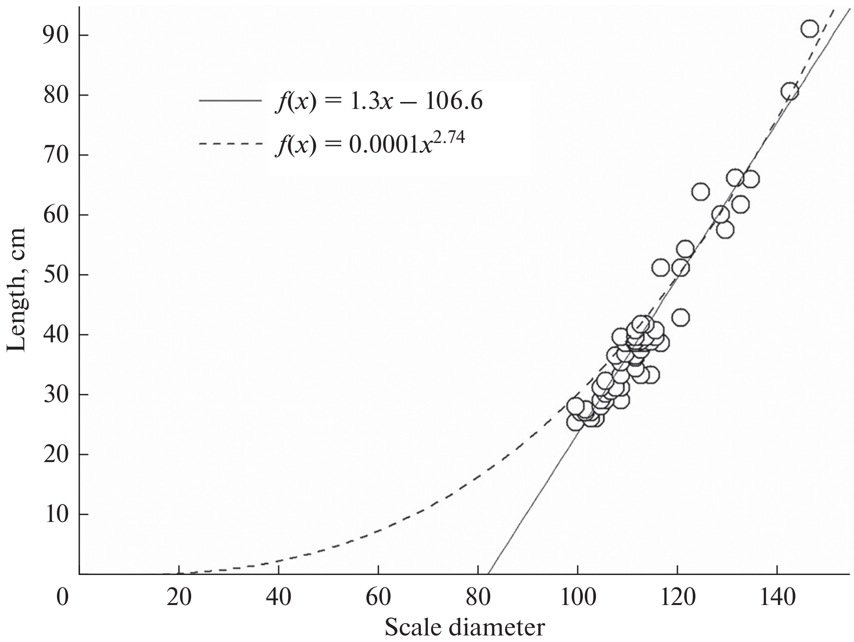

Fig. 2. Dependence of the length of the pikeperch *S. lucioperca* (cm) from the longitudinal diameter of the scale (ocular micrometer units), described by linear and power functions.

significance $\alpha = 0.05$, which allows us to accept the null hypothesis of equality of the shares of both sexes.

In Lake Necheritsa, pikeperch feeds on different types of fish; in the stomachs, 16 specimens of roach were found (~32% of the total number), 10 specimens of white bream (~20%), 7 specimens of perch (~14%), 4 specimens of ruff (~8%), 3 specimens of pikeperch (~6%), and 1 specimen of bream (2%). A total of 50 stomachs were analyzed. It was not possible to determine the species of fish in the stomachs of 9 pikeperch specimens (~18%); stomachs were empty in 24 specimens (~48%).

The choice of the Lea formula of direct proportionality for the procedure of inverse calculation is dictated by the fact that the linear regression line intersects the abscissa axis instead of the ordinate axis, and the curve of the power function comes out almost from zero (Fig. 2), which makes it impossible to apply the Lee formula. The specific growth rate of pikeperch in Lake Necheritsa calculated using formula (3) is presented in Table 1.

For each age class, a comparison was made between the actual lengths of pikeperch and the lengths of fish obtained by reverse calculation (Fig. 3a). The average proportion of deviation of sample lengths from those calculated inversely is 6% in absolute value, with a standard deviation $SD = 2\%$, which is a good indicator of the adequacy of the results of the reverse calculation. The linear growth curve with the values of standard deviations of lengths for each age class together for actual and calculated lengths is shown in Fig. 4. This graph is further used for comparison with the growth rate curves of pikeperch from other regions. Approximating the distribution of mean lengths of different age classes with a linear function yields a formal linear growth equation $L(t) = 5.4x + 0.2$, $R = 0.99$, where $L(t)$ is the length of the pikeperch at any given time t and 5.4 is the linear growth coefficient (Fig. 3b).

The frequency distribution of lengths of each age class (sampled and calculated together) was tested for compliance with the Gaussian distribution for the significance level $\alpha = 0.05$ using the Shapiro–Wilk test; hypothesis N_0 was accepted at $\alpha \le p$. For ten age classes, the hypothesis of the distributions corresponding to the normal law is accepted: age (1) year, sample size $n = 70$ individuals, $p = 0.54$; age (2), $n = 70$ individuals, $p = 0.88$; age (3), $n = 70$ individuals, $p = 0.76$; age (4), $n = 70$ individuals, $p = 0.44$; age (5), $n = 69$ individuals, $p = 0.39$; age (6), $n = 50$ individuals, $p = 0.55$; age (8), $n = 15$ individuals, $p = 0.05$; age (9), $n = 12$ individuals, $p = 0.24$; age (10), $n = 8$ individuals, $p = 0.62$; age (11), $n = 8$ individuals, $p = 0.57$. For age (7), hypothesis N_0 is rejected: $n = 8$ individuals, $p = 0.00$.

RESULTS AND DISCUSSION

Reconstructing the average lengths of age classes not represented in the catch, as well as age classes whose numbers in the catch are small, increases the sample to a statistically acceptable size and increases the likelihood of obtaining unbiased estimates of the linear growth of pikeperch from Lake Necheritsa. In particular, the reliability of the estimates is confirmed

Table 1. Actual and inversely calculated length of pikeperch *Sander Lucioperca* of different age classes from Lake Necheritsa

n	Age, years	Actual length, mm	Age, years	Calculated length, mm	Growth rate, shares*
–	0+	–	1	77(9) / 52–98	–
–	1+	–	2	135(15) / 101–172	0.345
–	2+	–	3	191(24) / 130–236	0.259
1	3+	270	4	245(30) / 185–338	0.184
19	4+	281(25) / 246–318	5	301(32) / 235–363	0.157
18	5+	355(32) / 280–380	6	340(32) / 274–425	0.116
17	6+	371(12) / 350–390	7	398(41) / 358–531	0.156
3	7+	411(7) / 398–510	8	433(57) / 397–593	0.120
1	8+	490	9	513(65) / 430–632	0.090
3	9+	508(36) / 481–701	10	549(71) / 486–590	0.098
4	10+	585(46) / 572–756	11	613(73) / 520–630	0.108
2	11+	632(113) / 610–633	12	688(81) / 610–784	0.138
1	12+	772	13	787	0.097
1	13+	870	14	–	0.045

n is sample size, individuals; the mean value and the error of the mean is above the line is (in brackets) and min–max is below the line.
* Value of the increase in the transition from the previous age class to the next.

by a comparison of the actual and calculated lengths of individual age groups: the average proportion of deviations of sample lengths from the calculated ones is 6% in absolute value ($SD = 2\%$). Another approach, which provides indirect evidence for the acceptability of back-calculation estimates, is to test the distributions of age-class lengths for normality. The analysis is based on general biological concepts about the nature of fish growth, namely, the frequencies of the lengths of a single-age group of one ecological form of a given species are distributed normally (Chugunova, 1959; Dgebuadze, 2001; Carlson et al., 2010). As is shown above, for ten age classes, the frequency distribution of lengths obeys the Gaussian law, and only for age (7) is the hypothesis of normality rejected. The fact that only 1 of the 11 distributions does not correspond to the normal law indicates the random nature of the given event, and the overall result can be considered satisfactory. A small error in the estimate when summing the sample and calculated lengths is possible if we take into account the fact that the reverse calculation gives the length for the age t •, while all individuals in the sample are of age t+.

The von Bertalanffy linear growth equation is widely used for quantitative assessments of fish growth parameters (Beaverton and Holt, 1969; Ricker, 1979), although it is valid only in the case of asymptotic growth. An approximation of the distribution of average lengths of differently aged cohorts of pikeperch in Lake Necheritsa (Fig. 3b) by the von Bertalanffy function of the form $L(t) = L_\infty(1 - \exp(-k(t - t_0)))$ in Statistica v. 10 gives an unreasonably large maximum length of 6513 mm, as well as a very small growth coef-

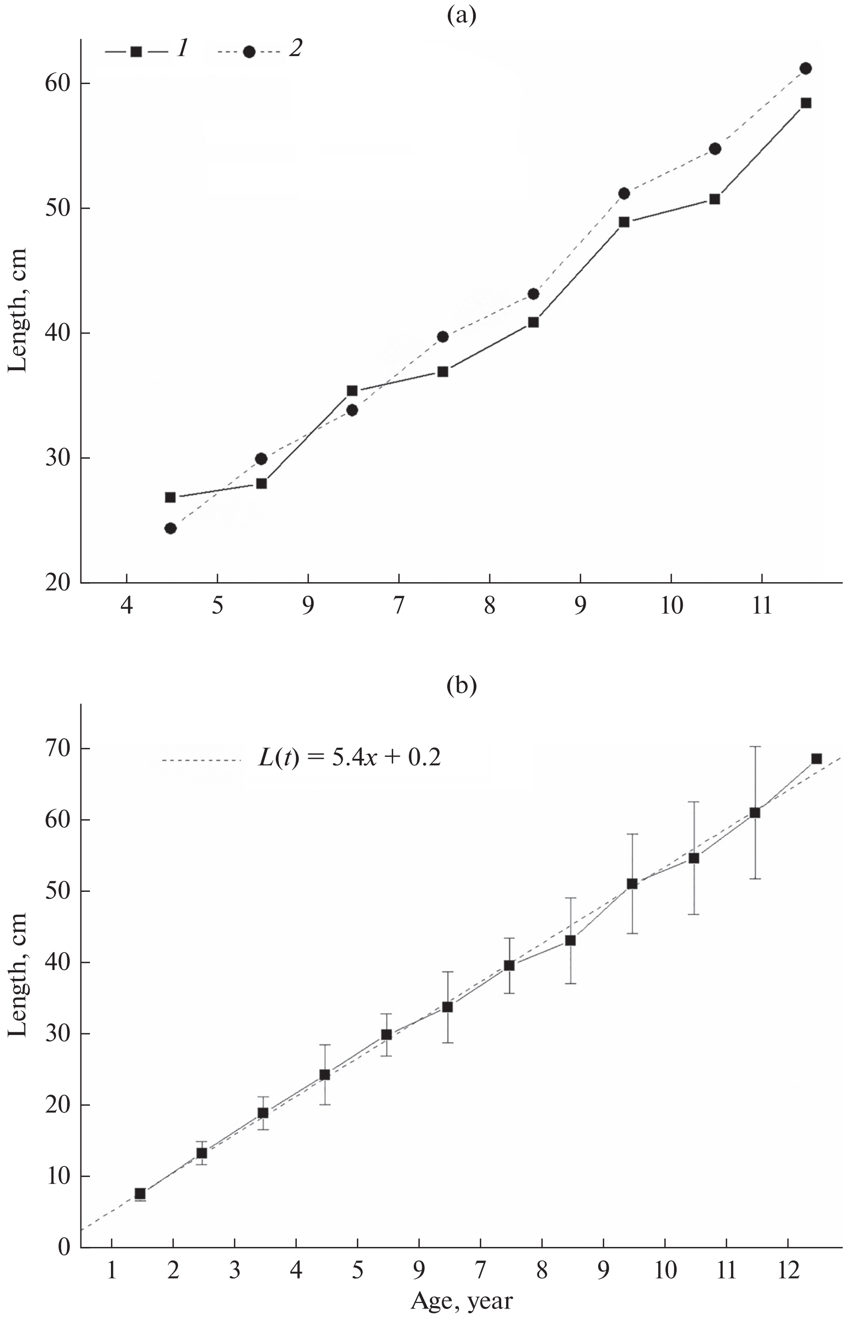

Fig. 3. Linear growth curves of pikeperch *S. lucioperca* in Lake Necheritsa (a), constructed on the basis of sample data (*1*) and inversely calculated lengths (*2*), and the linear growth curve of pikeperch (b), constructed jointly for actual and calculated lengths, with the values of standard deviations for each age class.

ficient $k = 0.008$ year^{-1} ($t_0 = 0.438$). Such a result, on the one hand, may call into question the accuracy of assessing age, and, on the other, may allow for a growth pattern that is different from asymptotic. To resolve this issue, we will provide literary data on the linear growth of pikeperch in regions with different climatic conditions.

Let us consider four populations of pikeperch from different reservoirs, including Lake Necheritsa. There are two lakes in Finland: Lake Pyhäselkä, with an area of 246 km^2 (62°20′ N, 29°33′ E) (Karjalainen et al., 1996), and Lake Saahajärvi, with an area of 2 km^2 (65°43′ N, 25°28′ E) (Vinni et al., 2009); Lake Necheritsa (56°13′ N, 28°44′ E) (our data); and the lower reaches of the Akhtuba River (47°45′ N, 46°95′ E) (Kuzishchin et al., 2016); growth graphs of pikeperch from four populations are presented in Fig. 4a. The approximation of the length distributions of pikeperch

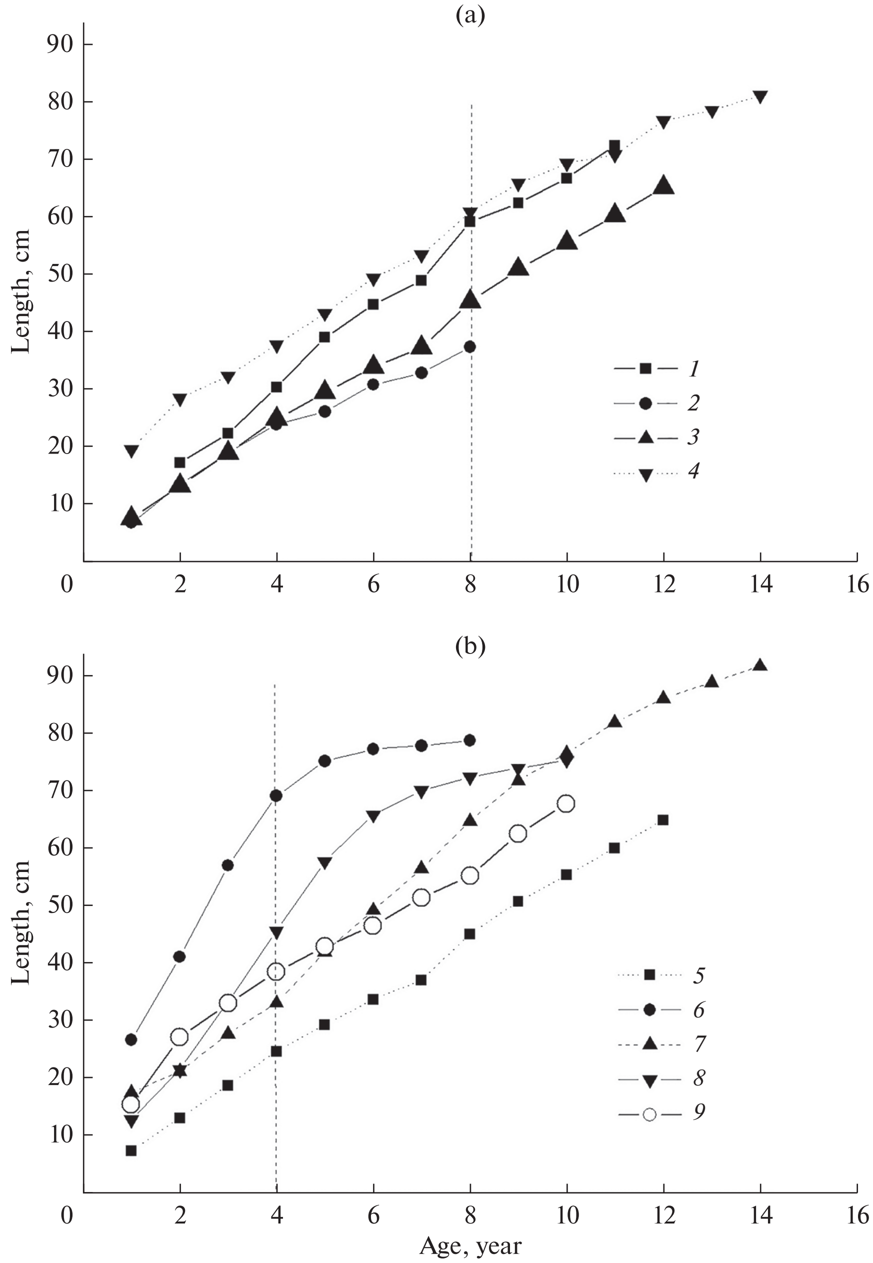

Fig. 4. Linear growth curves of pikeperch *S. lucioperca* from four different water bodies of Russia and Finland (a) and Russia and France (b). (*1*) Lake Pyhäselkä, (*2*) Lake Saahajarvi, (*3*) Lake Necheritsa, (*4*) Akhtuba River, (*5*) Lake Necheriitsa, (*6*) delta of the Rhône River, (*7*) Lake Castillon, (*8*) Lake Treignac, and (*9*) Rybinsk Reservoir.

from two lakes in Finland and the Akhtuba River by the Bertalanffy function gives the maximum lengths: 8117 mm (t_0 = –0.469, k = 0.007 year^{-1}) (Lake Pyhäselkä), 547 mm (t_0 = –0.049, k = 0.138 year^{-1}) (Lake Saahajarvi), and 1558 mm (t_0 = 0.048, k = 1.867 year^{-1}) (the Akhtuba River). For pikeperch from Lake Saahajärvi, the maximum length is biologically plausible, but the average lifespan is ~40 years—an implausibly long time interval; at the same time, for pikeperch from Lake Necheritsa, Lake Pyhäselkä, and the Akhtuba River, the ultimate lengths L_∞ themselves are unreasonably large. Thus, the von Bertalanffy linear growth equation will not be an adequate model for describing the growth functions of the species, for which a linear dependence is more suitable. The linear nature of growth is also confirmed by the distribution of shares of specific growth calculated using the Schmalhausen–Brodie formula (Table 1). Considering that the maximum length of pikeperch from Lake Necheritsa cannot be obtained by approximation, such an estimate is taken from catches. The maximum length of the pikeperch from the sample is 872 mm with a weight of 7080 g, which is apparently close to the maximum length. According to survey data (V.R. Khokhryakov), the mass of pikeperch from Lake Necheritsa reaches 10 kg.

As is known, when moving from high latitudes to low latitudes, the temperature of the environment as a whole increases, which in a certain way affects the growth rate of fish as a poikilothermic organism (Nikolsky, 1974; Odum, 1986; Bigon et al., 1989). However, the growth rate of pikeperch from Lake Pyhäselkä is similar to the growth rates of pikeperch from the Akhtuba River, although the lake is located ~1600 km to the north. Further, if we compare the linear dimensions of the pikeperch, choosing for convenience one age class, for example, 8 years (Fig. 4a), then the lengths of the fish will be different for populations living in the same region. For example, the average body length of an 8-year-old pikeperch from Lake Pyhäselkä is 37% longer than the average length of the same age class from Lake Saakhajärvi, located 200 km to the south, and it is also 23% longer than fish of the same age from Lake Necheritsa, located 500 km to the south.

Let us compare the linear growth of pikeperch from Lake Necheritsa with pikeperch from three water bodies in France, located on the southern border of the natural range of the species (Fig. 4b): Lake Treignac, area of 1 km^2 (45°57′ N, 1°83′ E), and Lake Castillon, 5 km^2 in area (Argillier et al., 2012)—both lakes are water bodies of the Weser and Verden rivers, respectively—and from the channels in the Rhône River delta of a width of 14 m and depth of 1 m (43°34′ N, 04°34′ E) (Poulet et al., 2003), as well as pikeperch from the Rybinsk Reservoir with an area of ~4580 km^2 and an average depth of ~6 m (Gerasimov et al., 2013).

Pikeperch from Lake Treignac and deltas of the Rhône River (Fig. 4b) demonstrate a pronounced asymptotic growth: the approximation of these distributions by the von Bertalanffy function gives biologically adequate limiting lengths and growth rates: L_∞ = 841 mm and k = 0.137 year^{-1} (t_0 = –0.413) for Lake Treignac and L_∞ = 904 mm and k = 0.466 year^{-1} (t_0 = –0.211) for the Rhône River. At the same time, for pikeperch from Lake Castillon, an estimated maximum growth of 5377 mm was obtained with a very small growth coefficient, k = 0.014 year^{-1} (t_0 = –1.063), which is biologically implausible. Thus, as in the case of pikeperch from the northern regions, the population of Lake Castillon shows a rather linear growth pattern, although growth slows down from age 10 onwards. As for the linear dimensions of the same age classes, for example, pikeperch from the Rhône River being significantly larger than that of the Akhtuba River, at the age of 4 years, the difference is almost 2 times. However, pikeperch in the Akhtuba River reaches the same maximum dimensions as in the Rhône River, but only until it reaches 14. At the same time, the growth of pikeperch from the Akhtuba River is similar to that of the Lake Castillon—the difference in average lengths at 14 years does not exceed 11%. Finally, the growth rate of pikeperch from the Rybinsk Reservoir is similar to that of pikeperch from Lake Necheritsa, as is evidenced by the almost parallel growth curves (Fig. 4b).

An analysis based on the relationship between growth rates and latitude does not reveal the full picture unless the area and depth of a particular reservoir are taken into account—characteristics that together determine key parameters such as trophic and oxygen indicators, the degree of eutrophication, species diversity, density parameters, etc. (Keskinen and Marjomaki, 2003; Zhivoglyadov and Lukyanov, 2018). As was shown above, pikeperch from the Lake Pyhäselkä, with an area of 246 km^2 and average depth of 10 m, is significantly larger than the pikeperch from the Lake Saahajarvi, with an area of 2 km^2 and average depth of 4 m, located to the south. The same can be said about pikeperch from the Lake Saakhajärvi when compared with pikeperch from Lake Necheritsa, area 12.8 km^2 and average depth of 6 m, although in this case the differences are not as significant. For populations of the species from France, the trends are similar: pikeperch from Lake Castillon, 5 km^2 in area, is larger and has a longer lifespan than the pikeperch from the Lake Treignac, area of 1 km^2, despite the higher growth rates in the second case. Sudak from Lake Castillon is also noticeably larger than the pikeperch from the canals in the delta of the Rhône River, although it exhibits a slower growth rate; at the same time, it has a significantly greater maximum length. Pikeperch from the Rybinsk Reservoir is on average 30% longer than that from Lake Necheritsa, located ~200 km to the south and ~352 times smaller in area (4580 km^2 and ~13 km^2, respectively). As in the above cases, larger fish live in a larger body of water.

It should be noted that all the southern water bodies under consideration, like the Akhtuba River, are flowing; the presence of a current generally stabilizes the oxygen regime even at high ambient temperatures, which has a positive effect on fish growth and the survival of their young, which in pikeperch is very sensitive to changes in oxygen concentration (Frisk et al., 2012).

In addition to the latitude and size of the reservoir, the proximity of a relatively warm sea, which moderates the climate, especially in high latitudes, is of no small importance. Thus, the regions of central Siberia, lying at the same latitude as Finland and extending beyond the natural habitat of pikeperch, are characterized by a much harsher climate, where pikeperch has a growth rate and maximum sizes significantly lower than in donor populations, despite the fact that it has successfully acclimatized (Semenchenko and Podorozhnik, 2014; Rostovtsev et al., 2016). It should be noted that southern populations of pikeperch generally show higher growth rates and more pronounced asymptotic growth compared to populations from northern regions. An analysis of data from a number of works (Ablak and Yilmaz, 2004; Milardi et al., 2011; Pe´rez-Bote and Roso, 2012; Nolan and Britton, 2018a) showed that a pronounced asymptotic growth of pikeperch occurs only at low latitudes, while growth close to linear is observed to varying degrees throughout the entire range. Data on Lake Necheritsa partially confirms this position. It is also noteworthy that in low latitudes the pikeperch reaches a greater maximum length with a weakly expressed asymptotic growth than with a characteristic asymptotic growth. This may be associated with a rapid "acceleration" of growth rates and subsequently an equally sharp slowdown, which is characteristic of asymptotic growth, as a result of which the growth potential of the organism is used up more quickly (Tytler and Calow, 1985). In the case of growth close to linear, a smooth "acceleration" of the growth rate maintains its uniformity throughout life, making it possible, all other things being equal, to achieve a greater maximum length. It should be noted that, in general, the shorter the lifespan of the pikeperch is, the less pronounced the asymptotic growth.

In addition to abiotic environmental parameters, growth rates may be associated with the density characteristics of the populations of both the pikeperch itself and the species that form the ichthyocenosis. According to research by the Pskov branch of the State Research Institute of Lake and River Fisheries, the share of pikeperch in the Lake Necheritsa in the total number of all species in 1998 was ~0.5% (Alexandrov and Afanasyev, 1998), while for catches in 2022 it reached ~4%. Given the representativeness of the samples, it can be concluded that the proportion of pikeperch in the ichthyocenosis increased 8 times in the period 1989–2022. Moreover, an increase in the proportion of the species is possible both as a result of an increase in the number of pikeperch itself and a decrease in the number of other fish species, for example bream. A final conclusion about the state of stocks in retrospect can only be made on the basis of an analysis of estimates of total abundance and biomass, since it is the density characteristics that serve as key indicators of the abundance of all species in the ichthyocenosis.

The quantitative shares of different species in the diet and catch of pikeperch are as follows: roach 32 and 56%, white bream 24 and 13%, perch 14 and 16%, bream 2 and 10%, and pikeperch 6 and 4%, respectively. A comparison of the shares for perch and pikeperch demonstrates their high similarity in diet and catch; for roach, white bream, and bream, significant differences between the shares in the food bolus and catch can be attributed to the small sample size, leading to bias in the sample estimate relative to general importance. This is indicated by the opposite fluctuations in the proportions of the same species in the catch and in the food bolus. In particular, the proportion of roach in the catch (32 and 56%) is ~0.57 times greater than in the lump, and the proportion of white bream (13 and 24%) is 0.54 times less. It should also be noted that pikeperch to a certain extent limits its own numbers in the ecosystem, since any predator regulates the numbers of species, including, in the presence of cannibalism, its own (Menshutkin, 1971; Nolan and Britton, 2018b; Rahmdel and Falahatkar, 2021).

An interpretation of the relationship between the linear dimensions of different age groups and latitude and the size of the water body and its food supply may seem too simple, since there are significantly more factors influencing growth. To understand the complex nature of the impact of environmental parameters on the size–age characteristics of a population, it is necessary to study a specific water body, which will allow us to take into account the contribution of each individual factor, as well as to identify key parameters that primarily determine growth dynamics. For example, energy expenditure on metabolic processes in poikilothermic organisms and fish decreases in the direction from north to south (Bigon et al., 1989), but the amount of oxygen dissolved in the water also decreases. A decrease in oxygen concentration, in addition to the direct physiological effects associated, in particular, with the suppression of reproductive functions (Lappalainen et al., 2003) and with energy expenditure on aeration of the gill epithelium (Frisk et al., 2012), leads to a change in the species composition of the biota and, consequently, the quantity and quality of food (*Species,* Biró, 2003; Sterligova et al. 2020; Pe´rez-Bote and Roso, 2012; Boussebaa et al., 2020). At the same time, the presence of a current promotes mixing, stabilizing the oxygen regime throughout the entire thickness of the water, which can partially neutralize the effect of elevated temperature on the concentration of dissolved oxygen. If in the southern regions relatively high temperatures are combined with a large area of the reservoir, as a result of which the diversity of biotopes with different quantitative combinations of environmental factors increases, then the growth rate and life expectancy can be high (Argillier et al., 2012). Organic pollution also has a significant impact. It almost always leads to eutrophication, which reduces the concentration of dissolved oxygen, which in turn slows down the growth rate of mainly younger age groups of fish (Sandström, Karås, 2002; Frisk et al., 2012). Finally, fishing is also an important factor, which to one degree or another always changes the average size of age classes (Gerasimov et al., 2013).

CONCLUSIONS

The distribution of average lengths of pikeperch of different age classes from Lake Necheritsa is well approximated by a linear function $L(t) = 5.4x + 0.2$,

$R = 0.99$. The pikeperch population is represented by 13 age classes, where the maximum sample length is 872 mm. Growth occurs against the background of the combined influence of climatic factors associated with latitude, as well as the size and food supply of the reservoir. The share of pikeperch in the 2022 sample reached 4% of the total number, which is 8 times higher than its share in Lake Necheritsa in 1998 and indicates a fairly high relative abundance of pikeperch in the ichthyocenosis. Six common fish species were found in the food bolus of pikeperch, including juvenile pikeperch itself: their ratio and comparison with the same species in the sample presumably indicate a lack of selectivity in the diet. When the abundance is high enough, pikeperch can act as a regulator of its own numbers. The absence of fishing pressure and sources of pollution allows us to assume that the pikeperch population from Lake Necheritsa does not experience strong anthropogenic impact, which makes it possible to consider it a natural standard of the population of this species in the Pskov Lake District.

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ETHICS APPROVAL AND CONSENT TO PARTICIPATE

Sampling methods were carried out in accordance with the ethical guidelines and rules approved by the Bioethics Committee of Moscow State University, regulated by the Russian Bioethics Committee (bioethics.ru/eng/rucommittee). Data collection protocols 163-02-2022 were approved at the commission meeting on February 18, 2022. The study was conducted in accordance with the ARRIVE guidelines (arriveguidelines.org).

CONFLICT OF INTEREST

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

REFERENCES

Ablak, O. and Yilmaz, V., Growth properties of pikeperch (*Sander lucioperca* (L., 1758)) living in Hirfanli dam lake, *Turk. J. Vet. Anim. Sci.*, 2004, vol. 28, p. 455.

Akbarzadeh, A., Farahmand, H., Shabani, A.A., et al., Morphological variation of the pikeperch *Sander lucioperca* (L.) in the southern Caspian Sea, using a truss system, *J. Appl. Ichthyol.*, 2009, vol. 25, p. 576. https://doi.org/10.1111/j.1439-0426.2009.01308.x

Aleksandrov, Yu.V. and Afanas'ev, E.A., Biological justification of amateur and sport fishing in the reservoirs of the state national natural park "Sebezhsky", 1998. https://github.com/Feodor1974/Sebezhsky-fish-biomass-1990year

Aleksandrov, Yu.V. and Kur'yanovich, V.I., Lampreys (Petromyzonidae, Cyclostomata) and fish (Pisces). Biodiversity and rare species of the Sebezhsky National Park, *Tr. S.-Peterb. O-va. Estestvoispyt.,* 2001, vol. 4, p. 199.

Argillier, C., Barral, M., and Irz, P., Growth and diet of the pikeperch *Sander lucioperca* (L.) in two French reservoirs, *Arch. Pol. Fish.*, 2012, vol. 20, no. 3, p. 191. https://doi.org/10.2478/v10086-012-0024-0

Begon, M., Harper, J.L., and Townsend, C.R., *Ecology. Individuals, Populations and Communities*, Oxford: Blackwell Sci., 1989, vol. 2.

Biverton, R. and Kholt, S., *Dinamika chislennosti promyslovykh ryb* (Dynamics of the Number of Commercial Fish), Moscow: Pishch. Prom-st., 1969.

Boussebaa, M., Ferrat, L., Ouahab, S., et al., Food preferences of Pike Perch, *Sander lucioperca* (Linnaeus, 1758) in Morocco, *E3S Web of Conferences*, 2020, vol. 150, p. 02011. https://doi.org/10.1051/e3sconf/202015002011

Carlson, S., Kottas, A., and Mangel, M., Bayesian analysis of size-dependent overwinter mortality from size-frequency distributions, *Ecology*, 2010, vol. 91, no. 4, p. 1016. https://doi.org/10.1890/09-0252.1

Chugunova, N.I., *Rukovodstvo po izucheniyu vozrasta i rosta ryb* (Guide to the Study of Fish), Moscow: Akad. Nauk SSSR, 1959.

Dgebuadze, Yu.Yu., *Ekologicheskie zakonomernosti izmenchivosti rosta ryb* (Ecological Patterns of Fish Growth Variability), Moscow: Nauka, 2001.

Frisk, P., Skov, V., and Steffensen, J., Thermal optimum for pikeperch (*Sander lucioperca*) and the use of ventilation frequency as a predictor of metabolic rate, *Aquaculture*, 2012, vol. 324, p. 151. https://doi.org/10.1016/j.aquaculture.2011.10.024

Gerasimov, Yu.V., Strel'nikov, A.S., and Ivanova, M.N., Dynamics of structural indices of populations of zander *Stizostedion lucioperca* (Percidae) of the Rybinsk Reservoir for 1954–2010, *Vopr. Ikhtiol.*, 2013, vol. 53, p. 57. https://doi.org/10.7868/S0042875213010050

Gladyshev, M.I., Biomanipulation as an instrument for water quality control in continental water bodies (Literature review over 1990–1999), *Biol. Vnutr. Vod,* 2001, no. 2, p. 3.

Jůza, T., Blabolil, P., Čech, M., Draštík, V., et al., Distribution patterns, annual density changes, growth and mortality of pikeperch (*Sander lucioperca* (L., 1758)) fry following oligotrophication of a reservoir, *Ecol. Freshwater Fish*, 2023, vol. 32, no. 4, p. 724. https://doi.org/10.1111/eff.12718

Karjalainen, J., Lehtonen, H., and Turunen, T., Variation in the relative year-class strength of pikeperch, *Stizostedion lucioperca* (L.), in two Finnish lakes at different latitudes, *Ann. Zool. Fenn.*, 1996, vol. 33, p. 437.

Keskinen, T. and Marjomäki, T.J., Growth of pikeperch in relation to lake characteristics: total phosphorus, watercolour, lake area and depth, *J. Fish Biol.*, 2003, vol. 63, no. 5, p. 1274.
https://doi.org/10.1046/j.1095-8649.2003.00249.x

Kovalenko, E.O., Pashinova, N.G., and Moskul, G.A., Morphological characteristics of pike perch (*Sander lucioperca* (Linnaeus, 1758)) of the Krasnodar reservoir, *Tr. Kransoyarsk. Gos. Agrar. Univ.*, 2014, vol. 5, no. 50, p. 58.

Kovtun, A.A., The age and linear growth of autumn chum salmon Oncorhynchus keta (Walbaum) on Sakhalin, *Vopr. Ikhtiol.*, 1981, vol. 21, no. 6, p. 1030.

Krpo-Ćetković, J. and Stamenković, S., Morphological differentiation of the pikeperch *Stizostedion lucioperca* (L.) populations from the Yugoslav part of the Danube, *Ann. Zool. Fenn.*, 1996, vol. 33, p. 711.

Kushnarenko, A.I., Fomichev, O.A., Sidorova, M.A., et al., Status of stocks and forecast of catch of semi-anadromous fish for 2005, in *Rybokhozyaistvennye issledovaniya na Kaspii. Rezul'taty NIR za 2003 god* (Fisheries Research in the Caspian Sea. Results of Research Work for 2003 Year), Astrakhan: Kasp. Nauchno-Issled. Nauchno-Issled. Inst. Khoz. Okeanogr., 2004.

Kuzishchin, K.V., Samoilov, K.Yu., Gruzdeva, M.A., and Pavlov, D.S., Distribution, population structure, and some biological distinctions of pikeperch *Sander lucioperca* of the channel part of the Akhtuba river (Volga-Akhtuba water system), *J. Ichthyol.*, 2016, vol. 56, no. 5, p. 702.
https://doi.org/10.7868/S0042875216050088

Lappalainen, J., Dörner, H., and Wysujack, K., Reproduction biology of pikeperch (*Sander lucioperca* (L.)) – a review, *Ecol. Freshwater Fish*, 2003, vol. 12, p. 95.
https://doi.org/10.1034/j.1600-0633.2003.00005.x

Lea, E., *On the Method used in the Herring Investigation*, Circonstance du Cons. Perm. Int. pour l`Expl. De la Mer, 1910, no. 30.

Ložys, L., Seasonal migrations of pikeperch (Sander lucioperca) from the Curonian Lagoon to the Baltic Sea and advantages of the phenomenon, *Acta Zool. Litu.*, 2003, vol. 13, no. 2, p. 188.
https://doi.org/10.1080/13921657.2003.10512562

Menshutkin, V.V., *Matematicheskoe modelirovanie populyatsii i soobshchestv vodnykh zhivotnykh* (Mathematical Modeling of Populations and Communities of Aquatic Animals), Leningrad: Nauka, 1971.

Milardi, M., Lappalainen, J., Malinen, T., Vinny, M., and Ruuhijärvi, J., Problems in managing a slow-growing pikeperch *Sander lucioperca* (L.) population in Southern Finland, *Knowl. Manage. Aquat. Ecosyst.*, 2011, vol. 400, p. 1.
https://doi.org/10.1051/kmae/2011010

Mina, G.A. and Klevezal', G.A., *Rost zhivotnykh (Animal Growth)*, Moscow: Nauka, 1976.

Nikol'skii, G.V., *Teoriya dinamiki stada ryb* (The Theory of Fish Shoal Dynamics), Moscow: Pishch. Prom-st., 1974.

Nolan, E.T. and Britton, J., Spatial variability in the somatic growth of pikeperch *Sander lucioperca*, an invasive piscivorous fish, *Ecol. Freshwater Fish*, 2018a, vol. 28, no. 2, p. 1.
https://doi.org/10.1111/eff.12456

Nolan, E.T. and Britton, J.R., Diet of invasive pikeperch *Sander lucioperca*: developing non-destructive tissue sampling for stable isotope analysis with comparisons to stomach contents analysis, *Knowl. Manage. Aquat. Ecosyst.*, 2018b, vol. 419, p. 1. 10.1051/kmae/2018037

Odum, E., *Basic Ecology*, Philadelphia: Saunders College, 1983, vol. 2.

Parés-Casanova, P.M. and Cano, L., Preliminary study of isometry in pikeperch (*Sander lucioperca*) from Ivars and Vilasana lake, Spain, *Ann. Exp. Biol.,* 2014, vol. 2, no. 3, p. 12.

Pérez-Bote, J.L. and Roso, R., Growth and length–weight relationships of Sander lucioperca (Linnaeus, 1758) in the Alcántara Reservoir, south-western Spain: comparison with other water bodies in Eurasia, *J. Appl. Ichthyol.*, 2012, vol. 28, p. 264.
https://doi.org/10.1111/j.1439-0426.2011.01918.x

Poulet, N., Forgeois, S., Critelli, A.J., et al., Life history traits of the pikeperch *Sander lucioperca* (L.) in the southern outskirts of its distribution area, *Proceedings of the 3rd International Percid Fish Symposium: Percis III*, Madison, 2003.
https://www.researchgate.net/publication/258110519

Pravdin, I.F., *Rukovodstvo po izucheniyu ryb* (Guide to the Study of Fish), Moscow: Pishch. Prom-st., 1966.

Rahmdel, K.J. and Falahatkar, B., Adaptation of pikeperch (*Sander lucioperca*) to formulated diets: A review, *Fish. Aquat. Life,* 2021, vol. 29, p. 1.
https://doi.org/10.2478/aopf-2021-0001

Rikker, U.E., *Metody otsenki i interpretatsiya biologicheskikh pokazatelei populyatsii ryb* (Methods for the Assessment and Interpretation of Biological Characteristics of Fish Populations), Moscow: Pishch. Prom-st., 1979.

Rostovtsev, A., Interesova, E.A., Babkina, I.B., et al., Fish harvest, age and growth of *Sander lucioperca* (Linnaeus, 1758) in the basin of the Middle Ob, *Vestn. Nauchn. Gos. Agrar. Univ.*, 2016, vol. 3, no. 40, p. 105.

Rukovodstvo po izucheniyu pitaniya ryb v estestvennykh usloviyakh (Guide to the Study of Fish Feeding in the Wild), Moscow: Akad. Nauk SSSR, 1961.

Sandström, A. and Karås, P., Effects of eutrophication on young-of-the-year freshwater fish communities in coastal areas of the Baltic, *Environ. Biol. Fishes*, 2002, vol. 63, no. 1, p. 89.
https://doi.org/10.1023/A:1013828304074

Semenchenko, N.N. and Podorozhnik, E.V., Obyknovennyi sudak Sander lucioperca (L) r. Amur: rezul'taty akklimatizatsii, *Chteniya pamyati V. YA. Levanidova* (Readings in Memory of V. Ya. Levanidov), 2014, no. 6, p. 611.

Shmal'gauzen, I.I., *Opredelenie osnovnykh ponyatii i metodika issledovaniya rosta* (Definition of Basic Concepts and Methods of Growth Research), Moscow: Biomedgiz, 1935.

Shorygin, A.A., *Pitanie i pishchevye vzaimootnosheniya ryb Kaspiiskogo morya* (Nutrition and Food Relationships of Fish of the Caspian Sea), Moscow: Pishchepromizdat, 1952.

Specziár, A. and Bíró, P., Population structure and feeding characteristics of Volga pikeperch, *Sander volgensis* (Pisces, Percidae), in Lake Balaton, *Hydrobiologia*, 2003, vol. 506, p. 503.

Sterligova, O.P., Ryukshiev, A.A., and Il'mast, N.V., The comparative biological characteristic of pike-perch *Sander lucioperca* (L.) in Lakes Onega and Vygozero, *Biol. Vnutr.*

Vod, 2012, no. 2, p. 55.
https://doi.org/10.1134/S1995082912020149

Strel'nikov, A.S., Population of zander Stizostedion lucioperca in Rybinsk reservoir in conditions of new commercial relations, *Vopr. Ikhtiol.*, 1996, vol. 36, no. 4, p. 481.

Tanasiichuk, V.S., On the adaptive capabilities of the pike perch *Stizostedion lucioperca* (L.), *Vopr. Ikhtiol.*, 1974, vol. 14, no. 5, p. 806.

Tesfaye, M., Souza, A., Soukalová, K., et al., Somatic growth of pikeperch (Stizostedion lucioperca) in relation to variation in temperature and eutrophication in a Central Europe Lake, *Fish. Res.*, 2023, vol. 267, p. 1.
https://doi.org/10.1016/j.fishres.2023.106824

Tytler, P. and Calow, P., *Fish Energetics. New Perspectives*, London and Sydney: Croom Helm, 1985.

Vinni, M., Lappalainen, J., Malinen, T., and Lehtonen, H., Stunted growth of pikeperch Sander lucioperca in Lake Sahajärvi, Finland, *J. Fish Biol.*, 2009, vol. 74, p. 967.
https://doi.org/10.1111/j.1095-8649.2009.02181.x

Vovk, F.I., *A single method for reconstruction of fish growth by scales, Tr. Biol. Stn. "Borok" Akad. Nauk SSSR*, 1956, vol. 2.

Zhivoglyadov, A.A. and Luk'yanov, S.V., Stock assessment of the current state of the zander *Sander lucioperca* population in the Azov sea basin, *Vopr. Rybolov.*, 2018, vol. 19, no. 4, p. 405.

Zykov, L.A. and Ivanov, V.P., Ecological and geographical variability of the pike-perch *Lucioperca lucioperca* (L.) growth within the natural habitat, *Vestn. Agrar. Gos. Tekh. Univ.,* 2008, vol. 3, no. 44, p. 26.

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