Intragroup variability of growth in perch, *Perca fluviatilis* L., 1758 (Percidae) in waterbodies in the watershed of the Middle Ishim

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ABSTRACT. As a result of the research carried out in 2016-2021 on the lakes of the Shchuchinsk-Borovoe resort area and on the Ishim River, material was obtained on the intragroup variability in the growth of perch. The absence of sexual variability was noted, which is explained by the relative stability and positive influence of environmental factors. The revealed generational variability of growth showed both a noticeable decrease in its rates in Lake Shchuchie and a significant increase in Lakes Borovoe, Katarkol and Tekekol. These processes of linear growth dynamics are caused by the interaction of hydrological and trophic factors. In all samples, a division of the general population into two clusters (incremental morphs) with different growth characteristics was observed. They correspond to the traditionally identified "coastal" and "pelagic" morphs of perch from the largest bodies of water (e.g. the former Aral Sea), but their differences are revealed statistically and not visually. Perch populations differ in the proportion of these clusters, which largely determines the average length per generation in general samples. Based on the characteristics of the back calculation of linear growth for clusters, all samples can be divided into two types, which in miniature resemble species-specific evolutionary r- and K-strategies (but not identical to it).

Keywords: perch, growth, variability, generations, clustering, environmental factors

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1. Introduction

Environmental conditions play a critical role in determining the development, behaviour and evolution of biological systems. Of course, this environment is not always homogeneous, and differences in factors such as temperature, food availability and light, among others, can lead to heterogeneous conditions and heterogeneous effects on organisms. These mechanisms can have a significant impact on the dynamics of performance, response norms and evolutionary processes in biological systems (Swartz, 1969; [Mayr, 1970;](#page-8-0) [Gilpin,](#page-7-0) [1987](#page-7-0); [Campeas et al., 2009;](#page-7-1) [Shinohara et al., 2022;](#page-8-1) da Silva Lima et al., 2022).

From an evolutionary perspective, environmental heterogeneity can serve as a catalyst for the development of new adaptations and traits. Organisms that can adapt to different environments have a greater chance of surviving and passing on their genetic characteristics to offspring.

However, it should be noted that environmental

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heterogeneity can also pose challenges for organisms. Some conditions can be extreme and require organisms to exert significant effort to survive. This can lead to stress, deterioration and reduced reproductive capacity (de Vries, 1971; [Fry, 1971](#page-7-2); [Nikolsky, 1974](#page-8-2); [Richards](#page-8-3) [et al., 2009](#page-8-3)). The adaptation of organisms to different conditions and the diversity of populations help to reduce risks and maintain the viability of species.

One of the most important adaptive mechanisms is the growth of an organism, defined as a change in its weight and linear dimensions over time [\(Mina and](#page-8-4) [Klevezal, 1976;](#page-8-4) [Jobling, 2002](#page-7-3)). The nature and rate of growth are adaptive functions. The body reacts to environmental changes and responds at the level of metabolic reactions. At the same time, most researchers agree that growth is one of the most variable properties of the body ([Mina and Klevezal, 1976;](#page-8-4) [Dgebuadze,](#page-7-4) [2001](#page-7-4); [Kuznetsova, 2003\)](#page-7-5).

This article is devoted to assessing intragroup variability in the growth of perch *Perca fluviatilis*

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Linnaeus, 1758, which is one of the most abundant species among the ichthyofauna of the waterbodies of the watershed of the Ishim River.

The dynamics of various growth indicators within populations in groups of different gender and generation were assessed. An attempt was made to determine the belonging of individuals to various ecological morphs, distinguished by growth rates, and to assess the differences between these groups.

2. Materials and methods

The data were collected during 2016-2021 from the Shchuchinsk-Borovoe lakes group (Lakes Bolshoe Chebachie (2016-2021); Borovoe (2016-2018); Shchuchie (2016-2019); and Tekekol (2016-2021), in Akmola oblast, Kazakhstan) and on the River Ishim (2018-2020) in the vicinity of Astrakhanka village (Akmola oblast, Kazakhstan) ([Fig. 1](#page-1-0)). The morphometric parameters of the waterbodies were assessed using standard methods [\(Kitaev, 2007](#page-7-6)).

An operculum was used ([Le Cren, 1947](#page-7-7)) when measuring along the fish's vertical ray [\(Krainyuk et](#page-7-8) [al., 2020](#page-7-8)) to determine age and back-calculate length. The back calculation of length was carried out using the simple Dahl-Lea proportions method, according to R.I.C.C. [Francis \(1990\).](#page-7-9) A total of 1159 specimens were examined.

To determine the variables of the von Bertalanffy equation (hereinafter referred to as VBGE), the Ford-Walford equation indices α and β were previously calculated based on the formula [\(Milovanov, 2019\)](#page-8-5):

*L*_{*i*+1} = $\alpha + \beta L$ ^{*i*}

where L_i is the length of the individual in the initial year of life and L_{i+1} is the length of the fish in the next year of life.

This equation is solved by the least squares method.

The asymptotic length of VBGE is determined by the formula:

*L*_∞ = $\alpha/(1-\beta)$

The growth constant VBGE is found by the formula:

k = *lnβ*

The initial age at which the length would be 0 is found for each age and then averaged:

 $t_o = 1 + ((ln(L_i/L_o)/k))$

Based on the indicators obtained, the Pauly-Munro growth-efficiency index is determined (growth performance index) ([Pauly and Munro, 1984](#page-8-6)):

 $\Phi' = \lg k + 2 \cdot \lg L$ _∞

The "growth potential realization coefficient" ([Krainyuk, 2023\)](#page-7-10) was calculated through the ratio of the arithmetic mean of the last calculated value (l_{max}) to the asymptotic length VBGE:

 $R = 1_{max}/ L_{\infty} \cdot 100\%$

This coefficient (R) allows us to correlate the elongation of the theoretical size-age series and back calculated length. This indicator is close to that used ([Kleanthidis and Stergiou, 2006](#page-7-11)), but in this case the calculated maximum length is used, not the observed one.

To identify incremental (Latin: incrementum – speed, tempo) morphs, the k-means clustering method was used. It was accepted that the data sets are a priori divided into two clusters, which corresponds to the presence of coastal and pelagic forms in perch ([Shatunovsky and Ruban, 2013\)](#page-8-7).

Clusters were identified from back-calculated growth data sets with separate endpoints for ranges of 1-4, 1-5, 1-6 years of life. The final cluster number of a particular individual was assigned based on the last, most extensive, aggregate in which it participated. The level of cluster mismatch was calculated when comparing pairwise adjacent sets. The maximum threshold percentage of mismatches should not exceed 15%, otherwise these data should be treated with caution. Individuals under four full years of age were excluded from the analysis.

Statistical processing of the material was carried out according to standard methods ([Plokhinsky, 1970;](#page-8-8) Zhivotovsky, 1991) using MS Excel 2003 [\(Korosov and](#page-7-12)

Fig.1. Map of location of investigated waterbodies

[Gorbach, 2007\)](#page-7-12) and IBM SSPS Statistics v. 22 (Bühl and Zöfel, 2005). The significance level was accepted as significant at $\alpha \leq 0.001$ for all types of variability (sex, generation, cluster).

3. Results

Of the six reservoirs studied, five are lakes and one is a river section (Table 1). The lakes vary in area (up to 1000 ha and more) and the average depth of three lakes is up to 3 m, two (Shchuchie and Bolshoe Chebachie) being deeper (at over 7 m). However, they also have differences that have a significant impact on the biota of the waterbodies. The floor of Lake Bolshoe Chebachie has a certain share of shallow waters and is subject to significant interannual fluctuations in water content, unlike Lake Shchuchie with its pit type.

The hydrochemical regime of the bodies of water is quite different: fresh, with mineralization up to $0.5\,\mathrm{g}/\mathrm{dm}^3$; brackish, with mineralization up to $1.0\,\mathrm{g}/\mathrm{dm}^3$; and brackish, with mineralization above 1 g/dm³. The water of the lakes is of the hydrocarbonate class; while in the river it is of the chloride class, mainly of the sodium group, and in two cases (Lakes Borovoe and Shchuchie – they are also less mineralized) calcium.

Sexual variability in the linear growth of perch in the studied waters is not evident (Table 2). The existing trends towards differences were not even at the level of $\alpha \leq 0.01$. A similar situation was also noted in previous articles ([Krainyuk et al., 2020](#page-7-8); [Krainyuk, 2022\)](#page-7-13).

Differences in growth between generations within the same waterbody were clearly expressed in only eight cases ($\alpha \leq 0.001$). To this, we can add four more cases where the reliability of differentiation was close to $\alpha = [0.001; 0.01]$. For aggregates from the Lake Bolshoe Chebachie and River Ishim, no significant differences in growth between generations were noted at all.

Figures 2-5 show the growth dynamics curves by generation. The linear regression trend vector (continuous line) is for illustrative purposes only.

In Lake Shchuchie [\(Fig. 2\)](#page-3-0), different generations show differentiation of growth in the mid-age period (5-7 years). At the same time, the trends in the dynamics of growth indicators are clearly negative, although at five years of age, younger generations show some improvement in performance.

The other three samples are characterized by increasing growth rates at certain stages. Thus, perch from Lake Tekekol ([Fig. 3\)](#page-3-1) demonstrate a significant increase in the average calculated indicators at two and three years over 11 generations. Naturally, the increase in indicators was not straightforward: significant deviations were also noted.

The increase in growth rates in individuals from Lake Katarkol [\(Fig. 4\)](#page-4-0) during the 2nd and 3rd years of life was almost linear, and only the last two generations of all those studied had some deviations. Another age at which the differences were significant (nine years) showed high fluctuations with a general increase in average scores.

A significant increase in the average calculated linear dimensions of perch from Lake Borovoe was observed in the range of four years – from two to five years of life over 10 generations [\(Fig. 5](#page-4-1)).

All studied groups of perch show a stable, reliable division into clusters (incremental morphs) in the range from the first year of life to generations 5-8 (Table 3).

Table 1. Description of water bodies

| Water body | Sex | Back calculated length, cm | | | | | | | | | | Number | | | | |
|---------------------------|------------|----------------------------|----------------|----------|----------------|------|------|--------------------------|------------------------------|----------------|------------------------------|--------------------------|----------------|----------------|------------------------------|-----|
| | | $\mathbf{1}$ | $\overline{2}$ | 3 | $\overline{4}$ | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | |
| Lake Katarkol | female | 5.6 | 8.9 | 11.9 | 14.3 | 16.5 | 18.5 | 20.6 | 22.6 | 24.4 | 26.7 | 28.7 | 31.1 | 32.2 | ٠ | 139 |
| | male | 5.6 | 8.9 | 11.7 | 14,2 | 16,4 | 18,6 | 20,6 | 22,6 | 24,5 | 27,2 | 29,2 | 30.0 | 31,6 | ÷, | 107 |
| | ANOVA, F | Ω | 0,5 | 0,9 | 0.9 | 0.1 | 0.,2 | Ω | $\mathbf{0}$ | Ω | 1.2 | 0.5 | | | \blacksquare | |
| Lake Borovoe | female | 5.7 | 9.3 | 12.0 | 14.2 | 16.1 | 17.8 | 19.9 | 22.0 | 24.3 | 26.4 | 28.6 | 30.0 | 32.5 | 34.1 | 88 |
| | male | 5.9 | 9.5 | 12.2 | 14.4 | 16.2 | 18.1 | $\overline{}$ | $\qquad \qquad \blacksquare$ | \blacksquare | | $\overline{}$ | | | $\overline{}$ | 48 |
| | ANOVA, F | 1.4 | 1.4 | 1.0 | 1.2 | 0.1 | 0.2 | $\overline{}$ | $\overline{}$ | \overline{a} | | $\overline{}$ | | | $\overline{}$ | |
| Lake Shchuchie | female | 5.6 | 8.9 | 11.8 | 14.5 | 16.6 | 18.4 | 20.5 | 22.0 | 23.6 | 25.9 | | | | \blacksquare | 57 |
| | male | 5,0 | 8.9 | 11.8 | 14.2 | 16.3 | 17.9 | 19.6 | 20.8 | \blacksquare | \blacksquare | \blacksquare | \blacksquare | \overline{a} | \blacksquare | 47 |
| | ANOVA, F | 0.2 | 0.1 | Ω | 1.6 | 4.5 | 5.7 | 7.4 | 3.0 | \blacksquare | | | | | ٠ | |
| Lake Tekekol | female | 5.9 | 9.0 | 11.4 | 13.6 | 16.0 | 18.1 | 20.0 | 21.7 | 23.3 | 24.8 | | | | | 88 |
| | male | 5.8 | 8.8 | 11.3 | 13.5 | 15.9 | 17.9 | 19.7 | 21.2 | 22.8 | 23.8 | $\overline{}$ | \blacksquare | | $\qquad \qquad \blacksquare$ | 62 |
| | ANOVA, F | 1.1 | 1.5 | 0.4 | 1.2 | 0.6 | 0.3 | 1.9 | 5.9 | 3.4 | 7.7 | $\overline{}$ | | | $\qquad \qquad \blacksquare$ | |
| Lake Bolshoe Chebachie | female | 6.0 | 9.1 | 11.9 | 14.5 | 16.5 | 18.6 | 20.7 | 22.6 | 24.3 | 25.9 | 27.3 | 28.3 | 30.5 | 31.7 | 189 |
| | male | 6.1 | 9.3 | 12.0 | 14.5 | 16.7 | 18.8 | 20.7 | 22.4 | 24.1 | 25.8 | 26.9 | | | ۰ | 182 |
| | ANOVA, F | 1.1 | 4.1 | 1.5 | 0.1 | 1.5 | 3.0 | 0.1 | 1.9 | 2.0 | Ω | 0.7 | | ٠ | ۰ | |
| River Ishim | female | 5.9 | 9.9 | 13.0 | 15.5 | 17.6 | 19.7 | 21.6 | 23.0 | 25.1 | 26.3 | | | \overline{a} | | 106 |
| | male | 5.8 | 9.8 | 12.8 | 15.2 | 17.3 | 19.1 | 22.5 | 23.6 | 25.3 | $\qquad \qquad \blacksquare$ | $\overline{}$ | | | | 46 |
| | ANOVA, F | 0.2 | Ω | 1.2 | 3.2 | 1.5 | 1.8 | 2.1 | 0.9 | 0.2 | $\overline{}$ | | | \overline{a} | | |

Table 2. Growth sex variability at perch from investigated water bodies

At the older ages, the differences between the morphs are smoothed out, mainly due to the statistical effect of their small number in the sample. It is worth noting a fairly strict division into morphs, shown by the low level of discrepancy in belonging to them between the adjacent set of generations – from 0 to 10.7%.

The ratio of clusters in the total sample is most often approximately equal (Table 3), with the exception of Lake Borovoe, where fast-growing ones predominate, and Lake Shchuchie, where individuals with slower linear growth dominate. This ratio has a fairly strong influence on the performance of the sample as a whole.

The indicators of the von Bertalanffy equation should be considered as special attributes of the population (sample) to some extent reflecting the averaged integral indicators of the interaction of the metabolism of individuals, environmental factors and more complex ecological and other processes.

The asymptotic length from the von Bertalanffy equation (Table 4) is quite illogical in a number of cases (if we still assume some kind of limit of this variable). However, it is worth remembering that they represent a specific attribute of the population and are not necessarily an achievable value. This is understandable when calculating the growth potential realization rate R, which varies between 39.2-78.7%. It is also worth noting the twofold increase in *L*∞ for cluster 2, compared to cluster 1, in the sample of perches from Lake Borovoe. An almost 1.5-fold excess is also typical for the sample from Lake Katarkol. In other populations, the difference is not so significant. The catabolic coefficient k behaves in exactly the opposite way. In gen-

Fig.2. Variability of average back calculated length at perch from Lake Shchuchie

Fig.3. Variability of average back calculated length at perch from Lake Tekekol

| Water | Cluster | Back calculated length, cm* | | | | | | | | | | | | | Clusters | |
|-------------------------------------|--|-----------------------------|-------------|------|------|------------------------------------|------|------|------|----------|----------|----------|------|------|--------------------------|-------|
| body | | $\mathbf{1}$ | $\bf{2}$ | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | ratio |
| Lake Katarkol | 1 | 5.7 | 9.3 | 12.4 | 15.0 | 17.0 | 19.2 | 21.2 | 23.0 | 24.9 | 27.1 | 28.9 | | | \overline{a} | 1:1 |
| | $\overline{2}$ | 5.3 | 8.2 | 11.0 | 13.6 | 15.9 | 18.0 | 20.0 | 22.2 | 24.0 | 26.5 | 29.0 | 30.7 | 31.9 | | |
| | ANOVA, F | 15.5 | | | | 110.7 191.7 211.9 153.7 | 97.2 | 54.2 | 18.8 | 7.6 | 1.8 | Ω | | | | |
| Lake Borovoe | $\mathbf{1}$ | 6.0 | 9.8 | 12.7 | 14.8 | 16.5 | 18.2 | 20.5 | 22.4 | 24.3 | 26.1 | | | | | 1:0.7 |
| | $\overline{2}$ | 5.3 | 8.4 | 11.1 | 13.6 | 15.6 | 17.5 | 19.7 | 21.9 | 24.3 | 26.5 | 28.6 | 30.0 | 32.5 | 34.1 | |
| | ANOVA, F | 23.3 | 100.5 157.5 | | 77.6 | 36.8 | 10.0 | 2.4 | 0.7 | Ω | 4.3 | | | | | |
| Lake Shchuchie | $\mathbf{1}$ | 6.1 | 10.0 | 12.8 | 15.1 | 17.1 | 18.8 | 20.5 | 22.1 | 23.7 | 25.9 | | | | \blacksquare | 1:1.8 |
| | $\overline{2}$ | 5.4 | 8.3 | 11.3 | 13.9 | 16.1 | 17.9 | 20.1 | 21.6 | 23.1 | | | | | \blacksquare | |
| | ANOVA, F | 19.6 | 90.7 | 94.8 | 65.5 | 63.9 | 25.9 | 1.5 | 1.4 | 0.3 | | | | | | |
| Lake Tekekol | $\mathbf{1}$ | 6.4 | 9.4 | 11.8 | 14.1 | 16.4 | 18.4 | 20.1 | 21.4 | 23.2 | 24.6 | 26.0 | 27.1 | | | 1:1 |
| | 2 | 5.3 | 8.3 | 10.7 | 13.0 | 15.4 | 17.6 | 19.6 | 21.3 | 22.9 | 24.3 | | | | | |
| | ANOVA, F | 67.8 | 68.3 | 60.7 | 86.6 | 38.1 | 12.7 | 5.3 | 0.2 | 2.0 | 0.4 | | | | | |
| Lake Bolshoe Chebachie | $\mathbf{1}$ | 6.3 | 9.8 | 12.7 | 15.2 | 17.2 | 19.2 | 21.0 | 22.7 | 24.4 | 25.9 | 27.1 | 28.3 | 30.5 | 31.7 | 1:1 |
| | 2 | 5.7 | 8.7 | 11.3 | 13.8 | 16.0 | 18.2 | 20.4 | 22.3 | 24.0 | 25.8 | | | | | |
| | ANOVA, F | 46.0 | | | | 162.0 382.0 463.7 231.7 113.0 39.2 | | | 9.5 | 4.0 | Ω | | | | $\overline{}$ | |
| River Ishim | $\mathbf{1}$ | 6.4 | 10.7 | 13.6 | 15.9 | 18.1 | 19.9 | 21.9 | 23.3 | 25.3 | 26.3 | | | | | 1:1.1 |
| | 2 | 5.3 | 9.0 | 12.1 | 14.9 | 17.0 | 19.1 | 21.0 | 22.8 | 24.4 | | | | | \blacksquare | |
| | ANOVA, F 50.4 137.5 97.5 52.4 35.1 15.1 19.1 | | | | | | | | 2.9 | 13.9 | | | | | | |

Table 3. Back calculated length of individuals from distinguishing clusters

* – significant differences between clusters are highlighted in bold ($\alpha \leq 0.001$)

eral, only the sample from Lake Shchuchie stands out somewhat from the overall picture of the relationship between VBGE constants.

The Poly-Munro growth efficiency coefficient *Ф*' for most populations is at an average level. It is slightly increased only for Lakes Katarkol and Borovoe.

4. Discussion

Intra-group growth variability is undoubtedly of interest in terms of studying the mechanisms of the dynamics of linear and weight indicators during the life cycle, as well as for assessing the influence and strength of factors influencing this process. This has very practical applications, including predicting the quantitative characteristics of commercial stocks.

Within-group variation in size can be considered at several levels. Differences are noted between generations, ages, sexes or ecological forms. Their manifestation should be related to the heterogeneity and variability of the habitat of a group of organisms.

Sex differences in growth rates in some cases may be related to the uniqueness of reproductive strategies of species and/or ethological characteristics [\(Henderson et al., 2003](#page-7-14); [Marshall et al., 2009;](#page-8-9) [Pompei](#page-8-10) [et al., 2012](#page-8-10); [Sandip et al., 2012\)](#page-8-11). According to G.V. [Nikolsky \(1965\)](#page-8-12), sexual variability in growth may be due to negative environmental conditions.

The data obtained by our research once again showed that perch populations in the region do not have sexual variability in growth. At present, there are no prerequisites for the formation of such dimorphism.

Fig.4. Variability of average back calculated length at perch from Lake Katarkol

Fig.5. Variability of average back calculated length at perch from Lake Borovoe

| Water body | Clusters | L_{∞} | \mathbf{k} | t_{0} | Φ | \boldsymbol{R} | \boldsymbol{n} |
|------------------------|-----------------|--------------|--------------|---------|--------|------------------|------------------|
| Lake Katarkol | total sample: | 58.0 | 0.058 | -0.74 | 2.29 | 55.0 | 246 |
| | $\mathbf{1}$ | 49.0 | 0.076 | -0.57 | 2.26 | 59.0 | 95 |
| | 2 | 69.3 | 0.045 | -0.79 | 2.33 | 46.1 | 94 |
| Lake Borovoe | total sample: | 75.9 | 0.040 | -0.94 | 2.36 | 44.9 | 136 |
| | $\mathbf{1}$ | 42.3 | 0.089 | -0.66 | 2.20 | 61.7 | 65 |
| | 2 | 86.9 | 0.033 | -0.87 | 2.40 | 39.2 | 48 |
| Lake Shchuchie | total sample: | 45.1 | 0.079 | -0.64 | 2.21 | 57.4 | 104 |
| | 1 | 38.0 | 0.106 | -0.55 | 2.19 | 68.1 | 36 |
| | 2 | 37.4 | 0.101 | -0.56 | 2.15 | 61.8 | 64 |
| Lake Tekekol | total sample: | 40.9 | 0.085 | -0.84 | 2.15 | 66.3 | 150 |
| | $\mathbf{1}$ | 39.2 | 0.090 | -0.99 | 2.14 | 69.1 | 54 |
| | $\overline{2}$ | 41.9 | 0.081 | -0.67 | 2.16 | 58.0 | 52 |
| Lake Bolshoe Chebachie | total sample: | 49.8 | 0.067 | -0.93 | 2.22 | 63.6 | 371 |
| | 1 | 45.1 | 0.081 | -0.76 | 2.22 | 70.3 | 172 |
| | 2 | 50.5 | 0.066 | -0.80 | 2.23 | 51.1 | 174 |
| River Ishim | total sample: | 35.6 | 0.128 | -0.38 | 2.21 | 73.9 | 152 |
| | 1 | 33.4 | 0.147 | -0.40 | 2.21 | 78.7 | 60 |
| | $\overline{2}$ | 35.4 | 0.126 | -0.27 | 2.20 | 69.0 | 63 |

Table 4. Bertalanffy equation indices for general samples and clusters

This may indirectly indicate a relatively positive characteristic of their habitat. However, this does not mean that, under certain conditions, sexual dimorphism in growth rates will not appear somewhere in the future.

Generational variability represents the dynamics of growth processes over time. Every year one generation replaces another. For convenience, we associate them with years of life. This is quite logical, given the cyclical nature of phenological phases.

Differences in the growth of generations are based on different mechanisms of differentiation of generations, which are based on their numbers and the degree of trophic competition, and in some cases, direct predation. A high population size of one of the age classes leads to a decrease in growth rates within it ([Post and McQueen, 1994](#page-8-13); [Boisclare and Rasmussen,](#page-7-15) [1996](#page-7-15); [Hjelm et al., 2000](#page-7-16); [Holmgren and Appelberg,](#page-7-17) [2001](#page-7-17); [Bobyrev, 2013;](#page-7-18) [Rask et al., 2014;](#page-8-14) [Roloson et al.,](#page-8-15) [2016](#page-8-15)) due to tension in trophic competition. This also cannot but affect adjacent age classes that are similar in type of nutrition.

By comparing the growth of alternating generations, one can see certain trends in their variability and associate them with certain operating factors. The increase in linear sizes of perches from Lakes Tekekol, Katarkol and Borovoe should be associated with an increase in water content in the second half of the first decade of this century.

An increase in the level of the waterbodies leads to an increase in feeding areas. New areas are being flooded, in which, due to their shallow water, there is an increased development of the food supply, i.e. zooplankton and zoobenthos. It is worth noting that it is younger generations that increase growth rates, mainly consuming invertebrates.

The situation is different in the case of Lake Shchuchie. The level is also rising here, and there are also flooded shallows. But, the main part of the lake bed is a natural pit with significant depth. Also, at the bottom of the reservoir there is a thick layer of sapropel. Accordingly, there are not so many realistic possibilities for the food supply to be increased.

At the same time, a decrease is already observed in facultatively piscivorous generations. Accordingly, its causes apparently lie in the food supply, and are not determined by the hydrological parameters of the water body. The food supply of these generations is largely composed of juveniles of their own species and species similar in ecological preferences in all water bodies of the region [\(Krainyuk and Assylbekova, 2013\)](#page-7-19), which has a certain impact on their growth.

Intrapopulation differentiation based on growth rates in fish has been known a long time [\(Nikolsky,](#page-8-12) [1965](#page-8-12)). For perch, the slow-growing form is usually designated as "coastal" and the fast-growing form as "pelagic" ([Berg, 1949\)](#page-7-20). A similar division is found not only in the European perch, but also in its Mountain-Asian variant, the Balkhash perch *Perca schrenkii* Kessler, 1874 ([Mitrofanov et al., 1989\)](#page-8-16). "Pelagic" and "coastal" morphs have significant differences in life expectancy, fertility and other indicators ([Shatunovsky](#page-8-7) [and Ruban, 2013](#page-8-7)).

The basic factor in the appearance of differences and the formation of these morphs is nutrition, the influence of which can be masked by a number of other reasons (ethological, environmental, etc.) and can manifest itself differently depending on any influence of external or internal nature ([Berg, 1949;](#page-7-20) [Nikolsky,](#page-8-12) [1965](#page-8-12); [Mitrofanov et al., 1989](#page-8-16); [Fontaine et al., 1997;](#page-7-21) [Craig, 2000;](#page-7-22) [Dgebuadze, 2001](#page-7-4); Svanbäck and Eklöv,

2002; [Krainyuk and Assylbekova, 2013;](#page-7-19) [Kestemont et](#page-7-23) [al., 2015;](#page-7-23) [Nakayama et al., 2017](#page-8-17)).

The presence of such incremental morphs indicates the existence of heterogeneity of the habitat and the distribution into new ecological niches within each generation anew. The larger the waterbody, the more contrasting the habitat and, as a consequence, the likelihood of the genesis of these forms and the degree of their differences is more likely and strong. For perch, for example, these morphs were once noted in the Aral Sea ([Nikolsky, 1940](#page-8-18)), for Balkhash perch – earlier in Lake Balkhash [\(Mitrofanov et al., 1989](#page-8-16)) and is still in the delta of the Yli River delta (Tsoy and Assylbekova, 2012). In smaller water bodies, their differentiation is difficult, including due to the high level of homing [\(Shaikin, 1989](#page-8-19)). However, here too one can observe a picture of intra-group division in these reservoirs (Svanbäck and Eklöv, 2002; [Krainyuk, 2022\)](#page-7-13), although not so pronounced.

Perch is a carnivorous species. Initially, in the larval and juvenile stages, it is characterized as a zooplanktivore (Glushakova, 1981; [Skrzypczak et al.,](#page-8-20) [1998](#page-8-20); Kratochvíl et al., 2008). The inclusion of zoobenthos in the diet occurs starting from the summer of the first year of life or later periods in the life of the perch (Tyutenkov, 1956; [Glushakova, 1981](#page-7-24); [Lappalainen et](#page-7-25) [al., 2001;](#page-7-25) [Amundsen et al., 2003;](#page-7-26) Adámek et al., 2004; [Krainyuk and Assylbekova, 2013](#page-7-19)). The onset of predation usually occurs at a body length of 10 to 25 cm, depending on feeding conditions. [\(McCormack, 1970;](#page-8-21) [Collete et al., 1977](#page-7-27); [Mitrofanov et al., 1989;](#page-8-16) [Amundsen](#page-7-26) [et al., 2003;](#page-7-26) [Ceccuzzi et al., 2011](#page-7-28)).

Within one generation, the transition to age-appropriate food items occurs unevenly, which ensures differentiation of the group according to growth rates. In addition, within a single population there is a division according to biotopic preferences ([Bobyrev, 2013\)](#page-7-18), largely related to the type of nutrition and foraging behavior in age (size) groups. Trophic factors and trophic behavior are quite logically the main ones when dividing a group into incremental morphs. They further determine the choice of habitat stations along a chain of other environmental factors.

When analyzing back-calculated growth, two types of population can also be distinguished. The first type includes cases of a longer age series and a higher growth rate in older generations in cluster 2 (Lakes Katarkol and Borovoe). They also have higher *L*∞ and *Ф*' exponents of the von Bertalanffy equation. They begin their life cycle from a "lower start", but by 7-8 years their linear dimensions are higher than those of other types of populations.

The second type consists of groups in which one cluster throughout its life has a higher growth rate and its life cycle is longer (Lake Shchuchie, Bolshoe Chebachie, Tekekol and the Ishim River). In the first years, their growth rate is better than that of populations of the first type but already at the end of their life cycle, their growth rate decreases.

These divisions to some extent resemble the rand K-strategies in miniature of an extra-taxonomic group with a scanty number (compared to taxonomic units), acting on scanty time periods, but not identical to it. We noted something similar, but at the population level, for the tench *Tinca tinca* (Linnaeus, 1758) from the reservoirs of the Irtysh-Karaganda canal (now named after K. Satpayev) ([Krainyuk et al., 2021](#page-7-29)).

5. Conclusion

As noted by Yu.Yu. [Dgebuadze \(2001\)](#page-7-4), not much attention is paid to intrapopulation growth variability and its analytical apparatus is quite insufficient. At the same time, if you use a number of conventional statistical techniques, you can reach quite interesting conclusions regarding ecological and microevolutionary processes.

The absence of sexual variability in height in the studied samples is quite logical, since there are no prerequisites for its appearance in the form of extreme changes in the environment. The presence of differences between generations is determined by a combination of hydrological and trophic factors.

The emergence of ecological forms that differ in growth rates occurs from the heterogeneity of environmental factors and the distribution of food resources, as well as age-related (size) behavioral reactions. However, specific reaction norms can vary within fairly wide limits. There is no single pattern in the formation of these incremental morphs, as can be seen from the two types of populations indicated.

Differences in relatively small waterbodies will not be so striking, but when using statistical-analysis methods they show high reliability of the differences. Most likely, this phenomenon is typical only for species where some environmental factors contribute to the gradient of the intrapopulation structure.

In general, studies aimed at studying intrapopulation differentiation in growth rates make it possible to assess the state of populations and determine mechanisms for their management, taking into account diversity within groups.

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Conflict of Interest

The authors declare no conflicts of interest.

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