Articles

MODEL OF FISH POPULATION DYNAMICS WITH CALCULATION OF INDIVIDUAL GROWTH RATE AND HYDROLOGICAL SITUATION SCENARIOS

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Introduction: Populations of commercially valuable fish species develop in aquatic ecosystems according to internal mechanisms of their evolutionary adaptations, which do not always suit the environmental conditions which can change due to anthropogenic pressure. Often the factors of reservoir eutrophication or introduction of new species into the ecosystem aggravate the competitive confrontation of the populations. The changes spread by domino effect and complicate the development of a strategy for rational exploitation of biological resources. Species under non-optimal anthropogenic conditions are vulnerable. **Purpose:** *Developing a model for introduced population dynamics, implemented as a group of scenarios for a volatile environment.* **Results:** *We developed a computational model of a population to describe the scenarios for its adaptation to environmental conditions. The scenarios include the pace of dimensional development and nutrition of fish. The model includes a unit for calculating diets, taking into account the hydrological situation factors: the oxygen content and the activity of hydrogen ions. The model is capable of operating in two modes: under standard environmental conditions (without specifying the hydrological situation) and with preset conditions for anthropogenic changes. Our approach allowed us to predict changes in the population structure with variability in abiotic factors. The model demonstrate the risk of taking out the fish which make the greatest contribution to the biomass growth rate.* **Practical relevance:** *The model was identified using the data on whitefish population in the Lake Sevan. It is suitable for computer simulation experiments, which made it possible to describe specific features of scenarios of population dynamics for the cases of increased fishing, limited feeding and changes in the hydrological conditions of the lake.*

Keywords — Nonlinear Models of Populations, Fish Growth Models, Energy Balance Calculation, Commercial Exploitation Scenarios, Eutrophication.

Introduction

In our previous work [1], we used mathematical methods to analyze the dynamic balance of the main biogenic elements which form the first level of an ecosystem. We developed a computational model for the consequences of excessive accumulation of nitrogen and phosphorus in the bottom sediments of a large reservoir. As more nutrients flow into the reservoir due to human economic activity, eutrophication processes start (algal bloom and oxygen deficiency). We successfully parameterized the model by real waterbody data and calculated a forecast of hydrochemical indicators. Ecosystems are highly prone to domino effect. Transformation of the trophic status of a reservoir from oligotrophic to eutrophic type after a certain time interval is also manifested in its aquatic community. Species adapted to the local conditions cannot change quickly, so the advantage is given to active unwanted invaders, less demanding of low oxygen content.

In another work [2], we developed a continuous-discrete model in the form of a differential equation system with a redefinable computational structure in order to describe sturgeon reproduction efficiency on the basis of various survival factors at juvenile development stages. For an exploited population with adaptive cyclicity, we described a computational scenario of degradation in the form of a sudden collapse. This paper is a logical continuation of our research in mathematical biology. It represents an aggregated model of fish population dynamics associated with environmental conditions by the key hydrological indicators through the efficiency of biomass accumulation and the rates of linear growth, taking into account unbalanced feeding. It should be noted that fishery forecasts are formed on the basis of statistical processing and averaged observation data for the previous period, but statistical methods for assessing the stock replenishment efficiency are often unpromising when the trophic status of a reservoir undergoes drastic

shifts. We took into account possible methodological errors in mathematical analysis [3, 4]. Note that *Coregonus* fishes are typical representatives of the Arctic ichthyofauna [5−9], therefore their habitat in middle latitudes is possible only in high mountain lakes like Issyk-Kul, Sorulukel or Sevan.

Characteristics and Components of the Model

The population model structure unites three submodels: 1) a model of individual weight dynamics; 2) a model of age group size dynamics; 3) a model of spawn yield dynamics with continuous calculation of fry loss. These submodels are adjusted for joint calculations, but they can be used independently to calculate particular problems, for example, analyzing the data on fish nutrition energetics and respiration (important for the case of reservoir eutrophication), or estimating the coefficients of natural and commercial mortality by fish age groups.

The interaction of the submodels is organized in such a way that they can describe important intrapopulation mechanisms: dependence of the diet and weight on the size of fish age groups; dependence of the fish spawn yield on the diet; dependence of the natural mortality coefficients on the actual diet; dependence of the natural mortality coefficients on the participation in spawning; dependence of the fecundity on the fish weight and age. To set up the initial state, parameters for the standard environmental conditions are specified.

We accept that abiotic factors directly affect two population indices: the diet of the fish and the mortality of their eggs; and indirectly they affect the weight of individuals, their mortality and fecundity, which was shown by the example of *Coregonus* fishes [4, 10, 11]. In our model, the temperature of the water and the concentration of dissolved O_2 affect the amount of food and the mortality of eggs; the water pH has a predominant effect on the egg mortality.

The general algorithm of our model implies that initially for all age groups, on the base of the initial data on individual weight, we determine the maximum amount of food, the expenditure on respiration, and the increase in fish weight corresponding to the maximum food amount. After that, based on the scenario data, the actual amount of energy received by a fish age group is calculated, and the weight value is corrected, taking into account the diet. The next step is to calculate the size of the age groups in accordance with the natural mortality and fishing seizures. It is assumed that all the fish that have reached the given weight by the time of spawning participate in the reproduction, and the spawn amount is proportional to the weight and age of the spawning fish.

Calculationunits for Individual Indicators

The maximum amount of food and the body weight gain for fish are determined within a month, provided that their nutritional needs are fully met. The internal time step of aunit is considered equal to a day. Since the mortality of juveniles is extremely high, the calculation of the daily amount of food is carried out according to their actual number taking into account the daily mortality. For other age groups, the food amount is calculated on the basis of a fixed abundance in each month. The weightgainis calculated as follows:

$$W_m(t+1) = W(t) + \Delta W_m(t+1),$$
$$\Delta W_m(t+1) = C_m \times U - R,$$

where W, W_m are the actual and maximum weights of a fish; ΔW_m is the maximum gain; C_m is the maximum amount of food; U is the food assimilation coefficient; R is the expenditure on respiration. The standard amount of food corresponds to an average monthly amount at which a fish gains the given standard weight. On the basis of biological data [12, 13], we define the food amount as a power function of weight:

$$C_m = \alpha_0 \times C_{ct1} \times W^{\alpha_1},$$

where C_{ct1} is the standard food amount for a fish weighing 1 kg; α_0 is acorrection for the excess of the maximum food amount over the standard food amount; $\alpha_1 \in [1/2, 2/3]$; C_m is the maximum food amount for a fish weighing W kg.

The standard amount of food is calculated based on the average monthly water temperature and oxygen content in water: $C_{ct1} = \alpha_2 \times A_t \times A_k$, where α_2 is a constant coefficient, and A_t, A_k are corrections for temperature and oxygen.

The dependence of the food amount on temperature is nonlinear; when the temperature is optimal for a given fish species, the curve has a maximum. When the temperature reaches the limit, the food amount drops to zero, and the nutrition stops. In the model, the dependence is approximated by the following formulas:

$$0 \le T \le T_{opt}, A_t = \alpha_3 \times T^2 - \alpha_4 \times T^3;$$
$$T_{opt} < T < T_{max}, A_t = 1 - \alpha_5 \times \left(T - T_{opt}\right)^2;$$
$$T > T_{max}, T < 0, A_t = 0.$$

Let us assume that when the oxygen concentration is more than a given limit value $O_2 > O_2$ lim, this factor is not a limiting factor anymore. As the oxygen content in water drops during eutrophication, the food amount first quickly decreases from normal down to 0.1, and then gradually decreases

down to zero. The dependencie sare approximated in the model as follows:

$$O_2\min < O_2 \leq O_2\lim, A_k = \alpha_6 + \alpha_7 \times$$
$$\times (O_2 - O_2\min + \alpha_8(O_2 - O_2\min)^2 - \alpha_9(O_2 - O_2\min)^3;$$
$$O_2 < O_2\min, A_k = \alpha_{10} \times O_2.$$

The calculation of energy consumption is based on the assumption that the expenditure on respiration consists of two components which are the expenditure related to the maintenance of the ichthyomass and the expenditure related to its growth according to the formula $R = A(W) \times (R_n - R_p)$.

Tofigure out the structure of the dependencies of expenditure on respiration, the Brett and Groves scheme was used [14], which defines the ratio of active and standard metabolism as a function of temperature. We took into account the data on the change in the ratio of active and standard metabolism, and the distribution of the energy supplied with food to biomass and respiration in fish ontogeny [15, 16].

It has been found that the maintenance expenditure is proportional to the biomass, increasingas the temperature increases according to the Krogh function: $R_n = K(T) \times W \times \alpha_{16}$, where $K(T)$ is the Krogh function, and α_{16} is an empirical coefficient. The expenditure related to growth is proportional to the food amount, decreasing linearly as the temperature increases, according to the law $R_p = C(1 - \alpha_{17}) \times \alpha_{18}$.

Food spectrum calculation unit. The model identification approach uses the data on the food biomass and the priorities of its consumption by whitefish age groups. The data are represented in tables of average annual changes in the food spectrum depending on the age of the fish. The unit calculates the actual food amount for the fish in accordance with the available food biomass, and with the requests for a particular food type from all the competing whitefish age groups [17]. The average monthly biomass of various food types is represented in proportion to their share in the diet, ensuring the constant tension in the food relations. The absolute value of the food biomass is given by a periodic function in order to provide the standard amount of food for the fish at their normal level of eating (30−40 % of the average monthly biomass). Note that a sharp change in conditions can force whitefish to drastically change their food spectrum, up to becoming predators sometimes [18−20].

Biomass increment correction algorithm. An iterative algorithm corrects the biomass increment and the expenditure on respiration, taking into account the actual diet:

$$W(t+1) = W(t) + \Delta W_m(t) \times C/C_m;$$
$$R(t+1) = R_m(t+1) \times C/C_m.$$

It is assumed in the calculations that the food distribution structure does not depend on the food amount. Separately, a weight correction is introduced after spawning for the age groups involved in reproduction.

Calculation of natural mortality coefficients. A very important component of the simulation model is the estimation of biological resource loss. The curve of natural mortality has a U-shape. Mortality in the first age group is large, then it decreases, reaching its minimum before spawning, and grows again, approaching the maximum during the 10th year of a whitefish's life [5, 21]. Let us assume that the mortality of fish depends on the degree of satisfying their nutritional needs. The loss from the lack of food can be simulated by the following dependence:

$$C/C_m \geq Kg, KCg = 0;$$
$$C/C_m < Kg, KCg =$$
$$= 1 - \exp(-\alpha_{18} \times (C_m/C - \alpha_{19}) \times$$
$$\times \Delta W(t+1)/W_m(t+1) + W(t)),$$

where KCg is the mortality coefficient which depends on starvation, and Kg is the starvation threshold. In the exponential factor we take into account the dependence between the mortality and the relative monthly increment. The natural mortality coefficient KC as a whole by groups can be found by the following formula:

$$KC = 1 - (1 - KCct) \times (1 - KCner) \times (1 - KCg),$$

where $KCct$ is the mortality without spawning, at normal feeding conditions; and $KCner$ is the spawning loss. We have to calculate the loss associated with density and competition.

Method for Evaluating the Reproduction Efficiency

Let us separately introduce an estimate of the loss at the earliest stages of development, which would additionally depend on the initial spawn density $N(0)$. The well-known Ricker function $R = \xi N(0)\exp(-bN(0))$ is not suitable here because the iteration trajectory shows chaotization properties with the increase of $\xi > e^2$ which is an unexplained mode for biology [2]. For our calculations we will use the implementation of a continuous segment in the iterative model construction. Here we apply a modification of our reserve-replenishment model for a decrease in the abundance from $N(0)$ down to $R = N(T)$ in the form of a system of equations on a time interval which makes up a continuous vulnerability interval $t \in [0, T]$:

$$\begin{cases} \dfrac{\mathrm{d}N}{\mathrm{d}t} = -\left(\gamma w(t)N(t) + \Theta(S)\beta\right)N(t); \\ \dfrac{\mathrm{d}w}{\mathrm{d}t} = \dfrac{g}{\sqrt{N^k(t) + \sigma}}, \; \Theta(S) = \left(1 - e^{-cS}\right)^{-1}, \end{cases} \quad (*)$$

γ is a coefficient of mortality which depends on the group density; β is a coefficient of neutral loss; $w(t)$ is a parameter of individual development in early ontogeny under the influence of group huddling. $\Theta(S)$ reflects the drop in spawning efficiency for a small population after overfishing: $\lim\limits_{S \to \infty} \Theta(S) = 1$. A computational solution of the Cauchy problem (*) will provide a calculation of the loss from spawn to fry, by a dependence with a pronounced maximum which will be the most efficient size of a spawning group. With an increase in the reserve size, the reproduction efficiency decreases, though with a non-zero horizontal asymptote.

Only the use of empirical dependencies for each type in tabular form can allow us to perform predictive calculations of the model in order to study the survival of spawn taking into account the changes in the environment parameters. The death of eggs, apart from predation, is associated with the water temperature and the amount of oxygen dissolved in the water. For the reservoir eutrophication scenario [5], we can use corrections based on the algorithm for calculating the oxygen content in the model of the biogenic element balance described in our previous paper.

In calculating the total number of eggs $N(0)$ for the system of equations (*), it is assumed that a fish participates in spawning if by the spawning time it reaches the weight $Wner$. The amount of spawn $N(0)$ is defined proportional to the fish weight and age: $N(0) = \alpha_{20} + \alpha_{21} \times W(L) + \alpha_{22} \times L$, where L is the age of a spawning fish; W is the fish weight, and $W > Wner$. If by the spawning time the fish gains a weight larger than $Wner$, it can spawn again; if not, it has to miss the spawning season.

The balance of the size of age groups is calculated at the end of each month, taking into account the natural mortality and the share $F \in [0, 1]$ of the fishery (which can be legal and unaccounted): $N(t + 1) = N(t) \times (1 - (1 - KC) \times (1 - F)$. Finally, the iterative algorithm calculates the transition of the fish to their next age group and the population replenishment by the fish which have survived the juvenile stage when they are most vulnerable. Mature whitefish have no natural enemies.

Identification of the Population Model

The population model was identified based on data on the whitefish population in the Lake Sevan, Armenia. This whitefish is a hybrid between *Core-gonus lavaretus maraenoides* and *Coregonus lavaretus ludoga* which were both introduced into the Lake Sevan during the 1920s. After their natural hybridization, many morphological and biochemical indicators allow us to consider Sevan whitefish as a single population in our model [22]. Long after their introduction, they did not play a large role in the fishery, but since the 1960s increased their abundance, and in 1980s became the most important fish for the local fishing industry. The fishery intensification has changed the population age structure, and now fish older than 8 years are rare. In accordance with this, the maximum age of afish in our model is specified as 10 years. The average weight of fish in catches is equal to 840 g at the age of 3 years. Available literature data describe the fish nutrition spectrum in the Lake Sevan quite fully [23]. We managed to determine the daily daily food ration SR for whitefish, calculating it according to A. V. Kogan's method [24]. It was found equal to 4.3 % of a fish body weight. The daily fullness index is 1/4 of a daily food ration. Taking into account the food in relation to the water temperature, a table of annual changes in the diet was compiled. On average throughout a year, a daily food ration is 1.9 % of a fish weight, and the annual ration is about 7 fish weights. Similar values describe the feeding of whitefish in a fry nursery model [4].

It is interesting to see how the energy obtained from food is distributed between body weight gain, gonads, respiration and other expenditures. Juvenile whitefish use their food most efficiently: the ratio of ichthyomass increment to assimilated food can be as high as 60 %; then it decreases down to 35 % by the end of the first year of their life and down to 20 % by the third year. The percentage of assimilated food in whitefish is about 80 % of their diet. With these ratios of energy expenditure for biomass increment and respiration, the fish can get the necessary food volume at plausible daily amounts of food. Theoretically, according to the model, whitefish have an opportunity to gain weight of 6 kg by 10 years of age. In fact, the maximum weight of whitefish varies within 2–4 kg, being limited by interspecific competition.

At the initialization, three age groups dominate in a spawning stock: 3+, 4+ and 5+, which together account for more than 80 % of the stock population. Males mature at the age of 2+ when they reach a weight of more than 480 g; females mature at the age of 3+ when they reach a weight of 650–1000 g. The model assumes that fish participate in spawning when they reach a weight of 700 g. With an equal sex ratio in the spawning stock, we assume that about 22.5 % of the spawning fish weight is consumed for reproduction. Each participation in spawning leads to a decrease in survival. Usually 1/3 of the spawning fish die. A similar post-spawning death of whitefish has been observed in nature [5, 6, 9, 11].

Our identification method was used to choose a step-by-step approach which presumed decomposing the model, overbuilding the unit structure, and subsequently taking into account the internal relationships, as well as external influences in simulation experiments.

At the **1st step**, the submodels were adjusted for the standard conditions. The submodel of individual weight dynamics selected and adjusted the functions which determine how the food amount and respiration expenditure depend on the fish weight, based on the data about standard diet, distribution of the energy obtained from food, and growth rate. A good agreement between the actual and calculated data was obtained when choosing power-law dependencies of the food amount and respiration expenditure on the fish weight with a constant distribution of the obtained energy for fish of 2–10 years of age. In the submodel of age group size dynamics, the value of natural mortality coefficient (*KC*) in a stable population was determined based on data about the age structure, the above-mentioned assumptions about the age changes in *KC* and the standard catch rate $F = 0.45$. The submodel of spawn yield dynamics determined how the number of spawned eggs depends on the fish weight and age based on data about the fecundity of whitefish in the Lake Sevan.

At the **2nd step** of the identification, the submodels were united and jointly adjusted. The influence of the population abundance on the fish weight was taken into account by introducing actual diet which depends on nutritional needs of the fish and the food availability. The maximum amount of food was considered equal to the amount which allowed a whitefish to gain the weight of 6 kg by 10 years of age. The natural mortality coefficient was decomposed into three components: normal mortality with the standard diet and no spawning, reproductive mortality, and starvation mortality. To determine the starvation mortality, we used the data on fluctuations in the fish weight over the age groups. Let us assume that the fish which fail to reach the minimum weight die. Mortality was determined depending on the ratio of the actual amount of food to the maximum one. The threshold is equal to the ratio at which a whitefish could only gain the minimum weight. Mortality is known to be higher in the situation of food deficiency and excessive juvenile density during the introduction into the reservoir [4], as our model for sturgeons confirmed.

At the **3rd step**, the identification closely considered the influence of external abiotic factors on the standard amount of food calculated by the average monthly water temperature and the content of oxygen in it determined by a balance equation according to G. G. Vinberg's method [12].

Eggs and juveniles are most sensitive to changes in the reservoir trophicity. Some environmental conditions suitable for mature fish can be disastrous for eggs. The model took into account the effect of temperature, pH and dissolved oxygen content on the egg mortality coefficients. When calculating the natural mortality of mature fish, it operated with the boundary values of abiotic factors known for this particular species.

Adjustment of the model showed that introduction of only few cause-and-effect relationships allowed us to reflect the main ecological aspects of a whitefish population in a certain stable state. Forage limitations keep the population from growing to infinity. The influence of population density on the growth rate allows the whitefish to gain their weight; malnutrition leads to a slower growth and late maturation of the fish; in extreme cases it can lead to their death. In the model, a fish almost never can get as much food as it wants, so the actual amount of the consumed food is equal to 0.6 of the maximum amount, on average. The model successfully took into account some well-known ecological facts: 1) the life expectancy of an individual depends on the age of its first spawning; 2) whitefish can miss some spawning seasons; 3) spawning reduces the chances for survival.

Results of Computational Experiments

Standard environmental conditions are chosen for the convenience of setting up the model and conducting experiments. For the initial state of the model population, the number *N* of the fish and their biomass *B* were taken (by age groups) from a population of 16.4 million fish with a total mass of 7124 tons, as estimated for 1980. After that, the age groups iteratively change their number / biomass. The greatest changes occur in the group of underyearlings where the average weight increases by 5 orders of magnitude and the number decreases by 3 orders of magnitude. With 6.64 billion larvae in the beginning, the total mortality of whitefish larvae and fry is 99.8 %. By the end of the year, out of all the larvae hatched 7800 million individuals remain. The high mortality rate cannot prevent a rapid increase in the population biomass. The weight gain rate drops sharply during the winter months. The relative weight loss caused by spawning is constant in all age groups from 3 to 10 and equal to 22.5 %.

The average annual expenditure on respiration is 31 % in the first age group and 68 % in the second one. In older groups, it almost does not change, making up about 80 % of the diet. The coefficient of food use efficiency (*P/A*) varies little with age, ranging from 19.4 to 19.8 %.

An important computational scenario considered how a whitefish population would react to changes in fishery and forage. Let us assume that intensive

fishing takesup the majority of the population, without selection between fish sizes. The abundance and biomass of the population fall sharply, decreasing in 10 years by about 100 times. Fishery undermines itself: by the 20th year it can take up just 0.7 tons when the population is about 1 thousand fish. In nature, such a decline in population size usually results in irreversible degradation; this is what happened to Canadian cod or Caspian starry sturgeon. Similar influence of overfishing was observed in the Lake Sevan during the 2000s. But some peculiarities of *Coregonus* fish population structure (formation of local subpopulation groups) give them chances to restore their abundance on the base of reproductively isolated groups which have partially survived. The population of the whitefish in the Canadian part of Lake Ontario successfully restored its abundance in the 1990s [25] after overfishing in the 1960s. In our model, a ban on fishing from the 21st year allowed the population to gradually restore its abundance. Calculations have shown that a population can be destroyed in 10 years, and the restoration would take more than 20 years without any fishing.

Fishery as intense as $\Delta F = [0,30; 0,45]$ keeps the population at the level of 20−40 million fish with a biomass of 12–18 thousand tons, maintaining stable catches at the level of 3000 tons. Increasing the intensity of fishing and reducing the minimum weight of fish caught rapidly deplete the biological resources. Excessive fishing decreases the population abundance especially badly in the case of sharp fluctuations in the food supply. The ecological niche is occupied by species-concurrent of lower value. Recent works on other *Coregonus* populations confirm the conclusions about the influence of density factors on the fish growth rate [26], the significance of eutrophication for the welfare of lake populations in Canada and Germany [27, 28], and the effect of temperature [29].

Conclusion

Using the data on the introduced Sevan white-fish, a segmented model has been developed which simulates the dynamics of abundance and biomass for fish population age groups depending on the fishery and such environmental factors asfood availability, temperature, pH of the water and dissolved oxygen concentration. The model can be classified as simulative, deterministic and discrete-continuous. The model was identified and verified with a mandatory biological substantiation of its results by the data on whitefish stock [17, 23]. The model can work in two modes: under standard environmental conditions (without specifying the hydrological situation) and with a scenario of anthropogenic changes. The scenario approach allows you to use lake eutrophication data for predicting changes in the fish population structure when abiotic factors change. Ultimately, a shift in the upper level of the trophic chain will affect the entire biotic community of the lake. Scenarios demonstrate that it is unreasonable to take out the individuals which make the greatest contribution to the biomass growth rate. A depleted population will recover with a rate lower than the anticipated value.

This research confirms the conclusion made in our previous RFBR projects on Caspian sturgeon reproduction efficiency. Even small fluctuations in fish mortality rate during early ontogeny lead to changes in the population size, which is difficult to take into account in fishery forecasts based only on statistical averaging of a data set which may be large but obtained under different conditions of the population existence and unstable hydrological situation caused by hydropower industry needs [30].

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Модель динамики популяции рыб с расчетом темпов роста особей и сценариев гидрологической обстановки

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Постановка проблемы: популяции ценных промысловых видов рыб развиваются в водных экосистемах по внутренним механизмам эволюционных адаптаций, не всегда соответствующим измененным из-за антропогенного давления условиям среды. Часто фактор эвтрофирования водоема или вселения в экосистему новых видов обостряет конкурентное противоборство популяций. Изменения распространяются эффектом домино и осложняют выработку стратегии рациональной эксплуатации биоресурсов. Виды в неоптимальных антропогенных условиях развития организма уязвимы. **Цель:** разработка модели динамики интродуцированной популяции, реализованной в форме группы сценариев для изменчивой среды. **Результаты:** разработана вычислительная модель популяции для описания сценариев ее адаптации к условиям среды. Сценарии включают темпы размерного развития и питания особей. В модель включен блок расчета рационов питания с учетом факторов гидрологической обстановки: содержания кислорода и активности ионов водорода. Модель способна работать в двух режимах: при стандартных условиях среды (без задания информации о гидрологической обстановке) и при задании условий антропогенных изменений. Подход позволил прогнозировать изменения в структуре популяции при вариативности абиотических факторов. Модель показывает опасность изъятия рыб, обеспечивающих наибольший вклад в темпы прироста биомассы. **Практическая значимость:** модель идентифицирована по данным для популяции интродуцента сига Севана и пригодна для имитационных вычислительных экспериментов, что позволило описать специфические особенности сценариев популяционной динамики при усилении промыслового изъятия, ограниченности питания и изменения гидрологических условий водоема.

Ключевые слова — нелинейные модели популяций, модели роста, расчет энергетического баланса, сценарии промысловой эксплуатации, эвтрофикация.

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