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Construction of the fitness function depending on a set of competing strategies based on the analysis of population dynamics

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Abstract. The *purpose* of this work is to construct a fitness function that depends on the set of coexisting competing hereditary elements based on population dynamics in the "predator–prey" model with the logistic growth of prey. *Materials and methods.* The work uses the generalized Volterra model. The planktivorous fish plays the role of a predator. Many different species of zooplankton are considered as prey, which differ from each other in the hereditary strategies of daily vertical migrations. The model takes into account the intraspecific competition of prey. The peculiarity of the model consists of the presence of pairs of hereditary strategies in which the carriers of the first can displace the carriers of the second and vice versa — the carriers of the second can displace the carriers of the first, depending on the set of competing strategies in which they coexist. To restore the fitness function, the ranking method is used, which is reduced to the classification of ordered pairs of hereditary strategies into two classes "the first strategy displaces the second" and "the second displaces the first". *Results.* The article presents a new methodology for constructing the fitness function. The technique involves two stages. First, the fitness function is reconstructed for a certain finite subset of elements on the basis of processing data on the long-term dynamics and comparing their competitive advantages. At the second stage, the form of the fitness function is derived for an arbitrary set of elements. It uses the features of interspecies interaction reflected in the model. With the help of the constructed fitness function, an evolutionarily stable regime of daily vertical migrations of zooplankton is modeled by numerically solving the minimax problem. *Conclusion.* The proposed method for constructing a fitness function that depends on a set of competing strategies is quite general and can be applied to a wide range of models of population dynamics. The strategy of diel vertical migrations of zooplankton constructed as a result of modeling is in good agreement with empirical data.

Keywords: fitness function, order, ranking, predator–prey model, zooplankton, daily vertical migrations, survival strategy, optimization.

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Introduction

Currently, mathematical modeling methods are widely used to study biological systems and processes [1–4]. The mathematical study of complex dynamics, along with the means of data mining, allows us to find an explanation for the observed phenomena, predict the behavior of a real system, and carry out a purposeful impact on it [5–9].

Modern approaches to evolutionary modeling in biology often rely on maximizing a certain criterion that reflects the competitive advantages of hereditary elements in the biological community (for example, genotypes, behavioral strategies, etc.) [10–12]. This methodology is a mathematical implementation of the fundamental Darwinian idea of "survival of the fittest" [13]. The corresponding criterion is called the fitness function. When comparing the fitness of different hereditary units, it is possible to predict the results of evolution, to investigate the direction of changes in ecological systems. Maximizing the fitness function makes it possible to identify evolutionarily stable hereditary behavioral strategies, that is, strategies that persist in the community indefinitely against the background of possible mutations [14].

However, there is a problem of mathematical formalization of the fitness function in the form of some mathematical expression. Different authors offer different understanding of the fitness function: the expected individual reproductive value, generalized entropy, some analogue of the Lyapunov function, etc. [15–19]. Different definitions of the fitness function sometimes lead to contradictory predictions of evolutionary results [12, 16].

A. Gorban proposed a general approach to the formalization of the fitness function, which defined it in the equations of the dynamics of measures with inheritance as the average time value of the reproduction specific rate [20–22]. The use of such a definition made it possible to solve a number of problems in general cancer therapy [23]. This approach was later developed in [24–26], where analytical algorithms for inferring fitness functions for wide classes of models were proposed. However, the parameters and coefficients that appear in the model cannot always be measured empirically. They involve identification, which makes it difficult to restore the fitness function. Therefore, it seems interesting to construct the fitness function directly on the basis of known population dynamics.

If fitness is understood as the average time value of the reproduction specific rate, then it can be formally calculated for each hereditary element based on the results of long-term population dynamics. But in this case, the prognostic effect of the fitness function will be small, since it will reflect the already known results of evolution. It is a priori impossible to obtain long-term population change data for all possible hereditary elements. In fact, it is possible to have information about the numbers only for some finite subset of such elements. Therefore, the problem of restoring the fitness function for the set of elements on the basis of population dynamics in a subset of elements seems to be more meaningful.

This formulation of the problem is a special case of the ranking problem, which is as follows [27, 28]. A finite subset of elements from a compact metric space is given. It determines the ranking order. The goal is to continue the introduced order over the entire space. The order can be determined by specifying the comparison function J. Its larger values correspond to the better elements (that is, $J(v) > J(w)$ if and only if v is better than w). In this case, the solution of the ranking problem is reduced to the identification of the comparison function J.

Currently, there is a wide range of different ranking algorithms based on machine learning methods [29–31]. The most popular is the pairwise approach, which consists in reducing the ranking problem to the classification of ordered pairs of hereditary elements "first, second" into two classes: "the first element is better than the second" and "the second element is better than the first" [32, 33].

Such algorithms can be successfully applied to reconstruct the biological fitness function from the observed population dynamics for a finite subset of competing elements [34]. These elements are ranked according to their competitive advantages [25]. The fitness function is introduced as a comparison function that reflects the established order of competitive advantages.

The problem of ranking hereditary elements was solved earlier, provided that fitness does not depend either on the initial state of the population or on a selected set of competing elements [34]. However, the competitive advantages and fitness function may depend on both. It is possible that in the same pair of hereditary elements, the first element may be both better than the second and worse than the second, depending on in which set of competing elements they coexist. This situation takes place in the "predator–prey" model with a logistical increase in preys [35]. A cyclic change in the ranking order may occur with a corresponding change in the sets of competing elements [24, 26, 36]. The direct application of machine learning technologies to solve the ranking problem in such cases is impossible, since the order of competitive advantages that is established for the training sample may not be preserved during the transition to a population with a richer set of hereditary elements. To establish the dependence of the order of competitive advantages on the set of coexisting elements, it is necessary to take into account the features of interspecific interaction, which are reflected in the equations of the mathematical model.

The purpose of this work is to construct a fitness function that depends on a set of coexisting competing hereditary elements, based on population dynamics and taking into account the hypotheses of interspecific interaction in the "predator−prey" model with a logistic growth of preys. The developed technique is used to model evolutionarily stable strategies of diel vertical migrations (DVM) of zooplankton.

The phenomenon of diel vertical migrations (DVM) of aquatic organisms was discovered two hundred years ago [15]. It was found that a large number of zooplankton species move up and down daily between the deep and near-surface layers of water [37–39]. The DVM of zooplankton play an important role in the dynamics of ocean organic matter. This phenomenon is considered as the most significant synchronous movement of biomass on Earth. It makes a significant contribution to carbon exchange and can potentially affect the climate on a planetary scale [40–45]. Identification of the causes and mechanisms of zooplankton DVM is an important problem in modern ecology. However, many aspects of DVM are still not understood. A large number of studies have been devoted to the study of the features of the hereditary behavior of zooplankton [13, 46–54]. The involvement of the concept of fitness allows us to explain a number of important features, for example, the dependence of behavior on the age of the organism [55, 56]. Thus, the task of constructing the fitness function is becoming increasingly important for modeling diel vertical migrations.

1. Materials and methods

1.1. Mathematical model. In this paper, the patterns of zooplankton DVM are investigated within the framework of the generalized Volterra model "predator−prey" with several types of prey and one predator [57]. Here the role of predator is played by a plankton-eating fish. As prey, we consider a set of n different zooplankton species that differ from each other by hereditary strategies of vertical migrations $v_i, i = 1, ..., n$; Q — the corresponding set of different hereditary strategies. Each strategy v_i represents a mode of periodic change of the vertical coordinate x of the zooplankton position during the day, that is, the function $x(\tau)$, where $\tau = 0$ corresponds to 12 o'clock in the afternoon, $\tau = 0.5$ corresponds to 24:00, and $\tau = 1$ corresponds to 12 o'clock the next day; x — migration depth, measured in meters, level $x = 0$ corresponds to the water surface. We assume that $x(\tau)$ is a continuously differentiable function on the segment $[0, 1]$ satisfying the conditions $x(0) = x(1)$.

Denote n — the number of different zooplankton species in the community implementing various hereditary behavioral strategies; $\rho = \rho_i(t)$ — the number of zooplankton subpopulation that implements the strategy v_i, $i = 1, ..., n$; $F(t)$ — predator population size, t — population dynamics time. The model is considered in the form of the following system of ordinary differential equations

$$\begin{aligned} \rho_i'(t) &= r_i\rho_i(t) - c_i\rho_i(t)F(t) - \rho_i(t)\sum_{j=1}^{n}\rho_j(t), \quad i = 1, \dots, n \\ F' &= F(t)\sum_{j=1}^{n} c_j\rho_j(t) - F(t). \end{aligned} \tag{1}$$

Here r_i — the reproduction coefficient of the i-th type of prey in favorable conditions in the absence of a predator and competition, c_i — the rate of predator attacks on the i-th type of prey; the last term in the first equation reflects the competition of zooplankton. Limiting the growth of the zooplankton community obeys the Verhulst hypothesis (additional mortality as a result of competition is proportional to the total population of the community). This number mathematically represents the sum of the numbers of prey subpopulations, where the summation variable is the number of the corresponding strategy. Accordingly, all coefficients of prey competition (both intraspecific and interspecific) are assumed to be equal to one. For simplicity, the mortality of the predator and the conversion rate of food into the offspring of the predator are set equal to one. The study of population dynamics for the "predator – two preys" model was conducted in [57]. However, the case of equality of competition coefficients was not considered separately. At work [58] a more detailed study was conducted, including this case. It was found that, depending on the ratios of the model coefficients, various qualitative dynamics can be observed: the survival of only one prey out of two or the indefinitely long coexistence of two preys. Similar results will be true with more preys. To determine which prey or pair of preys will survive, it is necessary to find the equilibrium states of the system and investigate their stability. In general, it is necessary to investigate the stability of $n + C_n^2 = n + n(n-1)/2$ equilibrium states. With a sufficiently large value of n, the solution to this problem becomes quite cumbersome. There is a second, more important difficulty. It is almost impossible to directly empirically measure the values of the coefficients of the model r_i and c_i. These characteristics are the consequences of the implementation of hereditary behavioral strategies. Here a different approach to the study of the limiting behavior of the model is being developed. It is based on the use of the fitness function. The theoretical foundations for constructing the fitness function are described in detail in [26]. Here are the main points that are necessary for further research.

1.2. Construction of the fitness function. The main hypothesis of the fitness comparison is as follows. The type i (and, accordingly, the hereditary strategy v_i) is considered more fit than the type j (strategy v_j) if the ratio $\rho_j(t)/\rho_i(t)$ tends to zero over time, that is

$$\lim_{t\to\infty} \rho_j(t)/\rho_i(t) = 0. \tag{2}$$

The advantage of this approach is the possibility of empirical comparison of fitness based on the observed dynamics of the numbers. In the case of a limited community (which is always the case in reality), it follows from (2) that the number of the j th (worst) species will tend to zero, that is, the worst species will be displaced from the community. From the relation (2) and the limitation of the value $\rho_i(t)$, the validity of the limiting transition follows

$$\lim_{t\to\infty} \rho_j(t) = \lim_{t\to\infty} \rho_i(t)\rho_j(t)/\rho_i(t) = 0. \tag{3}$$

Thus, a subpopulation that implements the v_i strategy will displace a subpopulation that implements the v_j strategy [26].

The established order significantly depends on the set of Q: in the same pair of strategies, it can change to the opposite when the set of Q changes [36].

In [26] it was shown that if there are average time specific rates of population growth

$$J(v_i) \equiv \langle \rho_i'/\rho_i \rangle = \lim_{T\to\infty} \frac{1}{T} \int\limits_{t_0}^{T} \rho_i'(t)/\rho_i(t)\, dt = \lim_{T\to\infty} \frac{ln(\rho_i(T))}{T} \tag{4}$$

and $J(v_i) > J(v_j)$, then ith view will be better than jth. Let

$$\langle \rho_i'/\rho_i \rangle - \langle \rho_j'/\rho_j \rangle > 0. \tag{5}$$

The inequality (5) taking into account (4) can be rewritten as

$$\lim_{T\to\infty} \frac{ln(\rho_i(T)) - ln(\rho_j(T))}{T} > 0. \tag{6}$$

It follows from (6) that

$$\lim_{T\to\infty} ln(\rho_i(T)/\rho_j(T)) = +\infty, \tag{7}$$

from where, according to the definition (2), it follows that the i-th species is better than the j-th. Thus, the function $J(v_i)$ plays the role of a comparison function or fitness function. When comparing the values of this function for different species, you can find out which species will be more adapted.

From the equations of the model (1) , it is easy to obtain an expression for the time-average specific growth rate of the prey's population $\langle \rho_i'(t)/\rho_i(t) \rangle$. Adding the same constant to the fitness function does not change the order of competitive preference reflected by it. The function modified in this way will retain the properties of the same comparison function. As a result, the average time value of the sum of the numbers of species common to all species can be excluded from the resulting expression and a simpler expression for the fitness function can be used in the future

$$J(v_i, Q) = r_i - \langle F(t, Q) \rangle\, c_i. \tag{8}$$

Here $\langle F(t,Q) \rangle$ denotes the time average value of the predator's abundance. Further research is carried out under the assumption of the existence of a temporary average $\langle F(t,Q) \rangle$. If there is a limit to the function $F(t)$ with t tending to infinity, then its time mean $\langle F(t,Q) \rangle$ coincides with this limit. This limit is easily found by calculating the coordinates of the stable equilibrium state of the model. $\langle F(t,Q) \rangle$ is determined based on the surviving type of prey. It, in turn, is determined by a set Q competing strategies. If the set Q changes, then the best (surviving) strategy will be different. This will change the fitness function (1) and the competitive ranking order set by it.

Empirical data indicate that diel vertical migrations of zooplankton are mainly determined by the following environmental factors: distribution of food (phytoplankton) $E(x)$ in depth x, distribution density of predators $S_x(x)$, distribution of unfavorable habitat factors (temperature and hydrogen sulfide) $G(x)$, as well as the daily activity of the predator $S_\tau(\tau)$ [15, 16]. All these factors can be considered as continuous functions of the vertical coordinate x or the time of day τ. The following four macroparameters have the greatest impact on the survival of a zooplankton subpopulation [55, 56].

$$\begin{aligned} M_1(v_i) &= \textstyle\int_0^1 E(x(\tau))\, d\tau, \quad & M_2(v_i) &= -\textstyle\int_0^1 S_x(x(\tau)) S_\tau(\tau)\, d\tau, \\ M_3(v_i) &= -\textstyle\int_0^1 (\dot{x}(\tau))^2\, d\tau, \quad & M_4(v_i) &= -\textstyle\int_0^1 G(x(\tau))\, d\tau. \end{aligned} \tag{9}$$

The above parameters have the following biological meaning: M_1 — the amount of food consumed (phytoplankton) per day; M_2 — daily mortality from predation; M_3 — metabolic costs of vertical migrations (we assume that they are proportional to the kinetic energy of movement); M_4 — zooplankton losses at the entrance to near-surface or deep waters, which are characterized by unfavorable temperature and hydrogen sulfide conditions.

The coefficients of the model r_i and c_i are determined by these parameters. We will use the simplest linear approximations of the coefficients c_i and r_i

$$r_i = \lambda_1 M_1 + \lambda_3 M_3 + \lambda_4 M_4, \quad c_i = -\gamma M_2, \tag{10}$$

where the weighting coefficients λ_k, γ reflect the influence of each key factor and do not depend on the strategy v_i and the set Q.

In this case, the fitness function has the form

$$J(v, \rho_0) = \lambda_1 M_1 + \lambda_3 M_3 + \lambda_4 M_4 + \langle F(Q)\rangle \gamma M_2 \tag{11}$$

or, if you enter the designation $\lambda_2 = \langle F(Q)\rangle \gamma$, — type of linear convolution of the vector of key parameters $M = (M_1, ...M_4)$:

$$J(M, Q) = \sum_{k=1}^{4} \lambda_k M_k. \tag{12}$$

Then the problem of identifying the fitness function (11) with a fixed set of competing strategies Q is reduced to determining the values of the convolution coefficients (12). This problem can be solved on the basis of observational data.

1.3. Identification of fitness function coefficients. Let there be long-term data on the behavior of the ecosystem “fish–zooplankton” with some known finite set of hereditary strategies $Q_0 = \{v_1, ..., v_m\}$, that is, data on the dynamics of the numbers $\rho_1(t), \ldots, \rho_m(t)$ and $F(t)$. Let the functions $E(x)$, $S_\tau(\tau)$, $S_x(x)$, $G(x)$ of the external environment be known. Then we can find the values of the key parameters $M(v_i)$ for all strategies. Based on this data, it is possible to estimate the limits of the relations $\rho_j(t)/\rho_i(t)$ for all pairs (v_j, v_i) and arrange strategies according to their competitive advantages within a given set of Q_0. In the case when v_i is better than v_j, the inequality $J(M(v_i), Q_0) > J(M(v_j), Q_0)$ must be satisfied. Accordingly, the coefficients λ_k must satisfy the inequality

$$\sum_{k=1}^{4} \lambda_k M_k(v_i) > \sum_{k=1}^{4} \lambda_k M_k(v_j). \tag{13}$$

Each pair of strategies will yield an inequality similar to (13). Now it is possible to estimate the coefficients of the fitness function when solving the resulting system of linear inequalities with respect to the coefficients λ. After that, knowing the maximum value of the predator's abundance, it is possible to restore the coefficient γ by the coefficient λ_2.

Linear programming methods can be used to solve a system of linear inequalities of the form (13) [35]. However, classical methods are extremely sensitive to the accuracy of the values of key parameters. A small error in key parameters, which inevitably arises due to inaccuracy of measurements, can lead to incompatibility of the system of linear inequalities.

Here, to eliminate these difficulties, we use a pairwise ranking approach to find coefficients using modern image recognition methods [59]. Let's match the pair (v_i, v_j) with the point $(M(v_i), M(v_j))$, and a pair of (v_j, v_i) — point $(M(v_j), M(v_i))$ in a four-dimensional parameter space. Then the hyperplane

$$\sum_{k=1}^{4} \lambda_k M_k = 0 \tag{14}$$

should separate these points from each other. Let's consider all possible pairs of strategies from the set of Q_0. We get two sets of points in a four-dimensional space that should lie on different sides of the hyperplane (14). Thus, the problem of determining the coefficients λ of the fitness function is reduced to finding the components of the hyperplane normal that separates two sets of points in a four-dimensional space. This typical binary classification problem can be solved using well-established methods [59]. In particular, technologies that use neural networks can be applied [34].

The proposed technique allows us to restore the fitness function for the set Q_0. However, it does not make it possible to continue this function beyond the specified set. Within the framework of the model under consideration, the order of competitive advantages may change when the set of competing strategies Q changes. Thus, the question of constructing a single function that would express the order of competitive preference for any set of coexisting competing strategies Q remains open. By constructing such a function, one can find a surviving, evolutionarily stable strategy by maximizing this function on the set Q.

2. Results

2.1. Restoration of the fitness function for a fixed set of strategies. The problem of identifying the fitness function for daily vertical migrations of zooplankton was solved on the basis of empirical data collected as a result of long-term observations (July 2011, July 2014, October 2016, November 2019) of the behavior of zooplankton (Calanus euxinus, Pseudocalanus elongatus, etc.) in the Black Sea. Data reviews are given in the sources [38, 55, 60]. For comparison, the data presented in [61] was also used. To replenish the training sample of hereditary strategies, the technique described in [34] was also used, according to which additional obviously suboptimal strategies were generated.

Data on the behavior of plankton-eating fish (Sprattus sprattus, etc.), data on the distribution of phytoplankton and temperature distribution in water layers, levels of hydrogen sulfide concentration were involved [15, 16, 55]. Two types of approximations of functions of external factors E, S_x and G were used. The simplest are linear and quadratic approximations: $E = \sigma_1(x + D)$, $S_x = \sigma_2(x + D)$, $-D < x < 0$; $G = (x + D_0)^2$. Here D — the maximum depth of immersion, which is determined by the level of the hydrogen sulfide layer, there are no predators or food on it; D_0 — the most favorable depth for the existence of zooplankton, which is determined by the temperature and concentration of hydrogen sulfide; σ_1 and σ_2 — constants, which correspond to the rate of decrease in the amount of food and predators with increasing depth. The values of the corresponding constants were found from empirical data: $D = 140$ m, $D_0 = 80$ m, $\sigma_1 = 0.367$, $\sigma_2 = 0.833$.

Approximations by hyperbolic functions are more accurate

$$E(x) = \sigma_1(\tanh(\xi_1(x + D_1)) + 1), \quad S_x(x) = \sigma_2(\tanh(\xi_2(x + D_1)) + 1),$$
$$G(x) = \cosh\left(\xi_3\left(x + D_0\right)\right).$$

Here D_1, D_0 — characteristic depths, σ_1, σ_2, ξ_1, ξ_2, ξ_3 — constants. The following parameter values were used: $D_0 = 80$ m, $D_1 = 40$ m, $\sigma_1 = 0.25$, $\sigma_2 = 0.003$, $\xi_1 = \xi_2 = 0.025$ 1/m and $\xi_3 = 0.2$ 1/m.

In both cases, the approximation of the function $S_\tau(\tau)$ was used in the form of a sinusoidal dependence: $S_\tau(\tau) = \cos(2\pi\tau) + 1$, $0 < \tau < 1$.

To solve the problem of identifying the fitness function, a single-layer perceptron [34] was built. When creating and working with the network, the following software was used: the Scikit-learn machine learning library for Python; the Pandas library (for data processing and analysis) and the Numpy library (for working with large multidimensional arrays).

The training sample contained 202 different strategies. The sample in question was divided into a training part (70%) and a part for testing (30%) using the train_test module from the sklearn.modelselection

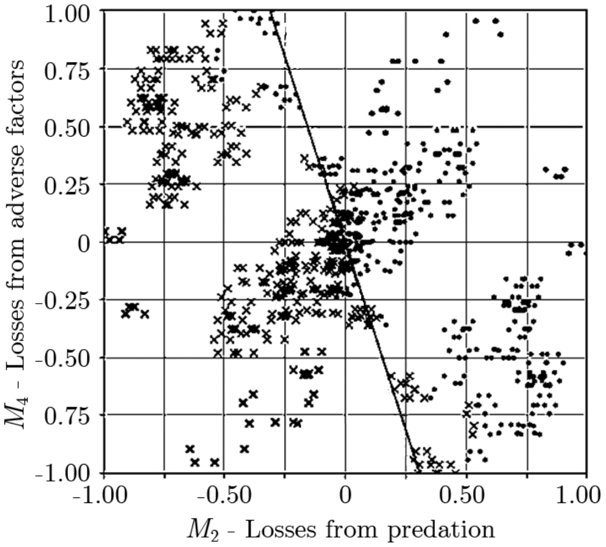

Fig. 1. Projections of the points of the training sample on the plain M_2, M_4. The crosses mark the points corresponding to the pairs (v, w) for which v is better than w; the black circles mark the points for which v is worse than w. The straight line corresponds to the intersection of the separating hyperplane and the plane of parameters M_2 and M_4

library. To evaluate the effectiveness of training, the Logloss module was used, which showed a good result (logloss = 0.01701). Another method of testing the effectiveness of training module was also used applying the sklearn.model module. In this case, the success rate of object detection is 99.89%.

In Fig. 1 the procedure for restoring the coefficients of the fitness function by solving the classification problem is illustrated. Here is a separating hyperplane constructed by a binary classifier for two classes of strategy pairs. The coefficients of this hyperplane are the desired coefficients of the fitness function.

The implementation of artificial neural networks for linear-quadratic approximation of external parametrization factors gives the following coefficient values: $\lambda_1 = 3$, $\gamma = 0.0017$, $\lambda_3 = 2.5e - 5$, $\lambda_4 = 0.01$; for hyperbolic approximation — the following values: $\lambda_1 = 3$, $\gamma = 1.2$, $\lambda_3 = 7.5e - 8$, $\lambda_4 = 0.1e - 4$.

The problem of identifying the fitness function was solved using a neural network for a fixed set of Q_0 (training sample). The obtained coefficients λ_1, γ, λ_3, λ_4 do not depend on this set. Their values will not change when moving to any other set of Q strategies that interest us. We will show how, based on the information obtained about the identified coefficients, it is possible to predict the best strategy v_0 for any set of competing strategies Q. Each strategy v of Q is characterized by the values of two coefficients r_v and c_v. Geometrically, this corresponds to a point on the plane of the variables r and c. The set of strategies Q will correspond to the set of points W on this plane. In this case, there may be a case when several strategies from Q correspond to the same point in W. The functional J, which is given by the formula (8), can be considered as a linear function of two variables c and r, given in the domain W; the coefficient $\langle F \rangle$ of this linear function depends on the domain W.

2.2. Restoration of the fitness function in the case of a single surviving strategy. Consider a situation where there is a single point (c_0, r_0) in W, which corresponds to the surviving strategies of v_0. We find the coordinates of the only stable equilibrium state of the model (1) and get an expression for the limit value of the predator quantity

$$\langle F(Q) \rangle = \frac{r_0}{c_0} - \frac{1}{c_0^2}. \tag{15}$$

The strategy v_0 will be the best in Q relative to another strategy w with the corresponding coefficients c_w, r_w if the inequality $J(w,Q) < J(v_0,Q)$ is satisfied, that is

$$r_w - c_w\left(\frac{r_{v_0}}{c_{v_0}} - \frac{1}{c_{v_0}^2}\right) < r_{v_0} - c_{v_0}\left(\frac{r_{v_0}}{c_{v_0}} - \frac{1}{c_{v_0}^2}\right) = \frac{1}{c_{v_0}}. \tag{16}$$

It follows from (16) that for the best strategy v_0, the equality will be valid

$$\min_{w\in Q}\left(\frac{1}{c_{v_0}} - r_w + c_w\left(\frac{r_{v_0}}{c_{v_0}} - \frac{1}{c_{v_0}^2}\right)\right) = 0. \tag{17}$$

If the strategy v is not the best for the set Q, then there will be at least one strategy w of Q for which the inequality holds

$$r_w - c_w\left(\frac{r_v}{c_v} - \frac{1}{c_v^2}\right) > \frac{1}{c_v}. \tag{18}$$

Inequality (18)in turn entails the validity of the following inequality

$$\min_{w\in Q}\left(\frac{1}{c_v} - r_w + c_w\left(\frac{r_v}{c_v} - \frac{1}{c_v^2}\right)\right) < 0. \tag{19}$$

Combining (17) and (19), we get that in order to find a surviving strategy v_0 in Q, we need to maximize the expression

$$J_0(v) = \min_{w\in Q}\left(\frac{1}{c_v} - r_w + c_w\left(\frac{r_v}{c_v} - \frac{1}{c_v^2}\right)\right) \tag{20}$$

for all strategies v in the set Q. The expression (20) can be considered as a generalized fitness function for the set Q. Given the linear dependence of the coefficients c and r on the key parameters, it is possible to express the function (20) through them

$$\begin{aligned} J_0(v) = \min_{w\in Q}\Bigg(&\frac{1}{\gamma M_2(v)} - (\lambda_1 M_1(w) + \lambda_3 M_3(w) + \lambda_4 M_4(w)) + \\ &+\gamma M_2(w)\left(\frac{\lambda_1 M_1(v) + \lambda_3 M_3(v) + \lambda_4 M_4(v)}{\gamma M_2(v)} - \frac{1}{(\gamma M_2(v))^2}\right)\Bigg). \end{aligned} \tag{21}$$

The generalized fitness function will change when the set Q changes. But the values of the coefficients that appear in its expression will not change. To find an evolutionarily stable strategy that corresponds to the selected set of competing strategies, it is necessary to solve an optimization problem.

It is necessary to emphasize another very important feature of the generalized fitness function J_0: on a survival strategy, its value is zero. Accordingly, for all non-optimal strategies, its value is negative. If, when solving the problem of maximizing the generalized fitness function, an answer with the negative largest value is obtained, then there is no single point in the set of W corresponding to surviving strategies.

The following Table shows an example of a set of four competing strategies with the corresponding values of c and r. For each strategy, the value of the function J_0 is calculated using the formula (20). From here it can be seen that this function does not take a zero value on any strategy. In this case, there are two different points in W that correspond to different survival strategies. It is impossible to find them by optimizing the J_0 functionality. This case requires a separate study.

Table. Example of the system with two surviving strategies

	c	r	J_0	J_2
v_1	2	2	-0.125	0
v_2	4.5	4	-0.104	0
v_3	3	2.5	-0.433	0.3
v_4	5	4	-0.380	0.4

2.3. Restoration of the fitness function in the case of a pair of surviving strategies. Let there be two different survival strategies v_0 and v^*, which correspond to two different points (c_0, r_0) and (c^*, r^*) in the set W and which have equal fitness values, that is

$$r^* - \langle F(Q)\rangle\, c^* = r_0 - \langle F(Q)\rangle\, c_0. \tag{22}$$

From the equality (22), we can get an expression for the limit value of the number of predators

$$\langle F(Q)\rangle = \frac{r^* - r_0}{c^* - c_0}. \tag{23}$$

Similarly to the case of the survival of one strategy, it is shown that for any best strategy v_0 (or v^*), the equality will be valid

$$\min_{w\in Q} J_2(v_0, v^*, w) = \min_{w\in Q}\left(\frac{r_0c^* - r^*c_0}{c^* - c_0} - r_w + \frac{r^* - r_0}{c^* - c_0}c_w\right) = 0. \tag{24}$$

If a pair of strategies v, u with the corresponding coefficients $(c_v, r_v), (c_u, r_u)$ is not the best for the set of Q, then the following relation will be valid for it:

$$\min_{w\in Q} J_2(v, u, w) = \min_{w\in Q}\left(\frac{r_vc_u - r_uc_v}{c_u - c_v} - r_w + \frac{r_u - r_v}{c_u - c_v}c_w\right) < 0. \tag{25}$$

We compare (24) and (25) and come to the conclusion that in order to find the best pair of strategies in Q, we need to maximize the expression

$$J_1(v, u) = \min_{w\in Q}\left(\frac{r_vc_u - r_uc_v}{c_u - c_v} - r_w + \frac{r_u - r_v}{c_u - c_v}c_w\right) < 0 \tag{26}$$

for all strategies v and u in the set Q with the corresponding coefficients (c_v, r_v) and (c_u, r_u), that is, maximize the functional J_1, which is given by the formula (26), on the Cartesian product Q^2. The expression (26) can be considered as a generalized fitness function for pairs of strategies from the set Q. Given the linear dependence of the coefficients c and r on the key parameters, it is possible to express the function (26) through them similarly (21).

Maximizing the functionality of J_1 allows you to find all possible surviving pairs (even if such a pair is not the only one). For the best pair, the value of the functional J_1 is zero.

The table shows the value of the functional $J_2(w, v_1, v_2)$ with different strategies w from the considered set of four strategies. From the values given, it can be seen that the smallest value of the functional J_2 is achieved at $w = v_1$ or $w = v_2$, where it is zero. Functional J_1 on the pair (v_1, v_2) takes the value 0. But zero is the absolute maximum of this functional, it never takes on a greater value. Therefore, the pair (v_1, v_2) the best.

If the set W contains more than two different points that correspond to surviving strategies, then at all these points the functional J takes an equal maximum value. Then, due to the linearity of the function J with respect to the variables r and c, all these points must lie on one straight line. All such points can be found by maximizing the J_1 functional and do not require the development of a different technique. However, in practice, such a case seems unlikely. After all, it requires precise linear matching of the values of the coefficients (and key parameters) for a set of more than two different strategies. Any arbitrarily small deviation from these values will lead to the destruction of coordination, which will entail the displacement of all strategies except two or even one.

2.4. The case of a strictly convex set of competing strategies. Let's prove another important property: if the set W is strictly convex, there is a single point in this set that corresponds to the best (surviving) strategies. When searching for a surviving strategy for such a set, you only need to solve the problem of maximizing the J_0 functional.

Suppose that in a strictly convex set W there are two distinct points (c_0, r_0) and (c^*, r^*), which correspond to the different survival strategies v_0 and v^*. In this case, the fitness function has the following form

$$J(w) = r_w - \frac{r^* - r_0}{c^* - c_0} c_w. \tag{27}$$

The function (27) is linear in the variables r_w and c_w, so it takes the same maximum value $J(v_0)$ not only at points (c_0, r_0) and (c^*, r^*), but also at all points of the segment that connects them. Since the set W is strictly convex, then all points of this segment belong to W and correspond to some strategies from the set Q, which will also be surviving. All points of this segment, except the ends, must be internal points of the set W, that is, any such point has a small neighborhood that is entirely included in W. Due to the linearity of J as a function of two arguments c and r, there are points in this neighborhood with larger values of J than $J(v_0)$, and this contradicts the fact that $J(v_0)$ — the maximum value of the fitness function in the domain W.

Consider the question of a survival strategy for the widest possible set Q that contains all possible smooth periodic time functions $x(\tau)$. The fitness function has the form (11). Here the value $\langle F \rangle$ represents some unknown constant in advance. In order to find a waiting strategy, we need to find a smooth function $x(\tau)$ that satisfies the condition $x(0) = x(1)$ and on which the functional (11) takes the largest value. The maximization problem can be considered as a classical calculus of variations (or optimal control) problem. Then, given the strict convexity of the function G and the convexity of the functions E and S_x, there is a unique solution to the variational problem. Accordingly, only one strategy will survive. This will be true for linear-quadratic approximations of environmental functions. If we take the sinusoidal approximation of the predator activity function $S_\tau(\tau) = \cos(2\pi\tau) + 1$, then the optimization problem can be solved analytically [14]. The only surviving strategy of zooplankton movement has the form of a sinusoid $x(\tau) = A + B\cos(2\pi\tau)$, where the constants A and B are explicitly expressed in terms of the coefficients of the fitness function and the parameters of the external environmental conditions

$$A = \frac{\lambda_1\sigma_1 - \langle F \rangle \gamma\sigma_2}{2\lambda_4} - D_0, \quad B = -\frac{\langle F \rangle \gamma\lambda_2}{8\lambda_3\pi^2 + 2\lambda_4}. \tag{28}$$

When substituting the obtained solution (28) into formulas for calculating the key parameters M (9), coefficients r and c (10), it is possible to calculate the corresponding stationary value of F by the formula (15):

$$\langle F \rangle = \frac{\lambda_1\sigma_1(A + D) - 2\lambda_3 B^2\pi^2 - \lambda_4(A + D_0)^2 - \lambda_4(B^2/2)}{\gamma\sigma_2(A + B/2 + D)} - \frac{1}{(\gamma\sigma_2(A + B/2 + D))^2}. \tag{29}$$

The solution of the resulting system of equations (28), (29) with respect to A, B, $\langle F \rangle$ allows us to find a surviving strategy.

2.5. Comparison with empirical data. For the previously introduced parameters of linear-quadratic approximations of the environment functions and the reconstructed coefficients of the fitness function, the following values of constants were found: $A = -55.2$, $B = -27.6$. The graph of the corresponding strategy is shown in Fig. 2, *a*.

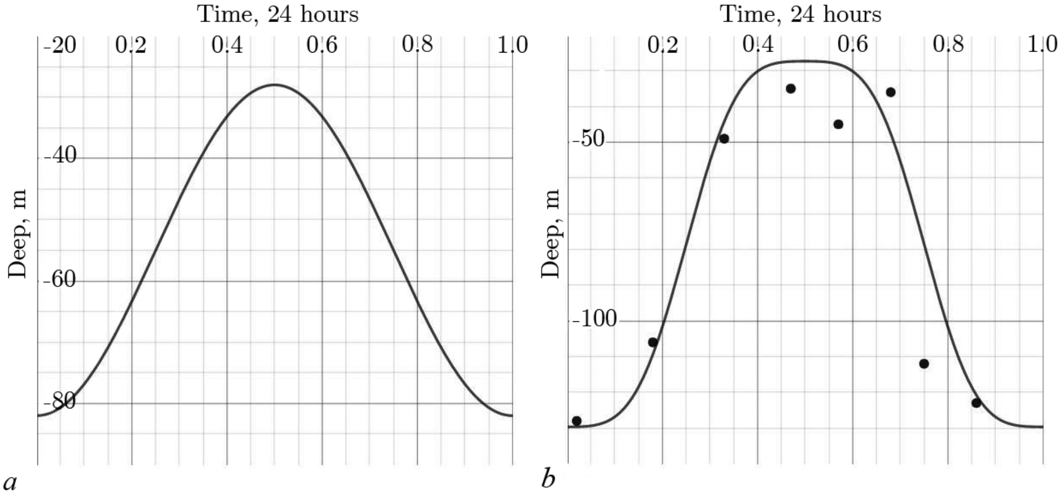

Fig. 2. Graphs of surviving strategies: *a* — graph of the surviving strategy in the case of linear-quadratic approximations of environmental factors; *b* — graph of the surviving strategy in the case of hyperbolic approximations of the environmental factors. The dots show the observed positions of the cladoceran Calanus euxinus on June 21, 2011 in the northeastern part of the Black Sea

For hyperbolic approximations of the functions of the medium, it is not possible to find an analytical solution to the variational problem. In this case, a numerical search for a surviving strategy was carried out in the form of a segment of a trigonometric series of the fifth order $x(\tau) = A_0 + \sum_{k=1}^{5}(A_k \cos(k2\pi\tau) + B_k \sin(k2\pi\tau)$. The problem of maximizing the value of the generalized fitness function (21) with the previously restored coefficients λ_1, λ_3, λ_4, γ relative to the coefficients of the series A_k and B_k was solved by the global optimization method [62]. As a result, the following best coefficient values were found: $A_0 = -78.5$, $A_1 = -57.6$, $A_3 = 6.5$, $A_5 = -0.2$, the remaining coefficients are zero. The graph of the corresponding strategy is shown in Fig. 2, *b*. For comparison, the observed positions of the cladoceran Calanus euxinus in the northeastern part of the Black Sea in the summer of 2011 are given. It can be seen that the constructed strategy is in good agreement with empirical data.

The possibility of an indefinitely long coexistence of two species of cladocerans was considered. Along with the strategy obtained, a strategy with coefficients was considered $A_0 = -80.8$, $A_1 = -49.5$, $A_3 = 4.2$, $A_5 = 0.2$. This strategy is an approximation of the movement of the cladocera on Pseudocalanus elongatus (Fig. **??**). The following values of the coefficients of the fitness function were considered: $\lambda_1 = 2.5$, $\lambda_3 = 2.5e-7$, $\lambda_4 = 1e-6$, $\gamma = 1.2$ and the system “predator–two victims”. Using the technique described above, it was found that both species survive in this system. This corresponds to the presence observed in nature of two dominant species of cladoceran Calanus euxinus and Pseudocalanus elongates in the northeastern part of the Black Sea.

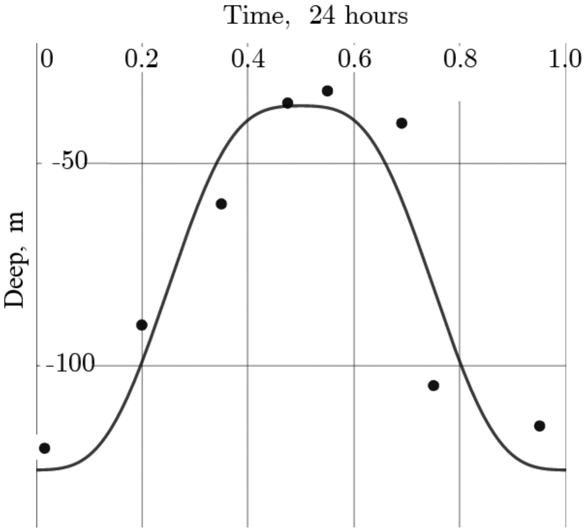

Fig. 3. Approximation of Pseudocalanus Elongatus motion. The dots show the observed positions of the cladoceran Pseudocalanus elongates on June 21, 2011 in the north-eastern part of the Black Sea

Conclusion

This article presents a new technique for constructing the fitness function in the case of its dependence on a set of coexisting hereditary elements — behavioral strategies. The technique involves two stages of the output of such a function. First, the fitness function is restored for some finite subset of elements based on data processing of long-term dynamics of their numbers and comparison of their competitive advantages. At the same time, the ranking problem is solved based on machine learning technologies. As a result, the values of the coefficients of the fitness function are identified. At the second stage, the form of the generalized fitness function for an arbitrary set of elements is derived. Here, the values of coefficients already found at the previous stage and the features of interspecific interaction are used, which are reflected in the model (the relationship of the values of phase coordinates in a stable state of equilibrium). The generalized fitness function has two different forms — for the case of a single surviving strategy and for the case of several surviving strategies. An example of a set in which two different strategies survive is given. Sufficient conditions for the uniqueness of the best point are proved.

The proposed method of constructing the fitness function, which depends on a variety of competing strategies, uses particular features of a particular model. At the same time, it is quite general and can be applied to a wide range of population dynamics models.

The strategy of diel vertical migrations of zooplankton constructed as a result of modeling is in good agreement with empirical data.

The search for a survival strategy is actually equivalent to determining a stable equilibrium state in the model. If the number of coexisting hereditary victim strategies in the studied community is large enough (for example, hundreds of thousands), then the number of possible equilibrium states of the system becomes very large and it is very difficult to solve the problem of studying their stability using classical Lyapunov methods. In this case, a search algorithm based on maximizing the fitness function seems to be a convenient alternative for the classical approach.

Using the constructed fitness function, it is possible to simulate an evolutionarily stable regime of daily vertical migrations of zooplankton by numerically solving the minimax problem.

The proposed method of constructing the fitness function, which depends on a variety of competing strategies, is quite general and can be applied to a wide range of models of population dynamics.

The ranking problem solved here is related to the key problem of artificial intelligence - the formation of the system's own goal, which determines its behavior. As a result of solving the ranking problem by artificial intelligence methods, a comparison function can be formed, which allows you to find the best behavior strategy. However, in the general theory of machine learning, the question of the source of the order of preference on the training sample remains open. It is assumed that this order is presented to the system by an external teacher. It is not always the order of preference, which is given on some subset, can be extended to wider sets. The present study, conducted for a special case of systems with expedient behavior — living systems, shows how the order of preference arises as a result of strategy competition. Here, in fact, the teacher is the very survival factor of the carriers of a particular strategy. Here it is shown how the objective function is formed even under conditions of dependence of the order of preference on a set of competing strategies.

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