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Modeling of adaptive counteraction of the induced biotic environment during the invasive process

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Abstract. *Purpose* is to develop a mathematical model for the analysis of a variant in the development of a population process with a non-trivially regulated confrontation between an invading species and a biotic environment. *Relevance.* The situation we are studying arises in invasive processes, but is a previously unexplored special variant of their development. The task of modeling is to describe the transition to a deep v-shaped crisis after intensive growth. The model is based on examples of the adaptive dynamics of a bacterial colony and the suppression of mollusk populations, carriers of dangerous parasitic diseases, after targeted anti-epidemic introduction of their antagonists. *Methods.* In our work equations with a retarded argument in the range of parameter values that have a biological interpretation were studied. The model uses a logarithmic form of species regulation, taking into account the theoretically permissible capacity of the medium. In the equation we included the function of external influence with flexible threshold regulation relative to the current and previous population size. *Results.* It is shown that the proposed form of impact regulation leads to the formation of a stable adapted population after the crisis, which does not have a destructive impact on the habitat. With an increase in the reproductive potential of an invasive species, a deep crisis becomes critically dangerous. The form of the crisis passage depends on the reproductive potential, on the size of the initial group of individuals, and also on the time of activation of the adaptive counteraction from the environment. It is established that at a sufficient level of resistance, a non destructive equilibrium is established. *Conclusion.* The actual scenario of sudden depression of an actively spreading population with a large reproductive r-parameter, which is caused by the delayed activity of its natural antagonists, has been studied. The threshold form of biotic regulation is characteristic of insects, the abundance of which is regulated by competing species of parasitic hymenoptera. The variant of rapid phase change considered by us in the model is relevant as a description of one of the forms of developing the body's immune response to the development of an acute infection with a significant delay. If the immune response is prematurely inhibited by the body itself, then the chronic focus of the disease persists. Examples of the dynamics of two real biological processes in experiments with biological suppression methods are given, which correspond to the invasion scenario obtained in the new model.

Keywords: models of isvasion processes, nonlinearity of regulation, threshold resistance of the biotic environment, cycles of COVID epidemic, anti-epidemic activities, CRISPR – CAS9.

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Introduction

In the article, continuing a series of works on modeling system changes, the author investigates nonlinear phenomena of ecodynamics caused by the introduction of aggressive species. Such invasive processes develop with active, but not constant, opposition from the biotic environment. As we have shown in previous works, a number of threshold effects lead to nonequilibrium and extreme situations in the development of population processes. The regulation and triggering of extreme invasion and the development of a response from the environment involves the action of previous states, as shown by the studies of population biologists [1]. However, there is no single answer to the question of what characteristics of the species themselves or the affected communities contribute to the success of the settlement and explain the dynamics

of the spread of the invaders [2]. The dynamics of invasions is very variable. By no means all species infestations (even purposeful acclimatization and release of individuals) end with successful occupation of the area.

A common feature of invasions is the time delay factor, which is observed between the initial colonization, the beginning of rapid growth of the local population and the expansion of the area. Temporary factors include the process of adaptation to a new habitat, the evolution of the characteristics of the life cycle, the elimination of genetic problems due to the small biodiversity of the original group (inbred depression factor). These factors causing lag effects have been investigated by many authors of [3], but the counter adaptation of the autochthonous biotic environment and the resulting reaction of counteraction is a less studied issue.

The purpose of the work is to analyze the scenario of an invasive process with counteraction factors created by a specially induced biotic environment to assess the duration of the passage of the crisis that has arisen. The author develops a phenomenological method of using functions with a threshold effect in population equations with a delay, where the regime of stable oscillations is not an actual solution. By consistent improvement, adequate inclusion of the lag factor in the functional components of the model is achieved. The novelty of the computational scenario of a deep crisis demonstrated by us is that the simulated impact does not remain linearly dependent on the state of the invasive population. The relevance of the modeling of flexible and threshold counteraction is justified by the methods of biological control of alien species. Targeted introduction of antagonists is carried out against an undesirable species. A competitive system of confrontation is being created, which, unlike many variations of the system «predators–victim», has adaptive mechanisms [4] — the number of regulatory antagonists depends on previous situations, and the effectiveness of attacks — on the current density of victims. The dependence of regulation on past states under the term «ereditarity of systems» was discussed in a biological context in the works of B. Volterra [5]. Actual example — lag time when starting a chain of response reactions in the first phase of infection — an important factor for the immune system that determines the course of the disease further. In conclusion, examples of scenarios described by the model from different fields are given — microbiology and zoogeography.

1. Delayed regulation — a method of describing biological nonlinearity

For the mathematical description of cyclic changes that do not follow from interactions (direct trophic interaction «predator–victim» or adaptive «parasite–host»), in population biology G. Hutchinson [6] proposed to consider the effect of the delay — of some previous state of the biosystem $N(t-\psi(t))$— on the speed of modern reproduction. Fluctuations can be observed under constant conditions in isolated populations of [7]. Models and equations are not presented in the theoretical review on the ecology of cyclic biosystems [6].

The model itself in the form of an equation was first proposed by W. Wright [8] in this form (we keep the notation):

$$y\prime(t) = -\alpha y(t-1)[1+y(t)]. \tag{1}$$

In (1) α is equivalent to the reproductive parameter r, and the notation $y(t)$ corresponds to $N(t)$ in (2). Later «Hutchinson's equation» was written out by R. May [9] in the modern form familiar to environmentalists:

$$\frac{dN}{dt} = rN(t)\left(1-\frac{N(t-\tau)}{K}\right), \tag{2}$$

where r is— traditionally the reproductive potential of the population. Initially, r is the difference between natural mortality and fertility per unit of time. The parameter K is borrowed from the limited growth model $N(t) \to K$ Ferhulsta–Pirla [10], where reflects the saturation level of the ecological niche [11]. In fact, (2) is a modification of $\dot{N} = rf(N(t-\tau))$ with a delay of τ for the equation

$$\frac{dN}{dt} = rf(N(t)) = rN(t)\left(1 - \frac{N(t)}{K}\right). \tag{3}$$

The textbook parameter K borrowed later in other models in (3) set the available level of non-destructive filling of the medium: at $0 < N(0) < K$, $\max N(t) = K$ is performed/ The level K is considered a stable capacity of the ecological niche for the species at $t \to \infty$.

In different modeling works, K should actually be interpreted with different aspects for different scenarios, depending on the situation and properties of the selected $f(N)$. Behind the different interpretations of K is the theory of environmental regulation [12]. The capacity of the medium can act indirectly on mortality, for example, through the growth rate of larvae. In ecology, there are fundamental and realized ecological niches [13]. The interpretation of K in models for analyzing different transients will be ambiguous. With the development of extreme processes in biosystems, the number of aggressive invader significantly exceeds the hypothetical balance capacity for the biosystem. For a lethal pathogen, there is no balance capacity in our body[1]. For many ecodynamic phenomena, the use of K as an optimal niche capacity or limiter level in their modeling is only an instrumental tool.

The (2) model was intended to visually describe the fluctuations of $\forall N(0) > 0$, since at $r\tau = \pi/2$ there is a bifurcation of the birth of the cycle [14], the cyclic trajectory is denoted by $N_*(t)$. The saturation capacity of the ecological niche K at $r\tau > \pi/2$ becomes the center point for the resulting cycle $N_*(t; r\tau)$co by the property $\forall N(0)$, where the capacity of the niche K acts as the average value of $\overline{|\max N_*(t) - \min N_*(t)|} \approx K$. The equation (2) has been investigated by many authors [15] and often in one-parameter form $\dot{x} = \lambda x(t)(1 - x(t-\tau))$ without interpretation [16].

Studies of (2) have not solved many problems in adequately describing a variety of population fluctuations. The development and complication of (2) has led to the emergence of a direction in modeling — the development of equations with a deviating argument in problems of modeling biological processes [17]. The equations with $N(t-\tau)$ have become relevant not only for the dynamics of populations [18]. They are also used in the study of the rate of transcription of DNA →RNA for protein synthesis. The development of the direction is associated with problems that are not particularly interesting from the point of view of theoretical mathematics, but are significant for computational modeling in the biological field.

M. Smith proposed [19] an alternative model for (2) of insect fluctuations in laboratory experiments, but this version of the equation was not developed. The lag of τ_2 in the reproductive multiplier $rN(t-\tau_2)$ — is an environmentally redundant inclusion

$$\frac{dN}{dt} = rN(t-\tau_2)\left(1 - \frac{N(t-\tau_1)}{K}\right) - \delta N(t), \tag{4}$$

where δ is the coefficient of competition-independent mortality from external factors of biotic aggression.

[1]Even in the case of long-term asymptomatic carriage of HIV and hepatitis C.

The direction of modeling growth limited by the resources of the environment (but not by the activity of antagonists) continues to develop in modern modifications and with unusual coefficients, for example

$$\frac{dN}{dt} = rN(t)\frac{(1-N(t))/(K+\vartheta N)}{(1-N(t))/K(1-\gamma)}. \tag{5}$$

Solutions of similar (5) models describe balancing processes $\forall N(0) > 0$. It makes sense to supplement not all such equations with the inclusion of $t-\tau$. An important practical difference between y solutions of various proposed models of limited population growth is the position of the inflection point $N_p \neq 0$ on the graph of the solution $N(t)$. For the (3) model, the ordinate of the inflection point is $N_p = K/2$, the abscissa is $t_p = r^{-1}\ln(K-N(0))/N(0)$. The position of the ordinate of the inflection point N_p is important to establish for the task of optimal operation and analysis of scenarios with withdrawal $\dot{N} = rf(N(t)) - Q$. The population growth at the point N_p is maximized. Then the population demonstrates better productivity, and all the excess growth can be withdrawn [20]. The concept is extremely dangerous for populations with critical threshold states.

Several modifications and variants of generalizations of the (2) equation are known for «Hutchinson model». For example, the modification in [21] is suitable for the case of different maturation times of y males and y females, who have different competition parameters c_1, c_2:

$$\frac{dN}{dt} = rN(t)\left(1 - \frac{c_1N(t-\tau) + c_2N(t-\tau_1)}{K}\right). \tag{6}$$

Modification of [22], where K-based regulation is enabled with a relative saturation value:

$$\frac{dN}{dt} = rN(t)\left(\frac{K-N(t-\tau)}{K+cN(t-\tau)}\right). \tag{7}$$

The model $\dot{N} = rf(N(t-\tau)) - F(N)$ with delayed regulation, but without the niche parameter $Kcf(x) = rx^{-bx}$ is proposed based on the study of experiments by entomologist A. Nicholson:

$$\frac{dN}{dt} = rN(t-\tau)\exp(-bN(t-\tau)) - \delta N(t). \tag{8}$$

A. Nicholson created competition for resources between the three stages of insect development and this factor caused fluctuations in the number of individuals with a large amplitude. Mortality δ was added to (8) arbitrarily, predators/parasites were not used in the experiment. With an increase in $r\tau$, the solution (8) demonstrates relaxation fluctuations [23], but with very small minimum values.

The essential interpretation of the occurrence of the τ delay of $t-\tau$ or generically $t-\psi(t)$ is important. The time value of τ originally referred to the regulation of reproduction efficiency through a delay in ontogenetic development. A change in the delay according to some law $\tau = \psi(t)$ can occur when there are adjacent generations with different duration of ontogenesis, when one of the generations undergoes wintering, which is a specific case. The length of a species' life cycle and the intervals between population peaks in its populations are not always comparable values on the time scale. We propose to divide the lag in the interpretation of models into three types. Let's highlight the reproductive "ontogenetic" delay, the regulatory delay due to the exhaustion of resources or the search for new sources of nutrition. Separately, we will consider the third type - adaptive lag, as the time needed by the system to develop a response.

1.1. Problematic aspect — approaching zero cycle minima. The method of obtaining oscillating solutions in models with $t-\tau$ has a problem from the point of view of the ecological validity of the behavior of solutions. If we increase $r\tau > \pi/2$ in (1), then the cycle $N_*(t; r\tau)$ will quickly take the form of inharmonic oscillations [24]. The relaxation cycle with increasing amplitude as $r\tau$ increases will take the form of Λ-shaped peaks $\max N_*(t) \gg K$. Then the trajectory in the minima of the cycle begins to approach arbitrarily close to the values in the neighborhood zero. It is known that for a model in one-parameter form $\dot{N} = \lambda N(t)(1 - N(t-\tau))$ in progress

$$\min N_*(t,\lambda) = \exp\left(-e^{\lambda} + 2\lambda + \frac{1+(1+\lambda)\ln\lambda}{\lambda} + O\left[\frac{\ln^2\lambda}{\lambda^2}\right] - 1\right).$$

Neighborhood of minima $N(t_{\min}) \approx \min N_*(t;\lambda\tau)$fluctuations, where the trajectory runs for a long time near-zero values $\min N_*(t;\lambda\tau) \to 0+\varepsilon$, become extremely long — for the population interpretation, the solution is unrealistic.

The following modification option (1) was analyzed in [25]:

$$\frac{d\,N}{d\,t} = \lambda N(t) f\left(N(t-1)\right), \tag{9}$$

where $\lambda \gg 1$ is assumed, a $f(x)$ is a differentiable function decomposable into an asymptotic series for which the conditions are satisfied

$$f(0) = 1, \quad f(x) = -a_0 + \sum_{k=1}^{\infty} \frac{a_k}{x_k}, \quad x \to \infty, \quad a_0 > 0. \tag{10}$$

The conditions (10) correspond to the biologically interpreted function in [25] with relative regulation of reproduction

$$f(x) = \frac{(1-x)}{(1+\varsigma x)}. \tag{11}$$

The coefficient ς in (11) complements the number of parameters that determine the characteristics of the relaxation cycle $N_*(t)$. Under transformations from the original equation (9) to the singularly perturbed $\dot{x} = F(x(t-1),\varepsilon)$ and to the limit relay equation $\dot{x} = R(x(t-1))$ for (9)c (10) in [25], the existence of a unique and orbitally stable cycle $N_*(t;\lambda\tau\varsigma)$. The correspondence of the properties of the $N_*(t)$ cycle to the well-known population process in (9) with (11) from the restrictions introduced there (10) is difficult to justify, since from the statement about the characteristics of oscillations in [25] it was established:

$$\min N_*(t,\lambda) \sim C_1 \exp\left(-\lambda a_0\right), \quad C_1,\ a_0 = \text{const} > 0.$$

The parameter λ was specified in [25] initially large. The problem of population interpretability of the cyclic regime persists in other modifications of the $cN(t-\tau)$ models. Serial outbreaks of the number y of insect pests cannot be described with the property of minima: $\min_{0<t<T_*} N_*(t,r) \to \varepsilon$, and $\varepsilon \ll 1$. This is especially evident for active invaders with large values of r. The cycle $N_*(t,r)$ reaches too small values to quickly re-achieve high numbers. The inclusion of more than two variables with a large delay in the model is not biologically convincing. The scenario of the formation of a relict species occurs with a gradual decrease of the previously dominant species to equilibrium, which turns out to be stably separated from zero.

Extreme population fluctuations of y Arctic rodents with large amplitude and small minima [26] are known, but these are *unstable* regimes and 4-year periods are regularly disrupted with the possibility of the death of local groups [27]. Such fluctuations of the species in the environment are endogenous [28], they are not a consequence of the interaction «predator–victim», therefore «Volterra» systems of equations are not described.

2. Specific new models of formation and destruction of fluctuations

The interpretation of the parameter K as a balancing limit and the volume of the niche in our modifications is changing. We previously proposed [29] equation for a special pulsating outbreak of abundance — the phenomenon of sawtooth oscillations of a dangerous pest *Choristoneura fumiferana* in the forests of Canada:

$$\frac{dN}{dt} = rN(t)\left(\frac{K - N^k(t-\tau)}{K + cN^m(t-\tau)}\right), \quad m = k+1. \tag{12}$$

In the modification (12), during a pulsating flash between short peaks of fluctuations, the number is kept at a significant level. In the computational scenario c $k = 2$, the effect of a rapid decrease in minima is eliminated $\min_{0<t<T_*} N_*(t,r) \to \varepsilon$, $\varepsilon \ll 1$.

Another modification proposed by the author in [30] is based on the idea that the $N(t-\gamma) transition is important for control mechanisms$ through the precritical threshold of the number of H. The model is designed for cases when the amplitude of the cycle of a dangerous invader cannot become higher than a certain value acceptable for the environment. In the scenario, the dynamics of the invasive process is influenced by the deviation $[H - N(t-\gamma)]$. The deviation value can be either positive or negative. In the modification proposed by us in [30], a variant of the destruction of unsteady oscillations with increased r, $H = 1/3K$, $\gamma = 2/3\tau$, $r\tau > \pi$:

$$\frac{dN}{dt} = rN(t)\left(1 - \frac{N(t-\tau)}{K}\right)(H - N(t-\gamma)), \quad \gamma < \tau. \tag{13}$$

The value of H in (13) is interpreted as the threshold state of «pre-saturation» of the medium when at $N(t) \to H+\varepsilon$ the invader population is already beginning to have a destructive effect on the environment.

In immunological interpretation, with such a viral load, the body, after a short delay interval, encounters dangerous symptoms that can become lethal. After the formation of fluctuations, when the maximum value of the cycle exceeds the limit level for the ecosystem, the trajectory of $N(t)$ tends to infinity with a stop of calculations. The scenario of the destruction of the c (13) cycle did not require an increase in r directly during the computational experiment. The (13) model described a computational scenario with «outlier» of the trajectory from the cycle, which, according to our initial hypothesis, corresponds to a demographic catastrophe of overflow due to the destruction of the environment. However, the dynamics of the destruction of the cycle is more consistent with the development of the epidemic of a volatile virus.

Previously, the author did not have a graph with data to confirm the reality of the model scenario (13). In substantiation of the scenario, we have given only a hypothetical reasoning about the variant of the catastrophe of the human population on Easter Island. During the ongoing COVID-19 pandemic, epidemiologists observed several examples of the transition from regular

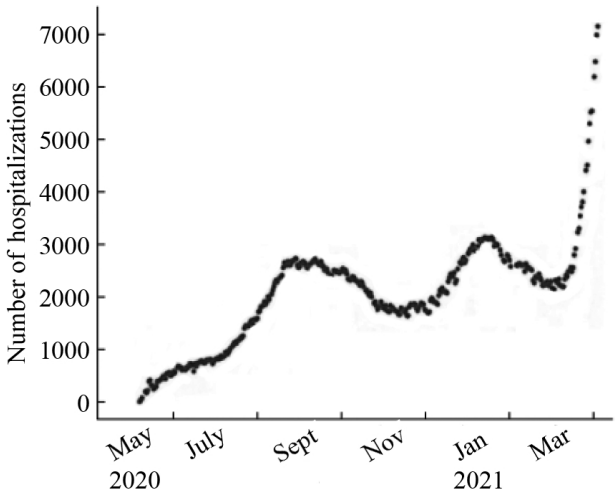

Fig. 1. Катастрофическое нарушение циклической динамики в ходе локальной эпидемии COVID-19 на Юге Бразилии по данным о госпитализации за день

Fig. 1. Catastrophic violation of the cyclical dynamics of the COVID epidemic in the South of Brazil according to hospitalization data per day

fluctuations in morbidity to a rapid Λ-shaped outbreak of the number of infections. The scenario with the destruction of the regime formed in the first phase of the process of fluctuations in the incidence of COVID-19 was noted in the spring of 2021 in the dynamics of the epidemic in Brazil. In Fig. 1 data on hospitalization of patients diagnosed with COVID-19 in 2020–2021 in the southern state of Brazil Rio Grande do Sul, from where the coronavirus epidemic spread to the rest of the country. It is obvious that the established cyclical regime was replaced by a rapid increase in the number of patients at the end of February 2021 (before the appearance of Delta and Omicron strains). In the epidemic interpretation, r is the basic reproductive number of the spread of the virus.

3. Models with active counteraction and minimum threshold

For the model of extreme population processes, the minimum number of the group that is theoretically necessary for the survival of the local population is relevant. In the work [31] A. Bazykin proposed an equation with a quadratic factor of external resistance $-\delta N^2$ to describe the scenario of population extinction with a threshold effect:

$$\frac{dN}{dt} = r\frac{\gamma N^2}{\gamma + \sigma N} - \varsigma N - \delta N^2. \tag{14}$$

The ecological principle of the «aggregated group» [32] says that for a population there is an optimal range for reproduction of the community size $\bar{\Delta}N$. This term is applicable to social animals. The critical minimum L threshold $L < \inf \bar{\Delta}N$ does not directly follow from this effect. The strict L threshold is poorly compatible with the rigid regulation function $rf(N^k)$, $k \geqslant 2$ in models.

From the hypothesis of weakening competition at $N \approx L$, we propose to use the multiplier $\sqrt[k]{(N-L)}$ c $rf(N^\theta)$, $1 < \Theta < 2$, $k \in 2^i - 1$ in this modification:

$$\frac{dN}{dt} = rN(t)\left(1 - \frac{N(t)}{K}\right)^\Theta \times \sqrt[3]{(N(t) - L)}. \tag{15}$$

In our new model (15) (no lag option), the range of exposure to the negative effect of the aggregated group (strong Ollie effect) begins directly at the yL threshold.

4. A model of the transition of an invasive outbreak into depression

Let's justify the new model $\dot{N} = rf(N(t-\tau)) - F(N(t-\tau_1))$ for an important situation that is not related to the emergence of a stable oscillation mode. Imagine a scenario where, with a large value of r, the potential for increasing the number of the emerging invasive population $N(t) \to K$, but the activation of the biotic resistance adapting all this time t_τ occurs.

Let's include the delayed factor of external loss with a delay of $\delta N(t-\tau)$ and use the logarithmic function in the equation for self-regulation of population growth rates

$$\frac{d\,N}{d\,t} = N(t)r\ln\left(\frac{u}{N(t-\tau)}\right) - \delta N(t-\tau_1). \tag{16}$$

For $\dot{N} = rN\ln(K/N)$, the ordinate of the inflection point $N_p = K/e$ on the solution curve lies lower than $K/2$ for the solution of the Ferhulst –Pirla model, so this regulation is better used for aggressive species. The parameter of a bounded medium in this model is not identical to the role of stable equilibrium in (3). In this new modification, $\dot{N} = rf(N;\tau u) - F(N;\tau_1)$ we use u in notation, since reaching the level of $N(t) = u$ is possible, but for large $r\tau$ only for a short time. In the computational scenario with (16), the death of the aggressive invader population is observed after two maxima of oscillations[2], as it was in the experiments of Georg Gause with the introduction of a predator into the victim's colony [33]

The aim of Gause's work was to experimentally test with the use of infusoria the solutions obtained in population models "predator–prey". There were no long-term fluctuations in the series of his experiments. After two periods, the experiment ended with $N_1(t_1) = 0$, $N(t_2) = 0$, $t_2 > t_1$. If the activity of the predator universe is not restrained, then the trophic system of the two species is unstable in reality. In (16) we sacrificed the property $\forall t$, $N(0) \geqslant 0$, $N(t) \geqslant 0$, but this is eliminated by the stop predicates in the numerical algorithm settings. When the r parameter decreases, the trajectory (16) demonstrates the usual harmonic oscillations of $N_*(t;\tau r)$, as well as (2).

Thus, the reduction of excessive reproductive activity contributes to the effective development of a new range by the species.

5. Modeling a deep crisis scenario

For real processes, a more complex form of counteraction is needed than in (16). We will not be able to describe directly the multi-species regulation in the natural environment, since parasites have their own natural enemies and regulatory factors — in reality, dozens of species participate in the fight. A high level of biodiversity stabilizes ecosystems. As a result, it is difficult to achieve complete destruction of the population, as it turned out in the laboratory of y Gause, in real adaptive systems [35]. All modern biosystems are the result of a long evolution in a competitive environment. The inclusion of pressure nonlinearity in the form $F(N) = -\delta N^k(t-\tau_1), k > 1, \tau \geqslant \tau_1$ is justified by the fact that the current exposure of parasites will be determined by the previous generation of the host population. But the modern impact, in turn, is associated with the

[2]We use the well-known algorithm Owren–Zennaro [34], a modification of the Runge–Kutta 5 method for systems with a delay.

concentration of victims available to them for infection [36]. Generations of insects are replaced discretely with a fixed time step.

Many invader populations overcome resistance in a situation of rapid crisis [37]. Consider the situation of active counteraction, which is formed after a certain time against an aggressively breeding population. Let's describe the confrontation in the form of the equation $\dot{N} = rN(t)f(N(t-\tau)) - F(N^k(t-\tau_1); J)$ for the case of regulated reproduction of the invader, which is able to affect its environment, but cause a response with some own the delay is $\tau_1 \leqslant \tau$.

Let's imagine that the situation of a sudden escalation of competitive confrontation develops for a population already when approaching a certain threshold of the number of J. This threshold of tangible impact on the environment J is significantly less than the theoretically permissible limit level $\mathfrak{K}$. Let's reflect two phenomena in the new model: the threshold effect and the adaptability of countering the active growth of the population of the invader with a coefficient of δ in the equation with logarithmic self-regulation, where q is the parameter of abiotic loss (for example, due to anthropogenic impact):

$$\frac{d\,N}{d\,t} = rN(t)\ln\left(\frac{\mathfrak{u}}{N(t-\tau)}\right) - \delta\frac{N^m(t-\tau_1)}{(J-N(t))^2} - qN(t),\ \delta > q,\ m \geqslant 2,\ N(0) < J < \mathfrak{u}. \qquad (17)$$

When approaching the threshold, competition with external influence becomes more acute. However, the pressure level depends on the state of the population non-linearly. With the emergence of a deep crisis, the pressure of antagonists weakens, but does not decrease to zero. Thus, J in the (17) model characterizes the tolerance threshold of the biotic environment of an invasive species.

In the computational scenario for (17), at the first stage, there is a «logistical» increase in the number of a small group of $N(0) < J$. But the growth stops after $N(t) > N_p$. In $\ln_K$-regulation, the ordinate of the inflection point is lower than for the quadratic one. Instead of the usual stabilization after a brief excess of equilibrium, then the stage of a sharp decrease in numbers begins with an increase in $F(N^2; J^{-1})$ at $N \to J$. The crisis comes before the moment when the growth potential is exhausted by intraspecific $\ln_K$-regulation due to the exhaustion of environmental resources. The impact of specific biotic external, but population-dependent $N(t-\tau_1)$ factors creates a threshold for the onset of depression. When approaching the threshold level of the population of the invader, it goes into a demographic crisis. A variant of the development of the studied situation of a special form of confrontation is shown in the computational scenario in Fig. 2. The Rand Model Designer computing environment with a library of numerical algorithms was used.

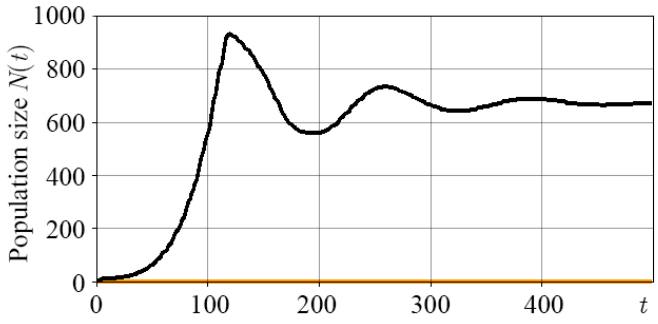

Fig. 2. Сценарий индуцированного средой краткого кризиса в пороговой модели (17) при $m = 2$, $r = 7.17 \cdot 10^{-3}$, $J = 10^3$, $\mathfrak{u} = 15 \cdot 10^3$, $\tau = \tau_1 = 48$, $\delta = 10$, $q = 4.2 \cdot 10^{-3}$, $N(0) = 10$

Fig. 2. Scenario of an induced brief crisis in the new model with the values of the parameters $m = 2$, $r = 7.17 \cdot 10^{-3}$, $J = 10^3$, $\mathfrak{u} = 15 \cdot 10^3$, $\tau = \tau_1 = 48$, $\delta = 10$, $q = 4.2 \cdot 10^{-3}$, $N(0) = 10$

The population goes through a stage of population depression, since the reaction of its opponents in a crisis is unstable and weakens at this time. As a result, the population crisis after transient fluctuations stabilizes at the level of $\lim_{t\to\infty} N(t) = P < J$ for small $q < \delta$. The parameter $\mathfrak{u}$ in (17) is the theoretical limit capacity of the depleted resources of the environment, which is initially not reached by a small local group. In the immunological interpretation, only a very high dose of infection $N(0) > J$ can become lethal. There is no equilibrium niche capacity for a pathogenic virus a priori, since the virus destroys the organism — its environment. The additional external impact of q in the (17) model is interpreted as the effect of therapy or artificial anthropogenic measures of influence.

The computational model (17) is ecologically applicable for the initially small group $N(0)<J/4$. At $N(0) = 2/3J$, $m > 2$, the development will show a sharp effect of a deep but surmountable crisis $N(t_m) \approx 0 + \varepsilon$, $\lim_{t\to\infty} N(t) = P$. If we reduce the environmental impact factor δ, on which the amplitude of the population reduction during the crisis depends, then the cyclical regime persists (around the level of P). The model has a variant of a cyclical solution without attenuation after the crisis, which in this case is not relevant for us. We consider scenarios without bifurcations and parametric changes. In biosystems, the parameters of species change slowly. With an increase in the parameters δ, τ in (17), we will observe a prolonged degradation — the effect of «bottleneck», a decrease in r then leads to death. The considered scenario differs from the situation when a newly formed population passes the stage of a long minimum with a stable small group of individuals with a small r. In our case, the reproductive potential is initially high $r > 1$. The long-term state of the minimal relic group is fundamentally different in evolutionary aspects from the transition to a sharp crisis with recovery. Increase in the number of $N(t) \to K$ in scenarios with a long minimum of $N(t) \approx L$ is associated with an increase in reproductive potential, where $r \neq \text{const}$. Recovery does not occur due to an increase in individual fertility, but due to an increase in survival in juvenile ontogenesis with the appearance of ways to avoid detection by enemies.

The proposed impact function $F(N^m(t-\nu); J)$ can be included in the model of sawtooth oscillations of pest outbreaks to describe their damping in the case of the existence of a limited forest resource and the counteraction of natural enemies-parasites:

$$\frac{dN}{dt} = rN(t)\left(\frac{K - N^2(t-\tau)}{K + cN^3(t-\tau_1)}\right) - \delta\frac{N^m(t-\nu)}{(J-N(t))^2} - qN(t), \quad \delta > q, \quad m \geqslant 2, \quad N(0) < J < K. \tag{18}$$

The equation (18) can be used as part of «Volterra» systems to describe trophic interaction with threshold effects. The (18) phenomenologically describes a complexly regulated reaction under the influence of the relative capacity of the medium.

The model with regulation $f(x) = rx^{-bx}$ is not suitable for our task:

$$\frac{dN}{dt} = rN(t-\tau)\exp(-bN(t-\tau)) - \delta F(N(t-\nu); J). \tag{19}$$

6. Biological justification for the obtained model scenario

The new model and computational scenario need to be justified in real examples. There are examples when biological invasions are created artificially and observations are made to account for the number of species. Most of the artificial invasions (introductions) were carried out in order to increase the commercial bio-productivity of ecosystems, as was the case in the Caspian Sea. There are more interesting examples for us when the introduction of a species into a competitive

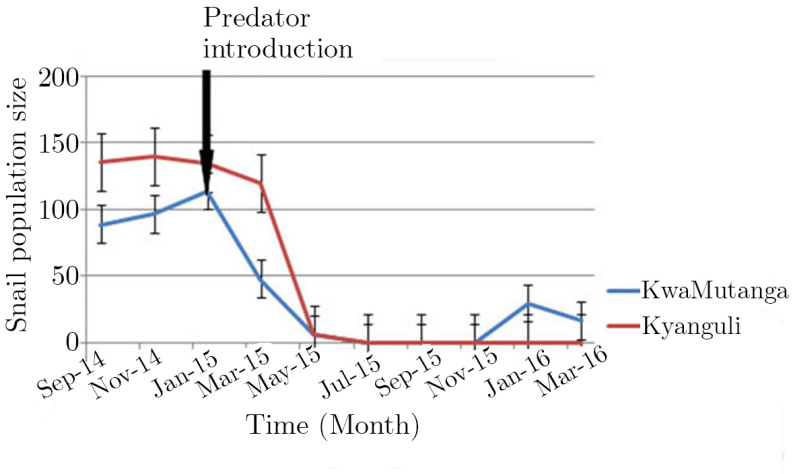

Fig. 3. Динамика популяции моллюсков рода Biomphalaria после выпуска эффективного хищника в двух реках Кении

Fig. 3. Dynamics of the population of mollusks of the genus Biomphalaria after the release of an effective predator in two rivers of Kenya

environment was carried out to create a biological struggle — targeted invasion against a specific harmful species.

6.1. Inducing species confrontation to combat local epidemics. Interesting anti-epidemic studies are being conducted in Africa. The introduction of the American cancer *Procambarus clarkia*, as a natural enemy of several species of mollusks of the genus Biomphalaria, carriers of parasitic worms of schistosomes, was carried out in two rivers of Kenya. In this way, experts tried to stop the spread of the dangerous parasitic disease schistosomiasis in Africa. After the introduction, the cancer suppressed the mollusks. But after a long depression, the populations of mollusks in one of the rivers recovered to a stable small state (Fig. 3), in another river some populations were completely destroyed [38].

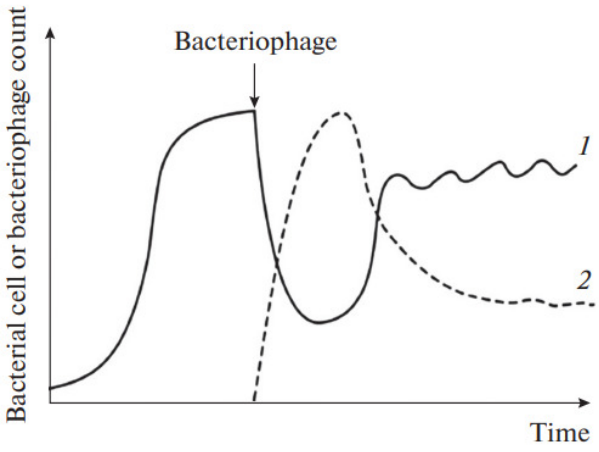

Fig. 4. Сценарий с коадаптацией: восстановление колонии бактерий после вселения бактериофага [39]: *1* — динамика бактерий; *2* — динамика вирионов

Fig. 4. Scenario with coadaptation: restoration of a bacterial colony after the invasion of bacteriophage [39]: *1* — dynamics of bacteria; *2* — dynamics of virions

6.2. Adaptive dynamics of species counteraction involving CRISPR – CAS9. It is known from many experiments since the 1930s that bacteriophage viruses cannot completely suppress a colony of bacteria, causing only a temporary crisis. In an experiment with the introduction of a bacteriophage into a colony of bacteria, the resulting depression effect was successfully overcome by bacteria when adapting their antiviral mechanism of endonuclease CRISPR – CAS9, dynamics The experiment is shown in Fig. 4. Now CRISPR – CAS9 is a promising method of genomic editing and a method for purposefully obtaining mutations, but initially it is a direct-acting adaptive immunity system in unicellular organisms. A special protein in the bacterial cell found and cut the DNA of the virus with molecular scissors, which it identified by a special short fragment. It takes time to isolate a suitable sample of foreign DNA. As a result, the methods of therapy of bacterial infections with bacteriophage viruses quickly lost their effectiveness and did not meet the expectations of [39], although a complete restoration of the bacterial colony was not observed. Now this adaptive defense mechanism is actively used by scientists for targeted genomic modification of organisms, including obtaining a mutation that ensures the immunity of cells to HIV infection.

There are several other examples in ecodynamics where there is no predator or parasite at all, but a crisis arises — a collision «type–environment» with a transition to a bottleneck state. The scenario obtained in (17) describes the dynamics of local deer populations introduced on islands in Arctic Canada [40]. The population multiplies in the absence of predators, but deer, with large crowding, destroy vegetation and destroy their environment. Nutrition becomes insufficient, epizootics occur and the mortality of young individuals increases. The population is entering a depression. Recovery after the crisis depends on the ability to regenerate their food resources, which happens with a delay. On Wrangel Island, the deer population died completely. Complete regeneration does not occur and so a threshold is created that is significantly less than the *initial* permissible capacity of the ecological niche. Two delays are present and competing in the system: the reproductive cycle of deer and the rate of restoration of the environment. This creates fluctuations with a decrease in the average value. The northern vegetation (a multi-species community) is recovering slowly. Interestingly, with artificial withdrawal, the deer population stabilizes, but fluctuations continue without withdrawal, which is confirmed by the model we have developed. Population structuring is another adaptation mechanism, which was shown in [41] on the example of a reproduction model of partially isolated sturgeon subpopulations of the Caspian Sea.

Practice shows that asymptotic oscillatory regimes are less relevant for active invasions or acute infections. There are alternative scenarios for the completion of the environment's struggle with the invader with threshold effects. For example, in HIV infection, the initial acute phase is suppressed by the immune response to the level of long-term balance equilibrium, as in the model scenario. As a result, with a decrease in the effectiveness of immunity, there is not a cyclic regime after bifurcation, but a rapid terminal phase of viral load growth.

There are interesting examples of crisis dynamics outside the field of population observations. So in oncology, it is known that the tumor cells remaining after immunotherapy suppression can suddenly switch back to rapid division [42], but these scenarios are the topic of a separate study.

Conclusion

Three models of specific population processes based on lag equations have been developed for situations of active resistance exerted by a biotic environment (possibly artificially induced) to an invasive species with a high reproductive potential. A specific (17) model for the scenario of

the crisis passing by an invasive population was developed on the basis of two phenomena of delay: in regulation due to the restoration of necessary resources and threshold delayed counteraction. The simulated crisis begins abruptly in the phase of rapid growth with active resistance of the biotic environment when approaching the threshold number. Increasing τ_1 will make the crisis more pronounced. The phenomena of a sharp change in rapid growth by deep depression were observed in the ecodynamics of different invader populations [43].

The considered (17) model can be further developed in the context of delayed immune response from CD8 T-lymphocytes to acute viral infection. The resulting scenario is consistent with the option of chronicling the focus of infection [44]. The mechanism of immune activation includes a group of multi-stage processes [45] and with the event component of the interaction of many cell types with the antigen [46]. In the primary immune response, there are three phases (afferent, central, effector), the change of which is difficult to consider in a completely continuous computational structure.

The (18) model, where three lag factors are included, is suitable for the situation of interaction of a mutating virus with the immunity of an organism reacting to already irrelevant antigens. In the case of a virus, the response of the immune system often depends on the initial dose of infection $Z(0)$ non-linearly. With a higher dose, the effector phase can begin faster. The models can be used to directly describe the counteraction in systems of equations, where in the function $F(N(t), Z(t-\xi))$ the number of the antagonist species $Z(t-\xi)$ is indicated directly. Equation $\dot{Z} = r_z\pi(Z(t-\gamma))$ should use a different functional regulation of reproduction with the aftereffect of ψ. A promising method for describing not completely predetermined situations when activating the immune response is a perturbation of the γ value of the delay $F(N(t-\gamma\tau_1))$ by a random variable.

In special cases (at the beginning of an epidemic), the spatial distribution of the initial group matters. In such situations, it is possible to use cellular automata [47] instead of equations, as for the epidemic dynamics model [49] A. V. Shabunin, or in the model of A. V. Nikitina [48], including with a delay in the algorithm for changing the state of cells [50].

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