KAPITEL 7 / *CHAPTER 7* [7]

MATHEMATICAL MODELING OF THE DYNAMICS OF BIOLOGICAL SYSTEM DEVELOPMENT

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Introduction

In the natural environment, in the absence of negative human influence, animal and plant species regulate their numbers according to the laws of competition, the amount of resources, the area of the territory, the presence of other species, etc. But there are few such territories left. In most habitats, populations experience a significant (often negative) impact of humans and the results of their activities. Under the conditions of such additional pressure, the number of populations can decrease to a dangerous number, when human intervention is already necessary for the purpose of their reproduction (positive influence). Such negative conditions also include natural disasters (earthquakes, floods, volcanic eruptions) and disasters caused by human activity (accidents with the release of large quantities of poisons or radioactive waste or military operations, as a result of which a large number of animals die and others migrate to other regions). . In such cases, after eliminating the consequences of a natural disaster or a disaster caused by man, it is necessary to reproduce the animal world that existed for a long time in this territory. And for this, first of all, it is necessary to model the dynamics of the development of the biocenosis, taking into account the connections between different groups of animals. This also applies to cases of establishment of animal and industrial production, nature reserves, forestry or fishing farms, hunting farms, etc., when it is necessary to start a system (biocenosis) that will further develop independently and be very stable.

As for Ukraine, both wild animals and farm animals are suffering and dying in it. Therefore, it will be necessary to reproduce both natural populations and entire biocenoses, as well as economic ones, which is why it is a problem of modeling the dynamics and relationships of populations, and the regulation of their number is

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considered extremely urgent. All these questions will become especially ripe after the end of hostilities in Ukraine and the cessation of shelling of the territories, which disturbed not only the social and public, but also the biological and industrial balance.

7.1. Modeling of the dynamics of biological system development

7.1.1. History of the question

For the first time, Thomas Robert Malthus used a mathematical apparatus for calculating the dynamics of population growth when he presented a simple one-species exponential model of the dependence of the number of the human population on time in the work “Experience of the Law of Population” in 1798 (the model of unlimited growth): $N(t) = N(0) \cdot e^{\mu t}$, where *t* – is the time, μ – is the value that is the difference bin a Mendelian single-locus diallel population for cases of stationary and fluctuating habitats [1]). In 1928 Vito Volterra published in the book “Mathematical Theory of the Struggle for Existence” equations that describe the interactions between a prey species with density and a predator that destroys it with density [2]. In the future, a significant contribution to the issue of modeling the calculation of the interaction of biocenoses was made by: Alexander Nicholson and Victor Albert Bailey (1930s, a discrete-time model for describing the population dynamics of the associated host-parasitoid system), Bill Ricker (1954, a deterministic model in fisheries economy), Michael Rosenzweig and Robert McArthur (1963, a simple graphic form of predator-prey interaction [3]), W. Anderson (1971), S. King, B. Clark, M. Balmer, L. Dimitrus, H. Barkai, P. Smoys, M. Stubbs, T. Nagilaki, R. Green, E. Frisman, E. Pianka (1978, models of interaction between different populations [4]), J. Murdie (models for three types of interactions [5]), O. Bazykin, M. Hassel, J. Varley [3], [6], Rogero Arditi and Lev Ginzburg (1989, [7], [8]). The following scientists calculated mathematical models of population development on a computer: J. Rygarden and B. Charlesworth (1971, a model of the dynamics of allele frequencies in a Mendelian single-locus diallel population for cases of stationary and fluctuating habitats [3]), S. Chernyshenko (1985, mathematical methods in the problems of optimal oppression of pest populations with pesticides [9]), R. MacArthur and E. Wilson (2001, the equilibrium model of island biogeography, that describes the number of species on an island as an equilibrium of immigration and extinction [10], O. Zhdanova (2014, models of natural selection in a structured population), E. Rasputina and G. Osypov (2017, mathematical models of population dynamics taking into account the saturation effect of their density on the basis of logistic functions and analysis of their stability parameters in the AnyLogic environment), A. Klymenko and A. Maltsev (2018, three-dimensional and four-dimensional modifications of the Lotka-Volterra equations in the Python programming language [11]), the authors of this article (2023, mathematical modulation of the relationships of biological systems [12]). The vast majority of researchers are busy developing models of population dynamics of specific species, which partially narrows the problem [13], [14], [15], [16].

7.1.2. Methods

Mathematical models used in mathematical ecology are usually divided into deterministic, stochastic, empirical-statistical and dynamic. Deterministic mathematical models are based on the internal description of the system itself and the relationships between the components of this system. Mathematical models that include random functions are usually referred to as stochastic. Empirical-statistical models use the described empirical information about the system to construct the necessary functional dependencies (regression models) between the input and output variables of the system. The methods of mathematical statistics and econometrics are used when constructing empirical-statistical models. Models that take into account changes in system parameters over time are called dynamic models. Models that describe the state of the system regardless of time are called stationary. There are also continuous and discrete mathematical models. Continuous models describe the change in system parameters at any random moment in time. Discrete models give the values of system variables at specific time intervals (hourly, monthly, annually, etc.).

According to the method of construction and types of solutions, models are divided into analytical and numerical. If the equations of the model can be solved analytically, that is, at the output we get certain explicit or implicit functions for the variables, then such models are called analytical. But usually, the circle of such models is quite limited, most real mathematical models often do not allow obtaining an analytical solution. In this case, finding the solution of the model is achieved by numerical methods, and the result is tabular functions that are specified in points.

Mathematical models are also divided into: 1) models based on differential equations; 2) difference models; 3) matrix models; 4) optimization models; 5) simulation models built on the edge of our knowledge about the object and implemented on a computer according to the block principle; 6) regression models (they provide functional relationships between input and output variables, based on the method of approximation of statistical data [17], [18]).

We will use continuous dynamic models and, in some cases, discrete and deterministic models.

7.1.3. Formulation of the problem

We denote by $y(t, \tau)$ the number of individuals of the population of age $\leq \tau$ at time t; $y(\tau, t)$ is the size of the entire population up to age τ at the time t, i.e., the capacity of the environment;

$S(\tau)$ – is the instantaneous mortality function of individuals aged ≤ τ;

$S_1(\tau)$ – is the mortality function of individuals of age τ (these functions can have the graphical form presented in Fig. 3);

T – is the maximum lifetime of an individual of this species;

A – birth rate of individuals (average) per unit of time;

$a_1(\tau)$ – is the birth rate for individuals of age τ (Fig. 1).

It is obvious that

$$S(\tau) = \frac{1}{\tau}\int_0^{\tau} S_1(t)dt; \quad a(\tau) = \frac{1}{\tau}\int_0^{\tau} a_1(t)dt; \quad A_{\max} = \frac{1}{T}\int_0^{T} a_1(\tau)d\tau .$$

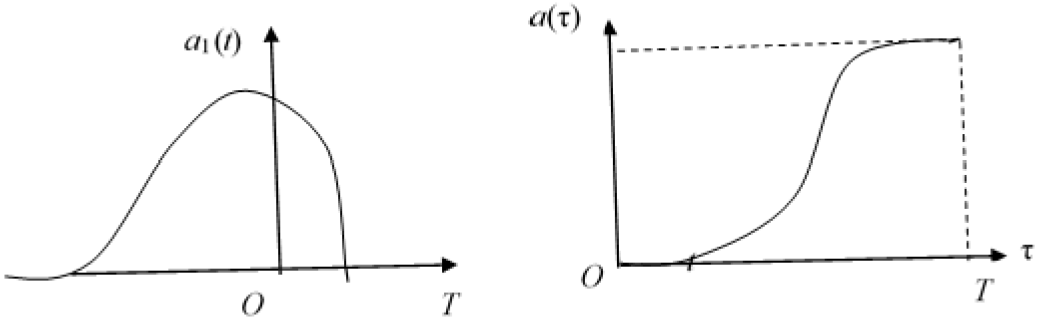

Fig. 1. Possible graphs of fertility functions

A source: author's development

We consider the birth rate $a(t)$ for the entire population to be constant, independent of the number of individuals of different ages (of course, in reality it can fluctuate depending on which age individuals predominate: the most fertile or already barren, that is, the number of species strongly depends on the initial age distribution. If old individuals predominate, then after n years $y_n = 0$, $i = 1, \dots T - 1$; if they are young, then after a year we will get a violent surge in the number of the species. However, the equation obtained taking this into account would be too difficult to solve and research). Similarly, let's set the mortality rate $S(\tau) = S$ for any τ. In other words, let's assume that it does not depend on age: old individuals die more often due to diseases and loss of running qualities, very young ones – because of their weakness and insecurity, and young ones – because of inexperience (Fig. 2). Survival is highest in middle-aged individuals, when they have gained a lot of experience and maximum running qualities, but it is partially reduced by seasonal mating battles for females and excessive risk-taking behavior caused by hormones. So it will not be an exaggeration to accept mortality as a constant value for all ages of both prey and predator.

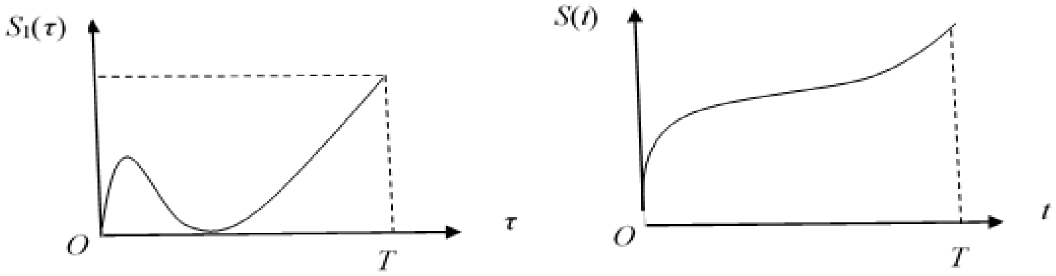

Fig. 2. Functions of mortality

A source: author's development

All these coefficients or functions (birth rates, mortality rates, eating victims) are determined for each species empirically, according to observational data, that is, by the tabular method. Similarly, we consider the functions $v(T)$ and $a(T)$ to be constant over time, that is, an increase in the number of individuals of a prey species invariably causes an increase in the number of predators that eat them. As $a(\tau)$ grows, $v(\tau)$ grows with some delay, and $S(\tau)$ grows without a delay, which reduces the value of $a(\tau)$, and equilibrium is restored.

Let's introduce a predator or competitor, or another positive or negative species (parasite) into the system.

$v(t, \tau)$ is a function of the instantaneous influence of another species on an individual of the first species of age τ in the form of an increase or decrease in its number at time t. That is, the number $l(\tau)$ of prey individuals of age $\leq \tau$, destroyed by a predator in a unit of time t, is included in the total number of prey individuals of age $\leq \tau$ (Fig. 3).

$$v(t,\tau) = \frac{l(\tau)}{y(t,\tau)}.$$

$v(t, \tau) > 0$, if the impact is negative (in the case of a predator or parasite);

$v(t, \tau) < 0$, if the impact is positive (in the case of symbiosis or the presence of the necessary resource for life);

$v_1(t, \tau)$ – is the function of the effect of one predator on the victim at age τ; at her birth and in old age, the influence of the predator is greatest. That is,

$$v(t,\tau) = \frac{1}{\tau}\int_0^{\tau} v_1(t,x)dx.$$

Therefore, we consider the functions $S(t, \tau)$, $v(t, \tau)$, $a(t, \tau)$ to be constant over time, since an increase in the number of individuals of a prey species invariably entails an increase in the number of predators that eat them, so that the percentage ratio in the function $v(t, \tau)$ will remain the same. As birth rate $a(t, \tau)$ increases, $S(t, \tau)$ increases and with some delay, the percentage of prey individuals eaten by the predator increases, which reduces the value of $a(t, \tau)$, and equilibrium is thus restored. It is assumed that there are enough resources and locations for all individuals of the prey and predator populations (that is, there is no self-limiting factor in the system).

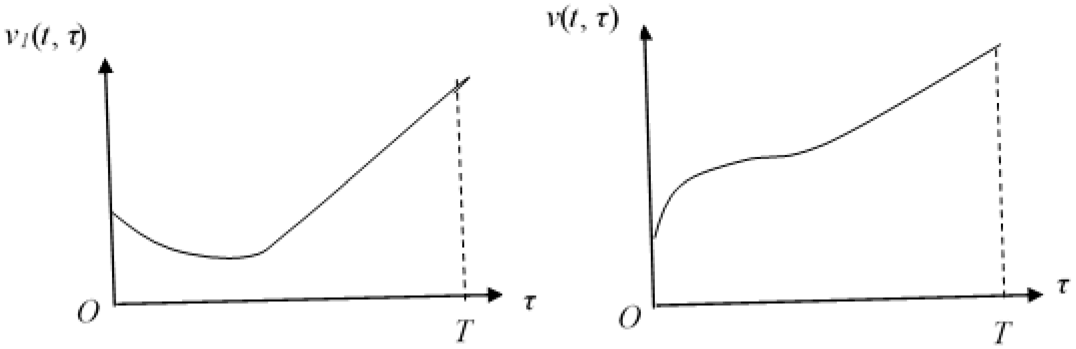

Fig. 3. The function of the effect of the predator on the victim

A source: author’s development

The number of individuals of a prey species of any age in any year can be calculated by knowing: the size of the entire population at the initial point in time, the birth rate relative to the entire population (the number of young born to each individual in the population), mortality of individuals from natural causes and predation their predators. In the case of competition, $y(t, \tau)$ is the number of individuals of age $\leq \tau$ of a given species that die at time t due to a lack of resources caused by the influence of a competing species, divided by the total number of individuals of a given species of age $\leq \tau$.

Our task is, based on the initial data (age structure, fertility functions, mortality from natural causes, death from predators, etc.):

- to build dynamic and discrete mathematical models of the interaction between prey and predator populations in single-species and two-species cases;
- check them for balance and stability;
- find solutions.

Note that a special case of the "victim-predator" model can be considered the “pollution-nature” situation, where nature plays the role of the victim, and pollution plays the role of the predator.

7.1.4. Solving the problem regarding the number of interconnected species

In ecosystems, late regulation is caused by one of three factors:

1) during development. If x is the number of adults, then the differential equation $\frac{dx}{dt} = f(x)$ describing the simplest population growth should be replaced by the equation $\frac{dx}{dt} = f(x_{x-T})$, where x_{x-T} is the number of sexually mature individuals at time $t–T$, T is the reaction time of the system to any change in the environment;

2) the discreteness of breeding seasons. Then the equation $x = f(x)$ should be replaced by $x_{n+1} = \alpha(x_n)$, where x_n is the population size in the nth year.

3) the delayed effect of factors limiting the number [12], [19].

Then, according to H. Hutchinson's equation, $x(t + 1) = x(t)\cdot a(t)\cdot(1 - b_{t-h})$, where h is the delay time, bt-h is the amount of division of the number of the species $x(t–h)$ on the capacity of the medium. As the density of a species increases, the resources available to it decrease. However, in a real ecosystem, resources are self-renewing, so the actual level of resources available over time will depend on the density of the regulated species at some time $t – T$ in the past, where T is the "lifetime" of the resource species. If $T \geq \frac{1}{a}$, then the Hutchinson equation (logistic with a delay) leads to divergent oscillations, although the equation with $T = 0$ always gives a stable equilibrium.

Let's find the size of the population at time $t + \Delta t$, age $\leq \tau$.

$$y(t + \Delta t, \tau) = y(t, \tau - \Delta t) + A\cdot y(t, T)\cdot\Delta t - S(\tau - \Delta t)\cdot\Delta t \cdot y(t, \tau - \Delta t).$$

Or

$$\frac{y(t+\Delta t,\tau) - y(t,\tau) + y(t,\tau) - y(t,\tau-\Delta t)}{\Delta t} = A\cdot y(t,T) - S(\tau-\Delta t)\cdot y(t,\tau-\Delta t).$$

At $\Delta t \to 0$ we get:

$$y'_t(t,\tau) + y'_\tau(t,\tau) = A\cdot y(t,T) - S(\tau)\cdot y(t,\tau). \qquad (1)$$

Boundary conditions: $y(0, \tau) = y_0(\tau)$; $y(t, 0) = 0$.

A more accurate equation describing the number of individuals at time t will look like this:

$$y'_t(t,\tau)+y'_\tau(t,\tau)=\frac{1}{T}\int_0^T a(t,\tau)\cdot y(t,\tau)d\tau-\frac{1}{T}\int_0^\tau S(t,x)\cdot y(t,x)dx \quad . \qquad (2)$$

If a predator is present in the system, terms will be added to equation (2):

$v(t,\tau-\Delta t)\cdot y(t,\tau-\Delta t)\cdot\Delta t$ – the number of individuals of age $\tau - \Delta t$ at time t, eaten by a predator during Δt in case $v(t, \tau) > 0$, or which increased their biomass in case $v(t,\tau) < 0$;

$\Delta t \cdot A \cdot y(t, T)$ – offspring during time Δt;

$v(t, \Delta t)\cdot \Delta t \cdot A \cdot y(t, T)$ – is the number of destroyed offspring of age $\leq \Delta t$.

The correction to the size of offspring due to the presence of a predator, instead of offspring under normal conditions $A\cdot\Delta t\cdot y(t, T)$ will be:

$$A\cdot\Delta t\cdot[y(t,T)-\int_{\tau-\Delta t}^{T} v(t,x)\cdot y(t,x)dx] \; .$$

This is the number of all destroyed individuals that could give offspring.

Taking into account all these corrections, we get the following equation, which determines the change in the number of the population during the time interval Δt:

$$y(t+\Delta t,\tau)=y(t,\tau-\Delta t)-S(\tau-\Delta t)\cdot\Delta t\cdot y(t,\tau-\Delta t)+A\cdot\Delta t\cdot\left[y(t,T)-\int_{\tau-\Delta t}^{T} v(t,x)\cdot y(t,x)dx\right]-$$
$$-v(t,\tau-\Delta t)\cdot y(t,\tau-\Delta t)\cdot\Delta t-v(t,\Delta t)\cdot A\cdot\Delta t\cdot[y(t,T)-v(t,T)\cdot y(t,T)].$$

Or, at $\Delta t \to 0$

$$y'_t(t,\tau)+y'_\tau(t,\tau)=A\cdot\left[y(t,T)-\int_{\tau}^{T} v(t,x)\cdot y(t,x)dx\right]-A\cdot v(t,0)\cdot[y(t,T)-v(t,T)\cdot y(t,T)]-$$
$$-v(t,\tau)\cdot y(t,\tau)-S(\tau)\cdot y(t,\tau).$$

Let's simplify the equation, taking into account that $v(t,0)=0$, and get the following partial differential equation:

$$y'_t(t,\tau)+y'_\tau(t,\tau)=A\cdot y(t,T)-A\cdot y(t,T)\cdot v(t,T)-y(t,\tau)\cdot(v(t,\tau)+s(\tau)) \; . \qquad (3)$$

Multiplier *A* does not make significant changes in the behaviour of the system, the nature of its stability and balance. Basically, the two equations with and without a predator differ by term $v(t,\tau)\cdot y(t,\tau).$ Now we will present more precisely the functions of intraspecific mortality *S*(*τ*) and interspecific influence *v*(*t, τ*).

$$
\begin{aligned}
y'_t(t,\tau)+y'_\tau(t,\tau)&=\int_0^T a(t,\,\tau)\cdot y(t,\tau)d\tau-\int_\tau^T a(t,\tau)\cdot v(t,\tau)\cdot y(t,\tau)d\tau-\\
&-\int_0^\tau v(t,\tau)\cdot y(t,\tau)d\tau-\int_0^\tau S(t,\tau)\cdot y(t,\tau)d\tau.
\end{aligned}
\tag{4}
$$

The integral equation (4) with partial derivatives was obtained.

Therefore, the influence of another species affects the characteristics of the regulated population:

1) it algebraically changes mortality within the population (according to *V*. Gompertz in the Gompertz-Meikham model of 1825, mortality increases exponentially with age;

2) affects fertility in a more complex way.

We differentiate both parts of equation (3) with respect to *t*:

$$
\begin{aligned}
&y''_{tt}(t,\tau)+y''_{\tau\tau}(t,\tau)=a(t,T)\cdot y(t,T)-a(t,0)\cdot y(t,0)-[a(t,T)\cdot v(t,T)\cdot y(t,T)-\\
&-a(t,\tau)\cdot v(t,\tau)\cdot y(t,\tau)]-y(t,\tau)\cdot v(t,\tau)+y(t,0)\cdot v(t,0)-S(t,\tau)\cdot y(t,\tau)+S(t,\,0)\cdot y(t,\,0).
\end{aligned}
\tag{5}
$$

Since $y(t,\,0)=0$, then

$$
\begin{aligned}
&y''_{tt}(t,\tau)+y''_{\tau\tau}(t,\tau)=a(t,T)\cdot y(t,T)-y(t,\tau)\cdot v(t,\tau)-y(t,\tau)\cdot S(t,\tau)]-\\
&-a(t,T)\cdot v(t,T)\cdot y(t,T)+a(t,\tau)\cdot v(t,\tau)\cdot y(t,\tau).
\end{aligned}
$$

We now differentiate both parts of the original equation (4) with respect to *τ* (the first term becomes zero):

$$
y''_{t\tau}(t,\tau)+y''_{\tau\tau}(t,\tau)=a(t,\tau)\cdot v(t,\tau)\cdot y(t,\tau)-y(t,\tau)\cdot v(t,\tau)-S(t,\tau)\cdot y(t,\tau)\,.
\tag{6}
$$

Subtract (5) from (6):

$$
\begin{aligned}
&y''_{\tau\tau}(t,\,\tau)-y''_{tt}(t,\,\tau)=a(t,\,\tau)\cdot v(t,\,\tau)\cdot y(t,\,\tau)-v(t,\,\tau)\cdot y(t,\,\tau)-S(t,\,\tau)\cdot y(t,\,\tau)-\\
&-a(t,\,T)\cdot y(t,\,T)\cdot v(t,\,T)+y(t,\,\tau)\cdot S(t,\,\tau)+a(t,\,T)\cdot y(t,\,T)\cdot v(t,\,T)-\\
&-a(t,\,\tau)\cdot v(t,\,\tau)\cdot y(t,\,\tau).
\end{aligned}
$$

After reducing similar terms of the equation, we get:

$$y''_{\tau\tau}(t,\tau) - y''_{tt}(t,\tau) = a(t,T)\cdot y(t,T)\cdot(v(t,T)-1) \tag{7}$$

or

$$y''_{\tau\tau}(t,\tau) - y''_{tt}(t,\tau) = \Psi(t,\tau)\,. \tag{8}$$

This is a differential equation with partial derivatives belonging to the hyperbolic type. Boundary conditions: $y(0,\tau) = y_0(\tau)$, $y(t,0) = 0$. (9)

Boundary conditions are set without taking into account the self-limitation of the number of victims. Equation (8) with boundary conditions (9) is solved by the finite-difference method (approximate). That is, according to equation (8), the difference between the acceleration of the change in the number of individuals by age at a fixed time moment and the acceleration of the change in the number of individuals of age $\leq \tau$ over time is obtained.

7.1.5. Perennial populations of a predator species

Suppose we know the number of predators up to τ years old in the $(i-1)$th interval of the year. And we want to know how many predators there will be in the i-th interval. We denote:

$v'(\tau, T_1)$ – is the number of all prey individuals eaten by a predator up to the age of τ during the year (this function characterizes the predator's hunting abilities);

$v''(T_2, \tau)$ – is the number of individuals of prey x age before τ, eaten by all predators during the year;

$f_2(T_2, \tau)$ – is the number of prey individuals under the age of τ that are eaten by all predators per unit of time or in 1 season;

$f_1(\tau, T_1)$ – is the number of all prey individuals eaten by predators under the age of τ per unit of time or in one season;

T_2 – the maximum lifetime of predators;

T_1 – maximum lifetime of victims;

$S_i(\tau)$ – is the mortality of predators of age $\leq \tau$ in the i-th interval of the year.

$$v'(\tau,T_1)=\sum_{i=1}^{\tau} f_1(i,T_1)\cdot\frac{1}{\tau},$$

$$v''(T_2,\tau)=\sum_{i=1}^{\tau} f_2(T_2,i)\cdot\frac{1}{\tau}.$$

Then

It is obvious that $v'(T_2, T_1) = v''(T_2, T_1)$, or $\frac{1}{T_2}\sum_{i=1}^{T_2} f_1(i,T_1)=\frac{1}{T_1}\sum_{i=1}^{T_1} f_2(T_2,i)$.

The number of individuals of the species in the following time period will be determined:

$$\begin{aligned} y_{n+1}(\tau) &= y_n(\tau-1)-S\cdot y_n(\tau-1)-v(\tau-1)\cdot y_n(\tau-1)+\\ &+a(T)\cdot\left[y_n(T-1)-S(T-1)\cdot y_n(T-1)-v(T-1)\cdot y_n(T-1)\right], \end{aligned}$$

where $y_n(\tau-1)-S\cdot y_n(\tau-1)-v(\tau-1)\cdot y_n(\tau-1)=\psi_n(\tau)-$ the number of individuals of age $\le \tau$ that survived to the next season,

$a(T)\cdot\psi_n(T)$ – is descendants born to all surviving individuals.

Let’s rewrite this equation in a more compact form.

$$y_{n+1}(\tau)=y_n(\tau-1)\cdot\left[1-S-v(\tau-1)\right]+a(T)\cdot y_n(T-1)\cdot\left[1-S(T-1)-v(T-1)\right]. \quad (10)$$

Boundary conditions: $y_n(0) = 0$; $S(\tau) < 1$; $v(\tau) < 1$.

It is obvious that $y_n(T + 1) = y_n(T)$ for any n, since the maximum lifetime of an individual does not exceed T years, after which it dies.

The offspring $y_{n+1}(T)$ in the next year will be

$$y_{n+1}(T)=a(T)\cdot y_n(T-1)\cdot\left[1-S(T-1)-v(T-1)\right]. \quad (11)$$

To make the population grow, it is necessary to $S(T-1)+v(T-1)<1$. This needs no further explanation. Otherwise, the population will die out.

Let’s write the expressions for $y_{n+1}(T + 1)$ according to the obtained formula (10).

$$y_{n+1}(T+1)=y_n(T)\cdot\left[1-S(T)-v(T)\right]+a(T)\cdot y_n(T-1)\cdot\left[1-S(T-1)-v(T-1)\right]. \quad (12)$$

Similarly

$$y_{n+1}(T)=y_n(T-1)\cdot\left[1-S(T-1)-v(T-1)\right]+a(T)\cdot y_n(T-1)\cdot\left[1-S(T-1)-v(T-1)\ \right].$$

After adding similar members, the expression takes the form:

$$y_{n+1}(T) = y_n(T-1)\cdot\left[1 - S(T-1) - v(T-1)\right]\cdot\left[1 + a(T)\right].$$

Where

$$y_n(T-1) = \frac{y_{n+1}(T)}{\left[1 - S(T-1) - v(T-1)\right]\cdot\left[1 + a(T)\right]}. \tag{13}$$

Substitute this expression into formula (12):

$$y_{n+1}(T) = y_n(T)\cdot\left[1 - S(T) - v(T)\right] + a(T)\cdot\frac{y_{n+1}(T)}{1 + a(T)}.$$

Or $$y_{n+1}(T) - y_n(T)\cdot\left[\frac{\left[1 - S(T) - v(T)\right]\cdot\left[1 + a(T)\right]}{1}\right] = 0.$$

So, we got equations in finite differences of the first order. Its solution will be:

$$y_n(T) = \left(-\frac{a}{b}\right)^n\cdot y_0(T);$$
$$y_n(T) = \left((1 + a(T))\cdot\left[1 - S(T) - v(T)\right]\right)^n\cdot y_0(T). \tag{14}$$

Here $b = 1$; $a = -\left[1 - S(T) - v(T)\right]\cdot\left[1 + a(T)\right]$.

$$\frac{y_{n+1}(T)}{y_n(T)} = \left[1 + a(T)\right]\cdot\left[1 - S(T) - v(T)\right].$$

Now let's make an equation relative to the number of individuals, divided by age

$$y_{n+1}(\tau) = y_n(\tau-1)\cdot\left[1 - S(\tau-1) - v(\tau-1)\right] + a(T)\cdot y_n(T-1)\cdot\left[1 - S(T-1) - v(T-1)\right].$$

Let's mark

$$1 - S(\tau-1) - v(\tau-1) = \varphi(\tau-1),$$
$$\psi_n(T) = a(T)\cdot y_n(T-1)\cdot\varphi(T-1). \tag{15}$$

Then we get a more compact equation:

$$y_{n+1}(\tau) = y_n(\tau-1)\cdot\varphi_n(\tau-1) + \psi_n(T).$$

For time $N \le T$

$$y_{n+1}(N) = y_{n-N}(1)\cdot\prod_{i=1}^{N-1}\varphi(i) + \psi_{n-N}(T)\cdot\prod_{i=2}^{N-1}\varphi(i) + \psi_{n-N+1}(T)\cdot\prod_{i=3}^{N-1}\varphi(i) + \ldots + \varphi(N)\cdot\psi_{n-1}(T) + \psi_n(T).$$

Or $$y_{n+1}(N) = y_{n-N}(1)\cdot\prod_{i=1}^{N}\varphi(i) + \sum_{j=2}^{N-1}\psi_{n-N+j}(T)\cdot\prod_{i=j}^{N-1}\varphi(i) + \psi_n(T). \tag{16}$$

N – is the age of the individuals we are interested in. Substituting expressions (11) and (14) into equation (16), we get:

$$y_{n+1}(N)=a(T)\cdot y_{n-N-2}(T-1)\cdot\varphi(T-1)\cdot\prod_{i=0}^{N-1}\varphi(i)+$$

$$+\sum_{j=1}^{N-1}a(T)\cdot y_{n-N+j}(T-1)\cdot\varphi(T-1)\cdot\prod_{i=1}^{N-1}\varphi(i)+a(T)\cdot y_{n}(T-1)\cdot\varphi(T-1).$$

$$y_{n+1}(N)=a(T)\cdot y_{n-N-2}(T-1)\cdot\varphi(T-1)\cdot\prod_{i=0}^{N-1}\varphi(i)+$$

$$a(T)\cdot\varphi(T-1)\cdot\left[\sum_{j=1}^{N-1}y_{n-N+j}(T-1)\cdot\prod_{i=j}^{N-1}\varphi(i)+y_{n}(T-1)\right]. \qquad (17)$$

According to the formula (13) $y_{n}(T-1)=\dfrac{y_{n+1}(T)}{\varphi(T-1)\cdot[1+a(T)]}$.

Then

$$y_{n+1}(N)=a(T)\cdot\frac{y_{n-N-1}(T)}{[1+a(T)]}\cdot\prod_{i=0}^{N-1}\varphi(i)+a(T)\cdot\frac{1}{1+a(T)}.\left[\sum_{j=1}^{N-1}y_{n-N+j+1}(T)\cdot\prod_{i=j}^{N-1}\varphi(i)+y_{n+1}(T)\right].$$

Applying formula (14), we finally get:

$$y_{n+1}(N)=a\cdot y_{0}(T)\cdot[1+a(T)]^{n-N-1}\cdot\varphi^{n-N-1}(T)\cdot$$

$$\left[\prod_{i=1}^{N-1}\varphi(i)+\sum_{j=1}^{N-1}\{[1+a(j)]\cdot\varphi(j)\}^{j+1}\cdot\prod_{i=j}^{N-1}\varphi(i)+\{[1+a(T)]\cdot\varphi(T)\}^{N+1}\right]. \qquad (18)$$

$y_{m+1}(1) = a\cdot(1 + a)^{n}\cdot(1 - S)^{n+1}\cdot y_{n}(T)$ at the condition that predators eat a constant percentage of individuals of the prey species – $v(T)$ – at any number; $S(T)$ and $a(T)$ do not depend on the size of the population (that is, there is a sufficient amount of resources and places to accommodate all individuals).

$$y_{n}(T)=y_{0}(T)\cdot\prod_{i=0}^{n-1}[1+a(y_{i}(T)]\cdot\prod_{i=0}^{n-1}[1-S(T,y_{i}(T)]. \qquad (19)$$

And now let's assume that the year is divided into w time intervals - the hunting period of predators. If during this interval the predator does not find a victim, then it dies; if he finds it, he lives until the next interval, when he will be forced to go hunting again. That is, the interval w is the time of eating, digesting and transforming the prey individual into the biomass of the predator. Generally speaking, the duration of the intervals w(τ) depends on the age differences of the predators. The number of predators under the age of τ in the (*i* – 1)th interval of the year is $y_{n+\frac{i-1}{w}}(\tau)$. If we denote by $x_n(T_1)$ the size of the population of the victim, at whose expense the predator lives, then in the *i*-th time interval the number of predators will be:

$$y_{n+\frac{i}{w}}(\tau)=\begin{cases} y_{n+\frac{i-1}{w}}(\tau-\frac{1}{w})-S_i(\tau)\cdot y_{n+\frac{i-1}{w}}(\tau-\frac{1}{w}), \text{ if } \dfrac{v'_i(\tau,T_1)\cdot x_n(T_1)}{y_{n+\frac{i-1}{w}}(\tau-\frac{1}{w})}>1 \\ v'_i(\tau,T_1)\cdot x_n(T_1)-S_i(\tau)\cdot y_{n+\frac{i-1}{w}}(\tau-\frac{1}{w}), \text{ otherwise.} \end{cases}$$

$\dfrac{v'_i(\tau,T_1)\cdot x_n(T_1)}{y_{n+\frac{i-1}{w}}(\tau-\frac{1}{w})}$ – the number of prey individuals eaten per predator.

In other words,

$$y_{n+\frac{i}{w}}(\tau)=\min\left\{y_{n+\frac{i-1}{w}}(\tau-\frac{1}{w}),v'_i\,\frac{\tau-1}{w},T_1)\cdot x_n(T_1)\right\}-S_i(\tau-1)\cdot y_{n+\frac{i-1}{w}}(\tau-\frac{1}{w}). \qquad (20)$$

With a sufficient number of victims, the maximum number of predators that will survive until the next season is determined by the formula:

$$z_{n+1}^{\max}(\tau)=y_n(\tau+1)\cdot\prod_{i=1}^{w}\left[1-S_i(\tau)\right]\cdot\frac{w-i}{w}. \qquad (21)$$

The minimum number of predators (with a constant lack of a resource, i.e. under the condition $\dfrac{v'_i(\tau,T_1)\cdot x_n(T_1)}{y_{n+\frac{i-1}{w}}(\tau-\frac{1}{w})}$ < 1 for any i) will be equal to:

$$z_{n+1}^{\min}(\tau)=x_n(T_1)\cdot\sum_{i=0}^{w-1}v'_{w-i}(\tau)\cdot(-1)^i\cdot\prod_{j=1}^{i}S_j(0-\frac{w-j}{w}-S_w(\tau)\cdot y_n\tau)\cdot$$

$$v'(\tau,T_1)=\frac{1}{w}\sum_{i=1}^{w}v'_i(\tau,T_1)<1 \quad \mathit{for}\ \forall i\ u\ \forall\tau. \qquad (22)$$

Let us determine the conditions for a sufficient number of victims (and the maximum number of predators) in the initial system.

$$\frac{v'_i(\tau,T_1)\cdot x_n(T_1)}{y_{n+\frac{i-1}{w}}(\tau-\frac{1}{w})}\geq 1 \quad \mathit{for}\ \forall i.$$

Then

$$\sum_{i=1}^{w} v'_i(\tau, T_1) \geq \frac{1}{x_n(T_1)} \cdot \sum_{i=0}^{w-1} y_{n+\frac{1}{w}}(\tau),$$

or

$$v'_i(\tau, T_1) \geq \frac{1}{x_n(T_1)} \cdot \frac{1}{w} \sum_{i=0}^{w-1} y_{n+\frac{1}{w}}(\tau)\,.$$

The larger the number of prey, the smaller percentage of its individuals can be eaten by predators for their survival, and vice versa.

Mortality $S(\tau)$ is a smoothed function; $S(T) \leq 1$.

$$S(\tau) = \sum_{i=1}^{\tau} S_1(i)\,.$$

Given this specification of the functions $a_i(T_2)$, $S_i(\tau)$ and $v'_i(\tau,\ T_1)$, which take seasonality into account, it is possible to move from the model (17) to (23). That is,

$$y(t+\Delta t, \tau) = \min\left\{ y(t, \tau - \Delta t) \cdot \int_t^{t+\Delta t} v'(\tau, t,\ T_1)dt \cdot x(t, T_1) \right\} - \frac{1}{\Delta t} \int_t^{t+\Delta t} S(t, \tau)dt \cdot y(t, \tau - \Delta t) +$$
$$\frac{1}{\Delta t} \int_t^{t+\Delta t} a(t, T_2)dt \cdot \left[\min\{ y(t, T_2 - \Delta t), v'(t, T_1) \} \cdot x_n(T_1) - S(t, T_2) \cdot y(t, T_2 - \Delta t) \right]. \tag{23}$$

So, we made two equations (prey and predator), based on which you can perform calculations and investigate the degree of mutual influence of species on each other depending on various conditions. Taking seasonality into account, the equation will take the form:

$$\begin{cases} x_{n+i}(\tau) = x_n(\tau-1) \cdot \left[1 - S(\tau-1) - v''(T_2, \tau-1)\right] + a(T_1) \cdot x_n(T_1 - 1) \cdot \left[1 - S(T_1-1) - v''(T_2, T_1-1)\right], \\ \qquad \partial e \quad a_i(T_2) = \begin{cases} 0, & i = 1,\ 2,\ 3, \ldots w-1 \\ a(T_2), & i = w \end{cases} \\ y_{n+\frac{i}{w}}(\tau) = \min\left\{ y_{n+\frac{i-1}{w}}(\tau - \frac{1}{w}), v'_i(\tau - 1, T_1) \right\} - S'_i(\tau) \cdot y_{n+\frac{i-1}{w}}(\tau - \frac{1}{w}) + \\ a_i(T_2) \cdot \left[\min\left\{ y_{n+\frac{i-1}{w}}(T_2 - 1), v'_i(T_2 - 1, T_1) \cdot x_n(T_1) \right\} - S'_i(T_2 - 1) \cdot y_{n+\frac{i-1}{w}}(T_2 - 1) \right], \end{cases}$$
$$v'_i(T_2, T_1) = v''_i(T_2, T_1). \tag{24}$$

Since all individuals of age τ next year will reach age τ + 1, then instead

$y_{n+\frac{i}{w}}(\tau-\frac{1}{w})$ it is logical to take at once $y_{n+\frac{i}{w}}(\tau-1)$.

In other words, we consider generations up to the (i – 1)th in the n-th year and trace their development up to the (n + 1)th year.

We believe (and it is logical to assume) that the hunting abilities of predators tend to be constant, that is, they are such that the predator finds the necessary number of victims even with a low population density of the prey species. Obviously, the evolution of species and natural selection lead to the fact that for prey and predator, the number of destroyed individuals tends to stabilize, which does not exceed the permissible value even at a low density of the prey population. That is, individuals of the victim, trying to survive, improve the parameters that save them from predators: they increase the territory of residence, the number of shelters, running qualities, and so on. And a predator at any minimum population density of its prey will always try, developing its hunting skills and increasing its search area, to find a constant number of victims necessary for its survival and reproduction. Over time, in a sustainable system, such numbers of prey and predator populations should be established, so that the number of eaten victims is such that they do not cause the extinction of one of the species. According to the parameter τ_1, the function $v(\tau_1,\tau_2)$ increases monotonically. According to τ_2, it has a reproductive-parabolic appearance since the hunting abilities of young individuals are still very small, then they begin to grow, reach a peak in adulthood, and in old predators, approaching the age of T_2, they fall sharply again. Then you can rewrite the system of equations in the following form:

$$\begin{cases} x_{n+i}(\tau)=x_n(\tau-1)\cdot\left[1-S(\tau-1)\right]\cdot v(\tau-1,T_2)\cdot y_n(T_2)+ \\ A\cdot\left[x_n(T_1-1)-S(T_1-1)\cdot x_n(T_1-1)-v(T_1-1,T_2)\cdot y_n(T_2)\right], \\ y_{n+\frac{i}{w}}(\tau)=\min\left\{y_{n+\frac{i-1}{w}}(\tau-1),\, v_i(\tau-1,T_1)\cdot x_n(T_1)\right\}-S'_i(\tau-1)\cdot y_{n+\frac{i-1}{w}}(\tau-1)+ \\ a_i(T_2)\cdot\left[\min\left\{y_{n+\frac{i-1}{w}}(T_2-1),\, v_i(T_2-1,T_1)\cdot x_n(T_1)\right\}-S_i(T_2-1)\cdot y_{n+\frac{i-1}{w}}(T_2-1)\right], \end{cases}$$
$$y_{n+1}(\tau)=\lim y_{n+\frac{i}{w}}(\tau)\quad npu\ i\to w. \qquad (25)$$

This model describes fluctuations in the number of species. By the way, the presence of shelters for the victim does not play the role of a stabilizing factor. So, let x_c is the number of victims avoiding the attack of predators in shelters during the winter. Then in the equations for (x_{t+1}, y_{t+1}) x_t will be replaced by the term ($x_t - x_c$). As simulation models show, the presence of refuges does not increase the probability of long-term coexistence of species, but, on the contrary, may even decrease it. As a result, an oscillating system that could remain stable for quite a long time turns into a system in which predators die out.

7.2. Equilibrium region

7.2.1. Equilibrium region for an annual species

We now study the system (population) in terms of equilibrium. First, let's take a species that is clearly independent of other species. Let the lifetime of individuals of the population $T = 1$ year. Leaving descendants, individuals die. The number of this species is expressed by the equation:

$$y_{n+1} = A\cdot(y_n - S_n\cdot y_n - v_n\cdot y_n),\ A = \text{const}.$$

Or $y_{n+1} = A\cdot y_n\cdot(1 - S_n - v_n)$.

These are the so-called non-overlapping generations. Then

$$\frac{y_{n+1}}{y_n} = A\cdot(1 - S_n - v_n)\ .$$

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Theorem. The equilibrium between species for the number y_n is stable (asymptotic), and deviations from it decay monotonically if

$$\frac{A'_y(y_n^*)}{A^2(y_n^*)} < S'_y(y_n^*) < \frac{A'_y(y_n^*)}{A^2(y_n^*)} + \frac{1}{A(y_n^*) \cdot y_n^*}.$$

Attenuating oscillations occur near y_n^*, if

$$\frac{A'_y(y_n^*)}{A^2(y_n^*)} + \frac{1}{A(y_n^*) \cdot y_n^*} < S'_y(y_n^*) < \frac{A'_y(y_n^*)}{A^2(y_n^*)} + \frac{2}{A(y_n^*) \cdot y_n^*}.$$

Deviation from equilibrium increases if

$$S'_y(y_n^*) < \frac{A'_y(y_n^*)}{A^2(y_n^*)}.$$

And the oscillations increase in amplitude, if

$$S'_y(y_n^*) > \frac{A'_y(y_n^*)}{A^2(y_n^*)} + \frac{2}{A(y_n^*) \cdot y_n^*}.$$

Proof

Taking into account the above iterative formula, we get $y_n = y_0 \cdot A^n \cdot (1 - S)^n$.

For the species to exist, it is necessary that $\frac{y_{n+1}}{y_n} \geq 1$. So, $S_n + v_n \leq 1 - \frac{1}{A}$.

Speed of reproduction $R = \frac{y_{n+1} - y_n}{y_n}$; $R = A \cdot (1 - S_n - v_n) - 1$.

At $S_n + v_n \leq 1 - \frac{1}{A}$ it is non-negative: $R \geq 0$.

The total function F of the negative impact on the species (S plus V) has the following graph (Fig. 4):

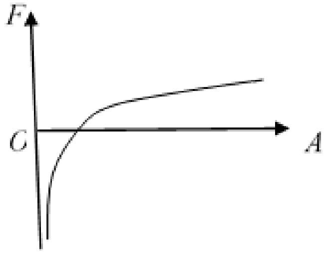

Fig. 4. Dependence of the birth rate on the total negative impact

A source: author's development

When $A < 1$, the species becomes extinct for any S_n, v_n. When $A = 1$, simple reproduction of the species occurs, when $A > 1$ – population growth.

Balance point:

1) $y_n = 0$ (unstable);

2) in the absence of predators ($v_n = 0$) $y_n = y_0$ (stand at which simple annual reproduction of the species occurs);

3) at $R = 0$, i.e. at $S_n + v_n = 1 - \frac{1}{A}$ simple annual reproduction of the species.

Let's plot the dependence of the reproduction rate R on the birth rate A, assuming that $1 - S_n - v_n = K$ is a constant. We get a directly proportional dependence.

$S_n - v_n < 1$. The larger $S_n + v_n$, the closer the graph of the function is to the abscissa axis (Fig. 5).

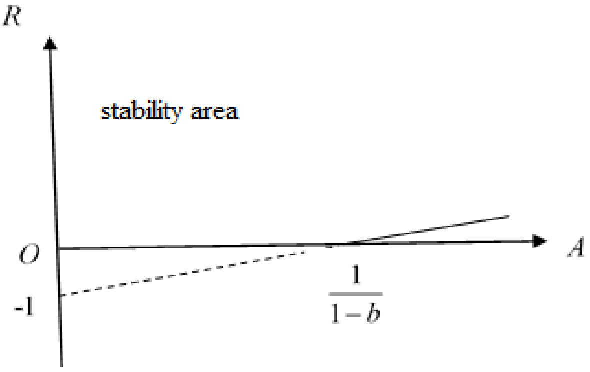

Fig. 5. Graph of the dependence of reproduction rate R on the birth rate of A

A source: author's development

The dependence of the reproduction rate R on the negative influence of $G_n = S_n + v_n$ has the following form (Fig. 6):

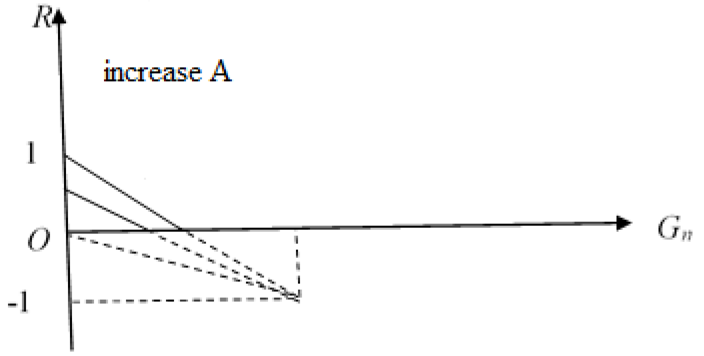

Fig. 6. Dependence of the reproduction rate R on negative influence

A source: author’s development

When the species is self-limiting and there are no predators ($v_n = 0$): $S_n = S(y_n)$, $A = A(y_n)$.

We receive: $\frac{y_{n+1}}{y_n} = A(y_n) \cdot [1 - S(y_n)]$.

In a separate case, $S_n(y_n) = S_n \cdot y_n$ (linear dependence).

Let's find the equilibrium point when $y_{n+1} = y_n$. It will be determined from the equation:

$$S(y_n^*) = [1 - \frac{1}{A(y_n^*)}],$$

Where $S(y_n)$ – is the probability of death of one individual given the number of y_n. It can be assumed that the indicators of a species do not change over time, but depend only on its number and environment (food, weather conditions).

The type of function $S(y_n)$ can be one of the following (Fig. 7):

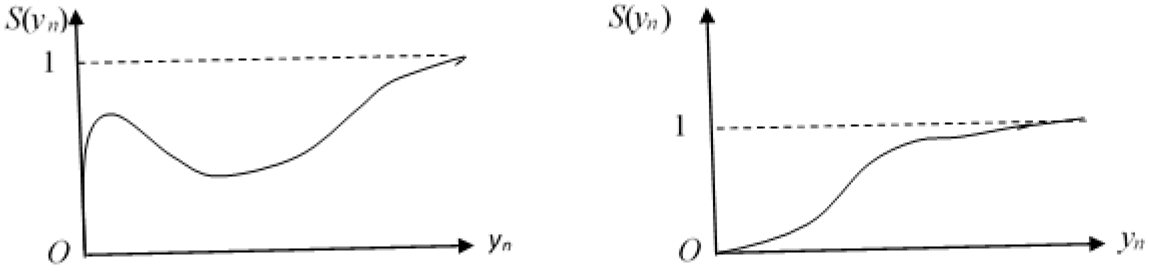

Fig. 7. Dependence of the function *S*(*y_n*) on the number of species *y_n*

A source: author’s development

For example, $S(y_n) = \frac{y_n}{1+y_n}$

$$S(y_n) \to 1 \quad at \quad y_n \to \infty;$$

$$A(y_n) \to 0 \quad at \quad y_n \to \infty.$$

The fertility function $A(y_n)$ can take one of the following forms (Fig. 8):

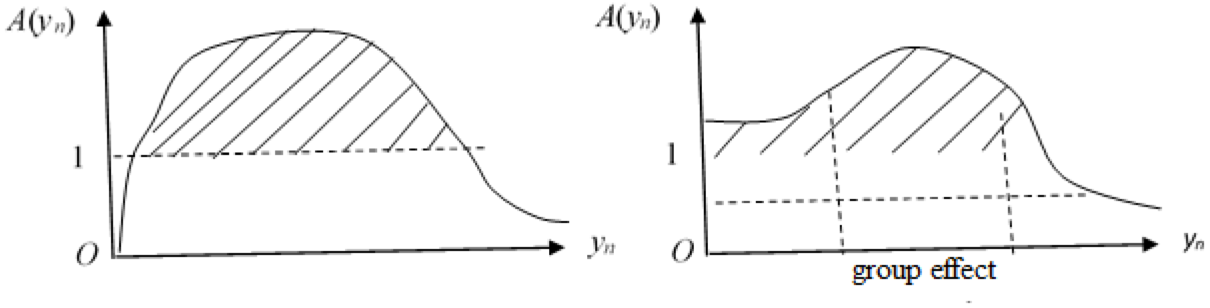

Fig. 8. Dependence of the function $A(y_n)$ on the number of species

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The shaded parts in the graphs show areas of stability.

The equilibrium equation can be solved by combining the graphs of the functions $S(y_n)$ and $G(y_n)$, or numerically, for example, by the iteration method [26]. Depending on these functions, there may be one equilibrium point or two. We are investigating this point y_n^* for stability. The equilibrium is stable (asymptotic) if $\left|\frac{dF}{dy}|_{y*}\right| < 1,$ where $y_{n+1} = F(y_n)$. In our case $F(y_n) = y_n \cdot (A(y_n) - A(y_n) \cdot S(y_n))$.

Because of $S(y_n^*) = 1 - \frac{1}{A(y_n^*)}$, then

$$\frac{dF}{dy} = A(y_n) - A(y_n)\cdot S(y_n) + y_n \cdot [A'_{y_n}(y_n) - A'_{y_n}(y_n)\cdot S(y_n) - A(y_n)\cdot S'_{y_n}(y_n)],$$

$$\frac{dF}{dy}|_{y*} = A(y_n^*)\cdot[1-(1-\frac{1}{A(y_n^*)})] + y_n^* \cdot [A'_{y_n}(y_n^*)\cdot[1-(1-\frac{1}{A(y_n^*)})] - A(y_n^*)\cdot S^*_{y_n}(y_n^*)],$$

$$\frac{dF}{dy}|_{y*} = 1 + y_n^* \cdot \left[\frac{A'_y(y_n^*)}{A(y_n^*)} - A(y_n^*)\cdot S'_y\,(y_n^*)\right].$$

At $0 \le \frac{dF}{dy}|_{y*} \le 1$ deviations from equilibrium disappear monotonically. These inequalities lead to the condition: $\frac{A'_y(y^*_n)}{A^2(y^*_n)} < S'_y(y^*_n) < \frac{A'_y(y^*_n)}{A^2(y^*_n)} + \frac{1}{A(y^*_n)\cdot y^*_n}$.

Because $A(y_n) \ge 1$ for any n, then $S(y_n) \ge 0$, $y_n \ge 0$.

At $-1 < \frac{dF}{dy}|_{y*} < 0$ damping oscillations occur near y^*_n, that is, these inequalities lead to the condition:

$$\frac{A'_y(y^*_n)}{A^2(y^*_n)} + \frac{1}{A(y^*_n)\cdot y^*_n} < S'_y(y^*_n) < \frac{A'_y(y^*_n)}{A^2(y^*_n)} + \frac{2}{A(y^*_n)\cdot y^*_n}.$$

At $\frac{dF}{dy}|_{y*} \ge 1$ or $S'_y(y^*_n) < \frac{A'_y(y^*_n)}{A^2(y^*_n)}$ the deviation from equilibrium increases, and at $\frac{dF}{dy}|_{y*} \le -1$ or $S'_y(y^*_n) > \frac{A'_y(y^*_n)}{A^2(y^*_n)} + \frac{2}{A(y^*_n)\cdot y^*_n}$ there are oscillations that increase in amplitude near y^*_n. The solution of the equation will be:

$$x_n = A^n \cdot x_0 \prod_{i=0}^{n-1}(1 - S(x_i)) . \qquad (26)$$

And now let's introduce a predator into the system. Let the number of victims eaten by all predators of age $\le \tau$, depending on the number of predators, as well as the number of victims, be expressed by the function $K(x_n, y_n)$. It is natural to assume that K depends linearly on y_n, i.e.

$$K(x_n, y_n) = \varphi(x_n)\cdot y_n .$$

Then the equation that determines the size of the predator population will take the form:

$$x_{n+1} = x_n \cdot A(x_n)\cdot[1 - S_n(x_n)] - \varphi(x_n)\cdot y_n .$$

Then the equation that determines the size of the predator population will take the form:

$$x_{n+1} = x_n \cdot A(x_n) \cdot \left[1 - S_n(x_n)\right] - \varphi(x_n) \cdot y_n .$$

Let f be the minimum number of victims needed by 1 predator per year to maintain its vital capabilities. If $\varphi(x_n) > f$, then all predators will have enough food. If $\varphi(x_n) < f$, then some of the predators will die of hunger, and only $\frac{\varphi(x_n) \cdot y_n}{f}$ predators will survive. Then the equations for prey and predator will look like this:

$$\begin{cases} y_{n+1} = A_2 \cdot \left[\min\left\{ y_n, \dfrac{\varphi(x_n)}{f} \cdot y_n \right\} - S_2(y_n) \cdot y_n \right] = A \cdot y_n \cdot \left[\min\left\{ 1, \dfrac{\varphi(x_n)}{f} \right\} - S_2(y_n) \right]; \\ x_{n+1} = A_1 \cdot x_n \cdot \left[1 - S_1(x_n)\right] - \varphi(x_n) \cdot y_n . \end{cases} \tag{27}$$

A_1 i A_2 – are birth functions for prey and predator, respectively. The equilibrium point at which $\frac{x_{n+1}}{x_n} = 1; \ \frac{y_{n+1}}{y_n} = 1$, is determined from the system of equations:

$$\begin{cases} y_n^* = \dfrac{1}{\varphi(x_n^*)} \cdot \left[A_1 \cdot x_n^* \cdot (1 - S(x_n^*)) - x_n^* \right]; \\ S(y_n^*) = \min\left\{ 1, \dfrac{\varphi(x_n^*)}{f} \right\} - \dfrac{1}{A_2}. \end{cases} \tag{28}$$

The appearance of the function $\varphi(x_n)$ can be: linear, as in the Volterra model; logarithmic; logarithmic with indentation (if the victim has storage) or exponential-logarithmic (for most vertebrates).

If a predator is independent of its prey and consumes it at a constant rate determined by its nutritional needs rather than the number of prey, then $\varphi(x_n) = C$ (straight line). (Fig. 9).

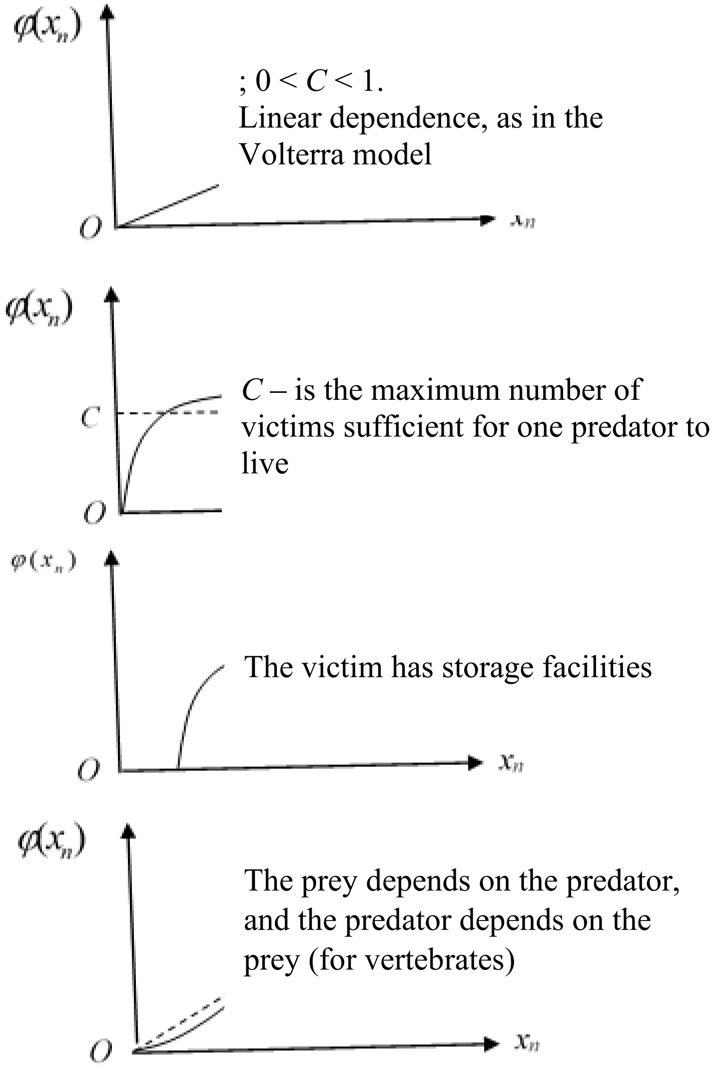

Fig. 9. Types of function $\varphi_{\min}(x_n)$, which determines the degree of prey eating by predators

A source: author's development

7.2.2. Equilibrium region for perennial species

The rate of reproduction of a species is expressed by the ratio:

$$R = \frac{y_{n+1}(T) - y_n(T)}{y_n(T)};$$
$$R = [1 + a(T)] \cdot [1 - S(T) - v(T)] - 1;$$
$$R = a(T) \cdot [1 - S(T) - v(T)] - [S(T) + v(T)].$$

Let's mark $b = S(T) + v(T)$. Тоді $R = a \cdot (1 - b) - b$.

It is obvious that when $a \ge \frac{b}{1-b}$ the population grows ($R \ge 0$).

When $R < 0$, the population, on the contrary, dies out (oscillations diverge). At the critical value $R = 0$, the size of the victim population does not change over time. It is clear that under any best conditions, $R < a$, $b < 1$.

Therefore, when $-1 < R < 0$, we get the region of instability, when $0 \leq R < a$ – the equilibrium coexistence of two species. In contrast to a species with a life time $T = 1$ year, a species with $T >> 1$ year does not die out even when $a(T) < 1$, if only $S(T) + V(T)$ meet the equilibrium conditions.

Obviously, for the existence of a prey species for a long time, it is necessary that $\frac{y_{n+1}(T)}{y_n(T)} \geq 1,$ from here

$$S(T) + v(T) \leq \frac{a(T)}{1 + a(T)},$$

$$a(T) \geq \frac{S(T) + v(T)}{1 - S(T) - v(T)}, \quad \text{or} \quad S(T) + v(T) \leq 1 - \frac{1}{1 + a(T)}.$$

This is a condition of equilibrium or a condition for the coexistence of two species: prey and predator.

The equilibrium condition of the entire population:

$$\frac{y_{n+1}(T)}{y_n(T)} = 1; \quad 1 = \left[1 + a(y_n(T)\right] \cdot \left[1 - S(T, y_n(T)\right].$$

And now we will get the equation for determining the equilibrium point $y_n^*(T)$.

$$S(T, y_n^*(T)) = 1 - \frac{1}{1 + a(y_n^*(T))}. \qquad (29)$$

We are investigating this point for stability.

Let’s mark $y_n(T) \cdot \left[1 + a(y_n(T)\right] \cdot \left[1 - S(T, y_n(T))\right] = F(y_n)$. Then

$$\frac{dF}{dy} = \left[1 + a(y_n)\right] \cdot \left[1 - S(T, y_n)\right] + y_n \cdot \left\{a'_{y_n}(y_n) \cdot \left[1 - S(t, y_n)\right] - \left[1 + a(y_n)\right] \cdot S'_n(T, y_n)\right\}$$

$$\left.\frac{dF}{dy}\right|_{y_n*} = 1 + y_n * \cdot \left[\frac{a'_{y_n}(y_n*)}{1 + a(y_n*)} - \left[1 + a(y_n*\right] \cdot S'_{y_n}(T, y_n*)\right] \qquad (30)$$

$0 < \left.\frac{dF}{dy}\right|_{y_n*} < 1,$ when

$$\frac{a'_y\,(y_n{*})}{\left[1+a(y_n{*})\right]^2} < S'_y\,(T, y_n{*}) < \frac{a'_y\,(y_n{*})}{\left[1+a(y_n{*})\right]^2} + \frac{1}{y_n{*}\cdot\left[1+a(y_n{*})\right]}. \tag{31}$$

Therefore, the equilibrium point $y_n{*}=Y$ is asymptotically stable, deviations from equilibrium disappear monotonically.

Summary and conclusions

We considered the predator-prey age system in the ecosystem with delayed regulation caused by: a) development time; b) the discreteness of breeding seasons; c) by the action of factors that limit the number. Usually, when modelling biological populations, the age of individuals is not taken into account, and the coefficients of birth, mortality, and the degree of predation by predators are considered constant, although they change depending on the age of the individual. We replaced the specified coefficients with functions that depend on the age of individuals. Using the method of continuous dynamic mathematical modelling, a system of differential equations with partial derivatives (for prey and predator) was built, which allows the calculation of the number of individuals of one or another species at any time moment. The resulting system is solved using the finite-difference method or the iterative method. We get the conclusion that the age distribution of the victim individuals after a number of years exceeding the maximum age of the individuals becomes independent of the initial age distribution, but depends only on the total number of the population (this is true for species that reproduce uniformly throughout their life - in mostly this applies to insects).

Despite expectations, in the obtained models, any shelters for the victim do not play the role of a stabilizing factor. Simulation models show that the presence of repositories does not increase the probability of long-term coexistence of species and may even decrease it. As a result, a system that, although it was fluctuating, but remained stable for a long time, turns into a system in which predators die out. Of course, in reality, the number of interacting species is much more than two: among them there may be parasites, competitors, predators of other populations, and people. However, as a rule, the influence of one or two predators on the prey species turns out to be decisive, and the rest of the interactions can be neglected. In the future, other influencing factors can be added, obtaining a more accurate system of equations. They can be used in hunting farms, industrial enterprises or when reproducing a chain of lost (dead or migrating) populations.