

Interaction of simulation and analytic methods in modelling of ecological and biological objects

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Abstract — A complex method of study is proposed, which includes a complete set of operations combining formal and informal methods, simulation and analytic approaches. This method has been used in construction and analysis of a set of models of tundra cenosis, i.e., ‘vegetation-lemmings-polar foxes’ (VLPF) model, an individual-oriented model (IOM) of a lemming population, and a simplified model in the form of a difference equation. Calculation formulas relating the parameters of the VLPF model and the difference equation are obtained, hypotheses concerning the principal mechanisms determining fluctuations in animal populations are formulated. Analysis of the properties of the difference equation and their manifestations in the VLPF and IOM models is performed.

1. Introduction

The foundations of quantitative ecology were laid in the pre-computer (analytic) period [2, 6–8, 13, 18]. However, the restricted capability of analytic methods could not satisfy the needs of ecologists. The development of ‘system dynamics’ by Forrester [4] consisting in creation of simulation models in a dialogue with experts, which removed the restrictions on the model type, increased essentially the potential of interdisciplinary interactions. Such approach allows one to use expert estimates and change them in the course of modelling. Therefore, a kind of an ‘ecological design (ED) game is implemented. The relative simplicity of modifying such models gives us the ability to perform comparative analysis of various sets of initial assumptions, data, or hypotheses. The algorithmic structure lying at the base of ED has the form

$$\frac{dF_x}{dt} = R_x - D_x - M_x \quad (1.1)$$

where R_x is the increase, M_x is the natural mortality, D_x is the disposition. The dynamics of the biomass of each trophic level is determined by the following three additive components: the rates of reproduction, disposition, and natural mortality;

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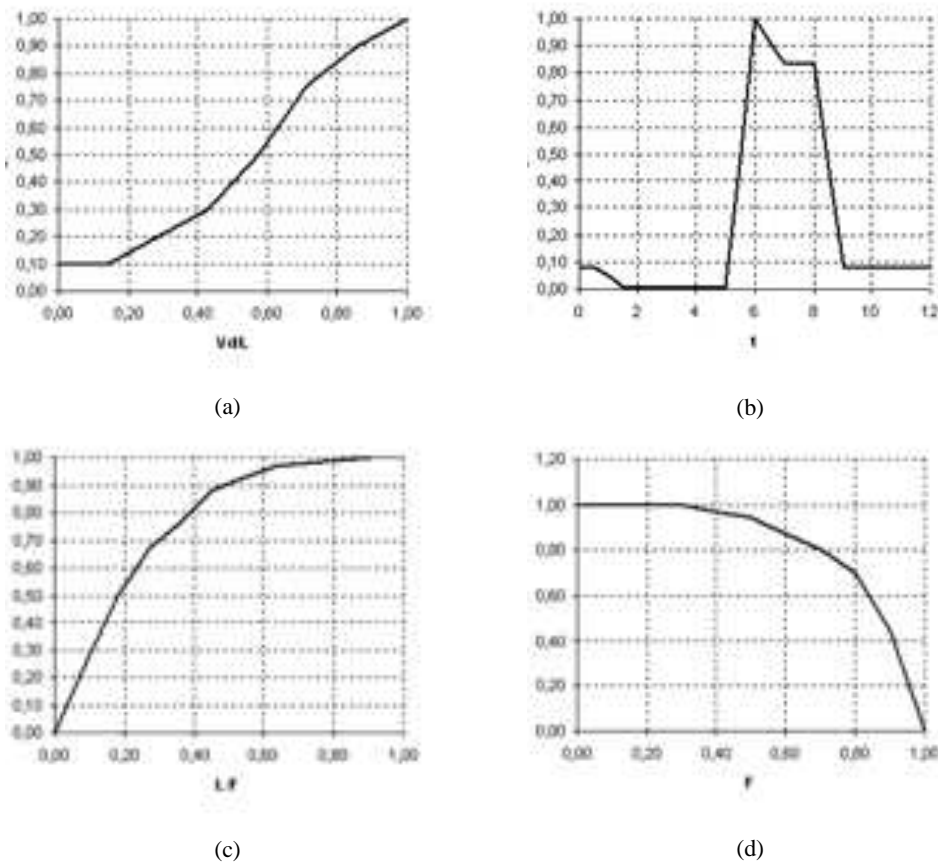


Figure 1. Expert-evaluated functions: (a) the function formalizing the decrease in the food value under its deficiency (g_2), (b) the function formalizing the mortality of lemmings during a year (g_3), (c) the function of eating saturation of lemming by polar foxes (g_4), (d) the self-limitation function of polar foxes (g_5).

each component, in its turn, is formed as a product of a constant and the corresponding function (including those of expert estimates). An example of functions with expert estimates in one of the latest versions of the model is presented in Fig. 1, the values of the constants are given below.

However, it is difficult to obtain a satisfactory description of the mechanisms of this phenomenon and to determine its principal mechanisms just by simulation tools, even under ideal conditions for interdisciplinary cooperation. A combination of the simulation and analytic approaches seems rather attractive. The search for implementation of such combinations has led to formation of complex studies (CS), including a complete set of operations, from sampling biological data to construction of interrelated models, including simplified ones admitting analytic (parametric) studies, which allows one to overcome the deficiency of purely simulation approaches (limitation by numerical calculations, ‘immensity of models’, etc.). An

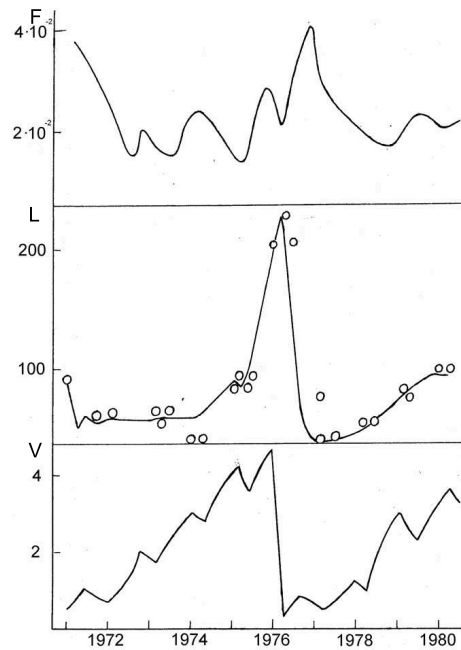


Figure 2. Results of a simulation experiment with the VLPF model [13] and the size variation dynamics of the ungulate lemming population registered on the Wrangel island [3] (marked by circles). Here V is the vegetation biomass, L is the mass of lemmings, F is the mass of polar foxes.

original detailed simulation model is used in justification of simplified models. The original model serves as a kind of a filter filtering the total spectrum of available biological information. The iterative modification process of the model leads to examination of possible variants. The modification and justification of simplified models proceeds under an expert control over utilized assumptions. Thus, possible doubts in justification of analytical models are replaced by the issues of confidence in the experts and initial biological data, and the ability of mathematical tools to represent the data, which has been significantly expanded with the use of computer technologies.

Based on expert-evaluated dependences, the 'vegetation-lemmings-polar foxes' (VLPF) simulation model was created taking into account seasonal variations of parameters. Interdisciplinary abilities of computer technologies and also the idea of ED were used in the initial formation of the model and its further modifications.

Figure 1 presents the expert estimates for the functions of a later version of the model. Various dynamic regimes and fluctuations in lemming and polar fox populations typical for the tundra were obtained as the result of numerical experiments [1, 5, 13]. The results of a particular experiment are presented in Fig. 2.

The dissatisfaction with the traditional result of simulation modelling consisting in a forecast of dynamic characteristics of the model under different scenarios of

external impacts [5, 13] and the desire to improve the understanding of the mechanisms forming the population dynamics of tundra animals resulted in the creation of the lemming population model [10] determining fluctuations in animal populations of the tundra community. This has given us the ability to justify a one-dimensional difference equation relating the size of the lemming population (the principal block in the VLPF model) for two adjacent years as a simplified model [5, 9, 13].

This difference equation allows us to determine the domains of the parameters in the original simulation problem, so that dynamic regimes of population variations are close to those observed in the nature, and to formulate hypotheses for principal mechanisms determining variations in the sizes of tundra animal populations. A special role of the simplified model in the study of tundra animal population variations has motivated a search for a closer relation between the difference equation and the original (simulation) VLPF model. Based on the joint analysis of ecological and biological information and the results of numerical experiments, we succeeded in the formulation and solution of the ‘inverse simulation problem’. It consists in the introduction of additional assumptions allowing us to obtain formulas relating the parameters of the original model of the community to the parameters of the difference equation.

The previous simulation experience has enabled us to reach another description level, i.e., the use of individual-oriented models [5, 11, 14].

2. ‘Vegetation-lemmings-polar foxes’ simulation model

Analysis of the structure of the pasture (surface) part of tundra biocenosis has shown the possibility of autonomous consideration of the VLPF community [13]. The model describes the population size dynamics of polar foxes F , lemmings L , and vegetation V :

$$\begin{cases} \frac{dV}{dt} = R_V - D_V - M_V \\ \frac{dL}{dt} = R_L - D_L - M_L \\ \frac{dF}{dt} = R_F - D_F - M_F \end{cases} \quad (2.1)$$

where R is the growth, M is the natural mortality, D is the disposition of biomass.

The effect of the time of year on the dynamics is described by the following variables: $S_1 = S_2 = 0$ in winter, $S_1 = 1, S_2 = 0$ in spring, $S_1 = S_2 = 1$ in summer. The winter lasts from September to January, the spring lasts from February to May, the summer lasts from June to August.

The dynamics of vegetation V is determined in summer by Verhulst’s formula, exponential mortality appears in winter, the growth and mortality are compensated in spring. Lemmings seize the vegetation if its available amount V_d forms the part \tilde{d} of its total biomass:

$$V_d = \begin{cases} \tilde{d} \cdot V, & \alpha > 0 \\ 0, & \alpha \leq 0 \end{cases} \quad (2.2)$$

$$R_V = a_4 \left(1 - \frac{V_1}{V_{\max}} \right) s_1 V_1 \quad (2.3)$$

$$M_V = a_3 (V_1 + V_2) (1 - s_2) \quad (2.4)$$

$$D_V = \begin{cases} L(a_1(1 - s_1) + a_2 s_1), & V_d > 0 \\ 0, & V_d = 0. \end{cases} \quad (2.5)$$

Here a_1 and a_2 are the vegetation seize coefficients: the first one is for winter and spring, the second one is for summer; a_3 and a_4 are the coefficients of growth and mortality of vegetation biomass, respectively, V_{\max} is the capacity of the econiche.

The change of the lemming biomass is calculated according to the formula

$$R_L = D_V g_2 \left(\frac{V_d}{L} \right) (b_9 s_2 + b_{10} s_1) \quad (2.6)$$

$$M_L = \begin{cases} 0, & L \leq \beta \\ b_5 g_3(t)L, & \frac{V_d}{L} \geq q \\ b_4 \left(1 - \frac{V_d}{L * q} \right) g_3(t)L, & \frac{V_d}{L} < q \\ b_2 g_3(t)L, & V_d = 0, s_2 = 0 \\ b_2 L, & V_d = 0, s_2 = 1 \end{cases} \quad (2.7)$$

$$D_L = \begin{cases} F g_4 \left(\frac{L}{F} \right) (b_6 + b_7 s_1), & L > \beta \\ 0, & L < \beta \end{cases} \quad (2.8)$$

where $g_2(V_d/L)$ is the trophic function (see Fig. 1a). The coefficients b_6, b_7, b_9, b_{10} characterize the seasonal changes. The function $g_3(t)$ describes the changes of mortality depending on the time of the year (see Fig. 1b); the function $g_4(L/F)$ describes the trophic function of polar foxes (see Fig. 1c), q is the critical specific weight of the vegetation below which there is a food deficiency; the mortality coefficients are the following: b_5 for sufficient food, b_4 for insufficient food, b_2 for absence of food in spring, b_β for absence of food in summer; β is the optimal biotope level of lemmings when lemmings always persist. The increase in the biomass of the polar foxes is generally provided by lemmings, however, in addition, other nonspecific kinds of food are present in the ration of polar foxes. The natural mortality, the loss due to hunting, and the increase of the biomass due to nonspecific kinds of food are taken proportional to the biomass of the polar foxes (with the coefficients c_4, c_5, c_2, c_3).

The change in the biomass of polar foxes is calculated by the formulas

$$R_F = c_1 g_5(F) D_L + (c_2 + c_3 s_1) F \quad (2.9)$$

$$M_F = c_4 F \quad (2.10)$$

$$D_F = c_5 F. \quad (2.11)$$

The function $g_5(F)$ reflects the limiting effect of high density (see Fig. 1 d).

The numerical study was performed with the following values of the coefficients:

$$a = (0.05; 0.16; 0.05; 1.2)$$

$$b = (500; 0.57; 0; 0.37; 0.05; 0.05; 0.1; 0.1; 5.6; 1.5)$$

$$c = (1; 0.025; 0.06; 0.055; 0.005)$$

$$\omega = 0.15, d = 0.6, \alpha = 2, V_{\max} = 30, q = 0.2, \beta = 2.5.$$

The initial conditions in numerical experiments were $V_0 = 10, L_0 = \beta, F_0 = 1$.

3. Inverse simulation problem (construction of simplified model)

In the process of solving the inverse simulation problem we managed to obtain formulas correlating the original VLPF simulation model and the difference equation on the base of the results of numerical experiments (and according to ecological and biological data).

In order to solve the inverse simulation problem, we accept the following simplifications:

1. the subsystem of polar foxes is removed from consideration, because their influence on the dynamics of lemmings is small;
2. we assume that in all periods except for winter and spring after the peak of the population size the food base (vegetation) does not restrict the dynamics of the lemming population;
3. we use the following assumption: at the end of the summer period the biomass of vegetation reaches its maximal value $V = V_{\max}$;
4. the trophic function $g_2(V_d/L)$ is equal to the constant \hat{g}_2^1 for insufficient food and to \hat{g}_2^2 for sufficient food; the dependence of mortality of lemmings on the food supply was described in two ways: either we have sufficient food (minimal mortality), or food is not available at all (maximal mortality). The function $g_3(t)$ representing the dependence of mortality of lemmings on the season was taken constant and equal to \hat{g}_3^1 in winter, \hat{g}_3^2 in spring, and \hat{g}_3^3 in summer.

The simplifying assumptions presented above have allowed us to obtain the required difference equation. It consists of three parts. The first part corresponds to the case when there is sufficient food all the year, the biomass (population size) of lemmings grows linearly; the third part is for the case when the food is insufficient even in winter, and then only the individuals from the optimal biotope survive, the biomass (population size) is constant within this range (a horizontal zone, a 'step'); and the second part is in between, this is the transition zone when the food is insufficient in spring.

Let us describe the first part. In accordance with the assumptions presented above, the change of the lemming population biomass in a ‘favorable year’ (the food is sufficient throughout the year) is described in each season by an autonomous first-order differential equation. As the result, we get the following difference equation connecting the lemming population sizes in two consecutive years:

$$\tilde{L}_{n+1} = P\tilde{L}_n.$$

Here $\tilde{L} = L/L_{\max}$, $P = \eta v \mu_1$ is the biomass increment in a favorable year; $\eta = \exp(p_s t_s)$ is the change in the biomass of lemmings during summer, $\mu_1 = \exp(p_p t_p)$ is the same change during spring, $v = \exp(p_w t_w)$ is for winter under the existence of food for the whole season; t_s , t_w , and t_p are the durations of summer, winter, and spring, respectively;

$$p_s = a_2(b_9 + b_{10})\hat{g}_2^2 - b_5\hat{g}_3^3, \quad p_{p1} = a_2b_{10}\hat{g}_2^2 - b_5\hat{g}_3^3, \quad p_w = -b_5\hat{g}_3^3$$

the parameters a_i and b_i are defined above.

Another portion of the difference equation describes the case when the food is insufficient even in the winter period. In this case only the individuals from the optimal biotope survive, the biomass (population size) is constant within this range (the horizontal part known as a ‘step’). The conditions of food shortage at the end of winter are determined by the parameter

$$B = \frac{V_{\max}z - \alpha}{a_1 t_w (1 + v)/2}.$$

Here $z = \exp(-a_3 t_w)$ is the ratio of the vegetation biomass at the end and at the beginning of the winter without the influence of lemmings, $B(1 - v)/2$ is the mean biomass of lemmings in the winter period.

A transition zone lies between the cases of excessive food and its shortage in the winter period, namely the case where there is no sufficient food in spring. Numerical experiments show that this zone is rather narrow. We describe it by a line segment joining the fragments of the difference equation indicated above.

Based on the difference equation presented above, which relates the sizes of the lemming population in two consecutive years, for the normalized variable $\tilde{L} = L/L_{\max}$ we have the form

$$\tilde{L}_{n+1} = \begin{cases} P\tilde{L}_n, & \tilde{L}_n \leq 1/P \\ 1 - r(\tilde{L}_n - 1/P), & 1/P \leq \tilde{L}_n \leq \tilde{B} \\ d, & \tilde{L}_n > \tilde{B}. \end{cases}$$

Here $\tilde{B} = B/L_{\max}$, $d = \beta \mu_2 / P$ is the portion of lemmings with guaranteed survival, $r = P(1 - d)/(BP - 1)$, $\mu_2 = \exp(p_p t_p)$ is the change in the biomass of lemmings in spring in the absence of food; β is the biomass of lemmings by the end of the winter provided the food shortage occurs in winter (the capacity of the optimal biotope).

The value L_{\max} is determined from the condition that the available food had been eaten by the end of spring:

$$L_{\max} = \left(\frac{V_{\max}z - \alpha}{a_1(t_w(1 + \nu) + t_p\nu(1 + \mu_1))/2} \right) \eta.$$

For comparison, Figure 3 presents the graph of the difference equation obtained as the result of numerical experiments with the original VLPF model.

Within the framework of integrated studies, we have succeeded in combining models of different classes. The simplification is not precise, because we applied a linearization of the original expert functions, however, it allows us to perform joint analysis of the models.

4. Use of difference equations

The analysis of the obtained difference equation has shown that there exist two principal (dimensionless) parameters forming the dynamic regimes of lemming population fluctuations, i.e., the rate of biomass increment P in favorable years and the survival rate in the most unfavorable conditions d . Whereas the estimation of the first parameter is comparatively reliable, the second one can be estimated from indirect data only. In order to reveal its impact, the corresponding numerical experiments were undertaken in [9] with a scenario where the parameter d varies from 1 to 0. It was found that stability zones with stable cycles successively appear in this case. The period of the cycles is constant inside a stability zone and changes as the natural series 1, 2, 3, 4 when passing from one zone to another. Stability zones are separated from each other by transition zones with more complicated regimes.

This result, i.e., the ‘order of the natural series’ with alternation of stability and transition zones where dynamic regimes change in finite times under small changes of the parameters, differs from the commonly accepted ‘doubling cascade’ with subsequent transition to ‘chaotic’ regimes [15, 16]. The presence of transition zones is in certain correspondence with the registered dynamics of actual populations. In the absence of a clear three-year cycle (in regions that are warmer than Taimyr) there are two- and five-year intervals between the population size peaks [3, 10, 12, 13].

5. Individual-oriented model

The studies of ‘vegetation-lemmings-polar foxes’ tundra community models performed previously, allowed us to apply a new description level, which is the method of individual-oriented modelling (IOM). The object of IOM application was the population of ungulate lemmings (*Dicrostonyx torquatus chionopyes*) in the West Taimyr. In this model a year is divided into two periods: the period of reproduction (from February 1 to August 31) and the winter period; lemmings are described by their age, sex, stage of sexual development, and vital capacity (VC). Population changes are related to migration.

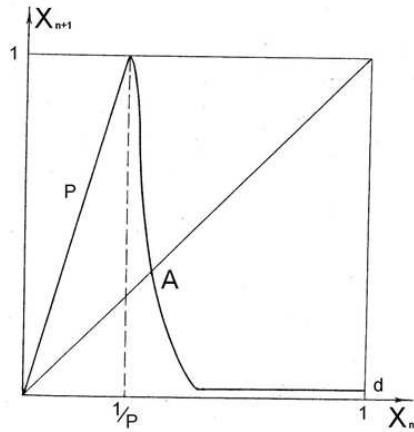


Figure 3. Graphic representation of the difference equation obtained as the result of numerical experiments with the VLPF model.

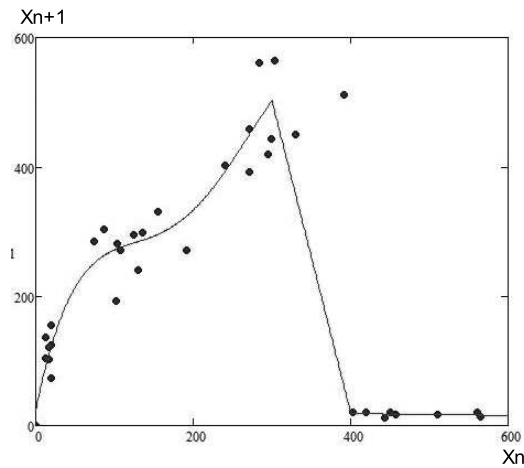


Figure 4. The form of difference equation obtained as the result of numerical experiments with the IO model.

A zooid goes out of the burrow and moves in an arbitrary direction. If a contact with other individuals occurs, a fight may happen, which decreases the VC. If the VC decreases to zero, the individual dies (this also occurs when the individual reaches the limit age). If individuals of different sexes meet in the reproduction period, the female capable of reproduction becomes pregnant with some probability.

The young are brought forth in a certain period of time and remain in the maternal hole for about two weeks. The stage of sexual maturity is achieved if the individual reaches a particular age and finds its own hole (the model is described in detail in [5, 11, 14]).

The numerical experiments with the IOM allowed us to reproduce the population fluctuations, including those with period 3 (see Fig. 5).

Figure 4 presents a graphical representation of the difference equation obtained as the result of a particular numerical experiment with the IOM (dots on the graph). This representation is qualitatively close to the form of the difference equation obtained for the VLPF model.

6. Simplified description in the form of differential equations

Many ecological systems, including tundra ones are characterized by seasonal factors. Such factors are taken into account in [1, 2, 13] using a generalization of the ‘predator-prey’ model. Since the IOM does not take into account the interactions of lemmings with vegetation and predators, a simplified description subject to seasonal factors can be done by the following equations. The Verhulst equation is used for the reproduction period:

$$\frac{dX}{dt} = rX \left(1 - \frac{X}{K} \right)$$

where X is the size of population, t is the time, r is the increment rate, K is the maximal size of the population.

For the winter period we use the equation

$$\frac{dX}{dt} = -aX$$

where a is the coefficient of the population decrease.

We succeeded in finding coefficients ($K = 500$, $r = 3$, $a = 0.1$, and $a = 0.6$ after the peak, $7/12$ in the reproduction period, $5/12$ the winter period) to obtain cycles with the period of 3 years similar to those obtained in numerical experiments with the IOM (see Fig. 5). (Solution of the differential equations was performed by the fourth-order Runge–Kutta method).

Figure 5 shows that the coincidence is good for a large population size at the end of the season and is much worse for a small population.

7. Integrated analysis of the models

As was indicated above, we succeeded in integrating the VLPF model and difference equation within solution of the inverse simulation problem. The analysis of the difference equation allowed us to select three principal factors forming the dynamic regimes of the lemming population fluctuations. These factors are the biomass increment rate in a favorable year P , the maximal population size B , and the survivability in the least favorable conditions d (or two dimensionless parameters, which are the relative increment rate of population and the share of animals with guaranteed survival). All these three factors were formed as the result of coevolution of the physiological and ecological characteristics of lemmings and the environment parameters.

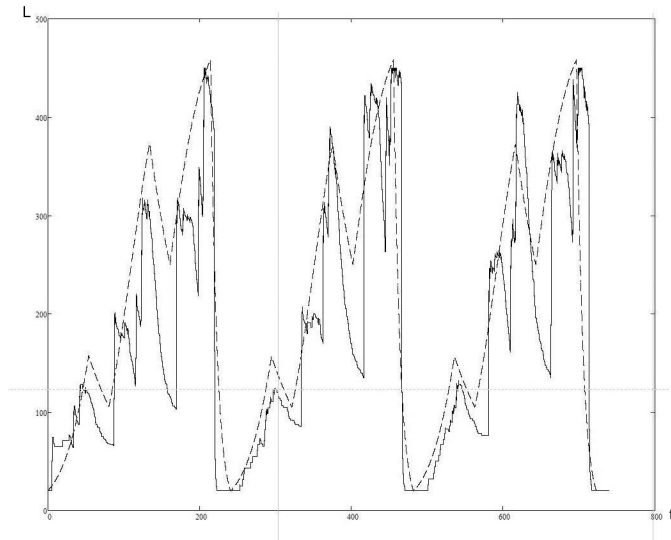


Figure 5. Comparison of lemming population dynamics (L) obtained by the complete IOM (solid line) and by the simplified model (dotted line).

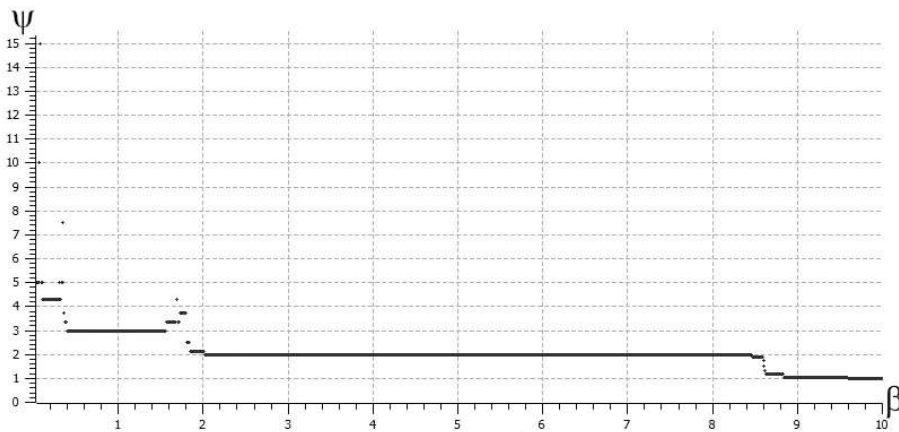


Figure 6. Dependence of the mean distance between population peaks (ψ) on the optimal biotope level (β).

The first factor characterizes the balance between the birth rate and mortality in all phases of development without 'environment pressure'. The second factor characterizes the ecosystem as a whole and is generally an indicator of lemmings and their food base coevolution. The third one characterizes the adaptive abilities of lemmings in extreme conditions and is mainly determined by local characteristics, in particular, by the terrain profile in the areas of their winter stay.

The conclusions obtained here are in good correspondence with the prevailing hypothesis that fluctuations in animal populations are formed not by a single fac-

tor, but by a certain combination of factors [3, 10, 12, 17]. Such combinations have been specified and it is (quantitatively) shown how these combinations affect the dynamics of animal populations.

In addition, we have succeeded in obtaining formulas for the transition between the VLPF model and the difference equation, which ensures a reverse compatibility of these models. Thus, the simplified difference equation can be used for adjusting the VLPF model (and other more detailed models) to the required modes of operation, and detailed models can be used for minute studies of the processes.

The analysis of the properties of the difference equation has shown that an alternation of stability and transition zones is observed under a variation of parameters. Numerical experiments with the VLPF model have also shown that the same effect takes place under a variation of such factor as the optimal biotope level β (see Fig. 6).

As is seen from Fig. 6, stability zones are observed for the following values of β : $[0, 05; 0, 17] - (4)$, $[0, 2; 1, 8] - (3)$, $[2; 8, 2] - (2)$, $[8, 9; 10] - (1)$ (the mean distance between the population peaks is presented in the parentheses). Transition zones are observed for the following values of β : $[0; 0, 05]$ $[0, 17; 0, 2]$ $[1, 8; 2]$ $[8, 2; 8, 9]$. Other parameters are defined above.

A similar pattern is observed for the individual-oriented model too.

8. Conclusion

Simulation modelling in the environmental and biological fields is an art of application of computer technologies in an interdisciplinary process creating mathematical models for incomplete, diverse, and inevitably distorted data concerning the properties of the studied objects. This is an art of searching for a compromise between the ecological and mathematical requirements, i.e., an efficient simulation requires not only a coordination of the informational base of the model with data and representations of the biologists, but also an appropriate choice of mathematical tools to represent the specificity of the studied object, and such tools are impossible to predict. Only a computational experiment with a completely (information-assembled) model can represent a time series related to the population size dynamics with a combination of the chosen structure of the model and the information base adjusted to it. The search for such successful combinations is based on the idea of ecological design (ED), which is an algorithmic structure allowing one to modify this model sufficiently easily. An implementation of this idea is based on the combination of Forrester's system dynamics with the Volterra–Kostitsyn hypothesis of the possibility of using systems of ordinary differential equations for description of ecological objects.

Within this approach, we are able to take into account practically all propositions of experts in a quantitative or a qualitative form. Moreover, the idea of ED implements the principle of modification ability, i.e., permanent readiness to revise the model and check various variants, assumptions, and hypotheses. This technology enables us to reconstruct the model in the course of numerical experiments and

to form several models for quantitative description of a phenomenon, which allows us to consider an object from different angles. The technology of simulation modelling allows us to start creating a model quickly enough and this process is based on expert data and model prototypes from previous stages. The ecological design allows us to implement different ideas sufficiently easily (on a formal level), to consider alternative variants, to use the knowledge of similar processes in other fields. Having assimilated the relevant field of study, the role of the mathematician in the model modification process is increased. The 'modeller-mathematician' takes certain expert functions upon himself and selects information from the viewpoint of simulation efficiency.

However, it is difficult to obtain a satisfactory description of the studied object and to reveal its principal mechanisms by pure simulation techniques, even under ideal conditions for interdisciplinary cooperation. A combination of simulation and analytic approaches looks attractive, the same is true for considering sets of inter-related models, including simplified ones admitting an analytic (parametric) study. The search for ways of implementation of such combinations has led to complex researches (CR). The original detailed simulation model is used to justify simplified models. This model serves as a kind of a filter for the whole spectrum of available biological information. The iterative process of modifying the model results in examination of possible variants.

The particular dependences and the set of functions kept changing in the process of construction and study of mathematical models of tundra community. Expert estimates were used and revised many times in the choice of different modifications of the model. In this paper we present a final stage of simulation. We describe a possible version of the model where we have succeeded in representing the fluctuations of animal populations close to actual ones. The stage of modification of the models and their coordination with the experts had been completed by the time of releasing this version (which is final at this stage). The figures present the functions used in the model, and the developers of the model (not the experts) are responsible for them. The final dependences have been proposed by the developers, but the opinion of the experts was taken into account in the construction.

The presence of simplified models admitting parametric studies completely changes the abilities and the potential of simulation. This is a tool for adjustment of the original simulation model to the corresponding dynamic regimes and, above all, this is a way to generate hypotheses on the principal mechanisms of the studied phenomenon. Using simplified models, we have succeeded in formulating the compatibility criteria for the original (basic) models and the population size dynamics registered in time series.

The presence of such criteria allowed us to remove the requirement of nonlinearity in the interaction of species and in strict intrapopulation regulation, and showed the possibility of periodicity due to seasonal peculiarities of the model.

The use of integrated approach in the simulation of tundra populations and communities has allowed us to justify a particular class of models taking into account the seasonal factors [1, 5] and also a new type of difference equations where for a

particular scenario of parameter variation, stability zones with stable cycles successively appear, and their periods vary according to the natural sequence [9].

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