================ TRANSLATIONS OF PUBLISHED ARTICLES ================

Dynamics of predator-prey community with age structures and its changing due to harvesting

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Abstract. The paper studies dynamic modes of discrete-time model of structured predator-prey community like "arctic fox – rodent" and changing its dynamic modes due to interspecific interaction. Possibility of shifting dynamic modes is analyzed. In particularly, 3-cycle emerging in prey population can result in predator extinction. Moreover, this solution corresponding to an incomplete community simultaneously coexists with the solution describing dynamics of complete community, which can be both stable and unstable. The anthropogenic impact on the community dynamics is studied. Anthropogenic impact is realized as a harvest of some part of predator or prey population. It is shown prey harvesting leads to expansion of parameter space domain with non-trivial stable numbers of community populations. In this case, the prey harvest has little effect on the predator dynamics; changes are mainly associated with multistability areas. In particular, the multistability domain narrows, in which changing initial conditions leads to different dynamic regimes, such as the transition to a stable state or periodic oscillations. As a result, community dynamics becomes more predictable. It is shown that the dynamics of prey population is sensitive to its harvesting. Even a small harvest rate results in disappearance of population size fluctuations: the stable state captures the entire phase space in multistability areas. In the case of the predator population harvest, stability domain of the nontrivial fixed point expands along the parameter of the predator birth rate. Accordingly, a case where predator determines the prey population dynamics is possible only at high values of predator reproductive potential. It is shown that in the case of predator harvest, a change in the community dynamic mode is possible as a result of a shifting dynamic regime in the prey population initiating the same nature fluctuations in the predator population. The dynamic regimes emerging in the community models with and without harvesting are compared.

Key words: *discrete-time mathematical model, community, predator-prey, stability, dynamic modes, age structure, harvest.*

INTRODUCTION

Modeling the dynamics of «predator-prey» community is a popular and interesting task: every year the number of articles on this topic is increasing. Figure 1 presents number dynamics of papers dealing with «predator-prey community» in Scopus. Searching by key-

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words (prey AND predator AND model) gives hundreds of papers, at that research interest to prey-predator models has significantly increased in the recent decades. Note, that the vast majority of them uses continuous-time models traditionally.
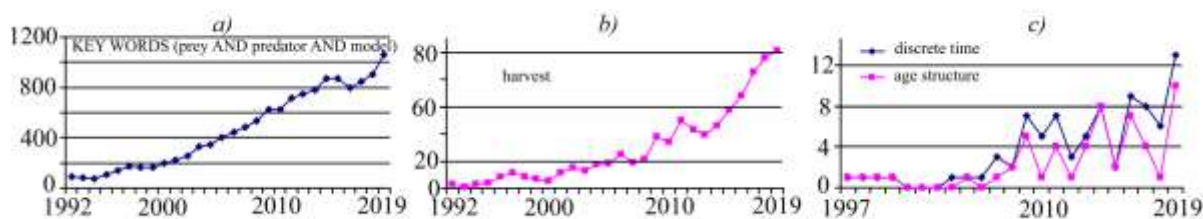

Fig. 1. Dynamics of paper number in the citation indexing service Scopus by the key-words (prey AND predator AND model) (**a**), among them the articles mentioning "harvest" (**b**), discrete time and age structure (**c**).

In our opinion, this is due to the fact that the first model proposed by Lotka and Volterra [1, 2] to describe the interaction between a predator and its prey uses differential equations. Consequently, many researchers continue developing on the basis of the founder's ideas. The development of this model by introducing additional terms and searching for new trophic functions ([3], e.g., Holing [4, 5], Bazykin [6]) provided it the capability of describing periodic oscillations in the population sizes caused by trophic interactions between species. Further development of these models followed the path of complication and generalization. There are stochastic [7–10], continuous [6, 11], algebraic and discrete time [12] modifications of the Lotka-Volterra model, and each of the modifications describes and takes into account specific features of interspecies interaction and a biological community development [13].

Equations with delay are often used to take into account the age structure of a community's populations in continuous time [14–19], where stage is described as a delay that corresponds to the time during which individuals of a predator [14–16] or a prey [16, 19] achieve maturity. As a rule, the age structure of the predator population is considered, since it is assumed that juvenile predators cannot feed themselves. Some papers describe age structure of community's populations using separate equations for each development stage of a prey [20, 21] or a predator [18, 22]. There are studies examining the influence of factors not related to the interaction of predator and prey on the community dynamics, for example, cannibalism [22] or a prey's refuge [21].

The main subjects of study of these models are the system stability [16, 18, 19], the hydra effect [20], bifurcations [16, 18, 19], the influence of optimal [18] and/or selective harvesting of prey or predator [18, 22–26]. Note that paper [18] studies the "prey – predator" model with stage-structured predator, while the selective harvesting of the predator is considered as a control parameter. In addition, the series of works [27, 28] merits attention, here differential-algebraic model of a "predator-prey" community with age structured prey under predator harvesting is investigated. The authors use a delay to separate in time the processes of feeding and reproduction in the predator population. They showed that increasing delay results in destabilizing dynamics of the model and emerging Hopf bifurcation.

Note that the number of studies analyzing the dynamics of "predator-prey" system with harvesting has increased in the last decade (Fig. 1). The harvest process in models with differential equations is assumed continuous. However, as a rule, harvesting is discrete in time and is confined to a certain season. Often harvest focuses on catching individuals of a specific age, which gives the greatest economic benefit [29–32]. Moreover, as a rule, models based on differential equations describe the processes of feeding and reproduction as interrelated and continuous ones, i.e. there is a continuous transition of the prey population biomass to the predator population one. However, many natural species have a pronounced seasonal breeding. Use of discrete–time models is seemed to be more adequate for describing dynamics of such populations. In addition, the description of development stages of

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individuals by discrete-time models is also more preferable [5]. However, as Figure 1 shows, a few papers investigate the dynamics of the predator-prey community with harvest using recurrent equations. Only the last decade has demonstrated an increasing interest to this approach.

Note that a number of very interesting papers among the modern studies consider temporal [33–35] and spatial [36–39] dynamics of prey-predator communities which are described by discrete-time equations. In particular, methods of the dynamic chaos theory were used to investigate fluctuations in discrete-time prey–predator systems considering either various biological effects [36, 39–41] as example «prey switching» [40, 41]. The paper [40] studies the community "polar bears and ringed seals" with switching between prey stages within the seal population, using matrix models. Prey switching is a phenomenon in which a predator disproportionately consumes the most abundant prey type, and switches to consume another prey type preferentially if the first becomes relatively rare [40]. There is also a very interesting paper [42], which studies the influence of different predation strategies on the response of age-structured prey populations to a changing climate. In particular, the study shows that the changing climate results in prey population fluctuations, while predator suppresses them. At the same time, ambush predators such as lions are more effective at suppressing fluctuations in their prey than cursorial predators such as wolves, which chase down prey over long distances [42].

The dynamics of specific communities is studied, such as host-parasitoid [43, 44] and plant-herbivore communities [45, 46], a community with age-structured prey [42, 44, 47]. The work [47] investigates a discrete-time model of a "predator-prey" community with an age-structured prey. This study showed that if the prey demonstrates chaotic fluctuations, then the increase in skill of predation can stabilize the prey dynamics, and in the case of large predation pressure, can transfer the population to another chaotic regime. This is true if the prey population reproduces, offspring once in a lifetime and its individuals are characterized by rapid maturation.

In the studies with community under harvesting, we note the following papers [48, 49] that focus on emerging bifurcations. Thus, [49] shows that a discrete-time "predator-prey" model with age-structured predator reveals Neimark-Sacker bifurcation and period doubling one, while the prey harvest stabilizes the community dynamics. The analysis of papers studying the harvest influence on a structured predator-prey community using discrete-time equations shows the importance of this field development, since the application of discrete-time models allows taking into account and describing a number of biological system features.

This paper continues the study of the discrete-time model of age-structured community of "predator-prey" describing dynamics of community like "arctic fox-mouse-like rodents" [50–52]. Given research focuses on analyzing the influence of interaction between species on the community dynamics. Harvesting impact on the community dynamics modes is also studied. Dynamic modes of a community model with and without specific harvest of a prey or a predator are compared.

MATHEMATICAL MODEL OF PREY-PREDATOR COMMUNITY

The community of "arctic fox – rodents" is evident natural example of prey-predator interaction. Natural populations of arctic foxes (*Alopex lagopus*) inhabit inland areas depend on small rodents, mainly voles whose populations are characterized by cyclic fluctuation [53]. Indeed, in years with low food supply, inland fox population demonstrates a very low rate of reproduction, by contrast, in years when prey species are abundant, number of pups in their litters is some-fold higher. At that, each species from the community at hand is age-structured, which is necessary to consider for modeling of the community dynamics.

A four-component model of prey-predator community dynamics describing the dynamics of the community "arctic fox – mouse-like rodents" and taking into account seasonality of the life cycle has been proposed in our previous paper [50]. It takes the form,

$$
\begin{cases}
X_1(n+1) = \left(a_1 X_1(n)\left(1 - \dfrac{\alpha_0 \cdot Y_2(n)}{X^* + X_1(n)}\right) + a_2 X_2(n)\right) \cdot e^{-\beta_1 \cdot X_1(n)\left(1 - \frac{\alpha_0 \cdot Y_2(n)}{X^* + X_1(n)}\right) - \beta_2 \cdot X_2(n)}, \\[4mm]
X_2(n+1) = s \cdot X_1(n)\left(1 - \dfrac{\alpha_0 \cdot Y_2(n)}{X^* + X_1(n)}\right) + v \cdot X_2(n), \\[4mm]
Y_1(n+1) = w \cdot \dfrac{X_1(n)}{X^* + X_1(n)} \cdot Y_2(n), \\[4mm]
Y_2(n+1) = Y_1(n)\left(1 - \dfrac{Y_1(n)}{M}\right) + c \cdot Y_2(n),
\end{cases}
\quad (1)
$$

where n is the reproductive season number. X_1 and X_2 denote the number of first-time participants in the reproductive process (or underyearlings) and the number of last year's participants in reproduction that have survived the winter, respectively (in the prey population).The variables a_1 and a_2 are their reproductive potentials, s and v are their survival rates; β_1 and β_2 are the coefficients of limitation characterizing influence of competition between mature individuals of different ages on the birth rate; $\alpha_0 \cdot Y_2(n) / (X^* + X_1(n))$ is the share of the underyearlings' number consumed by the predator, α_0 is average number of prey consumed by unit of predator per an year. Thus, the predator influences the processes of reproduction, competition and survival in the prey population. Y_1 and Y_2 are the numbers of individuals in the juvenile and reproductive part of the predator population, respectively; M is the carrying capacity or the maximum population number of predator that is sustainable, if it being exceeded the predator population becomes extinct; c is the survival rate of the mature individuals of the predator; w is maximal value of predator's reproductive potential, that is attainable with unlimited number of the prey. The function $X_1(n)/(X^* + X_1(n))$ describes a dependence of the predator reproductive potential on its satiation defined by the feeding quality. X^* is half saturation constant. Here we use the Holling type II functional response: $X_1(n) / (X^* + X_1(n))$

A substitution of the variables and coefficients,

$$
s\beta_2 X_1 \to x_1, \ \beta_2 X_2 \to x_2, \ Y_1/M \to y_1, \ Y_2/M \to y_2, \ a_1 \to r_1,
$$
$$
sa_2 \to r_2, \ \alpha_0 M\beta_2 \to \alpha, \ s\beta_2 X^* \to x^*, \ \beta_1/(s\beta_2) \to \rho, \quad (2)
$$

transforms model (1) to a more simple form:

$$
\begin{cases}
x_1(n+1) = \left(r_1 x_1(n)\left(1 - \dfrac{\alpha \cdot y_2(n)}{x^* + x_1(n)}\right) + r_2 x_2(n)\right) \cdot e^{-\rho \cdot x_1(n)\left(1 - \frac{\alpha \cdot y_2(n)}{x^* + x_1(n)}\right) - x_2(n)}, \\[4mm]
x_2(n+1) = x_1(n)\left(1 - \dfrac{\alpha \cdot y_2(n)}{x^* + x_1(n)}\right) + v \cdot x_2(n), \\[4mm]
y_1(n+1) = w \cdot \dfrac{x_1(n)}{x^* + x_1(n)} \cdot y_2(n), \\[4mm]
y_2(n+1) = y_1(n)(1 - y_1(n)) + c \cdot y_2(n).
\end{cases}
\quad (3)
$$

Model (3) has three fixed points:

1. A trivial fixed point that corresponds to the extinction of both populations: $\{\bar{x}_1 = 0, \ \bar{x}_2 = 0, \ \bar{y}_1 = 0, \ \bar{y}_2 = 0\}$.

2. A semi-trivial solution that corresponds to the prey population existence in the absence of a predator:

$$\left\{\overline{x}_1 = \frac{1-v}{\rho(1-v)+1}\ln\frac{r_1(1-v)+r_2}{1-v}\right\}, \ \left\{\overline{x}_2 = \frac{1}{\rho(1-v)+1}\ln\frac{r_1(1-v)+r_2}{1-v}\right\}, \ \overline{y}_1 = 0, \ \overline{y}_2 = 0.$$

3. A non-trivial fixed point corresponding to the sustainable existence of a predator-prey community is defined as solving a transcendental equation for $\overline{x}_1$:

$$\overline{x}_1(1-u)\left(\rho+\frac{1}{1-v}\right) = \ln\frac{(1-u)(r_1(1-v)+r_2)}{1-v}, \ \overline{x}_2 = \frac{\overline{x}_1(1-u)}{1-v}, \ \overline{y}_1 = W\cdot\overline{y}_2, \overline{y}_2 = \frac{W+c-1}{W^2},$$

where $1-u = 1-\dfrac{\alpha\cdot\overline{y}_2}{x^* + \overline{x}_1}$, $W = w\dfrac{\overline{x}_1}{x^* + \overline{x}_1}$.

Our previous studies [51, 52] present conditions for existence and stability of these fixed points. The papers show system (3) reveals transcritical, period doubling and Neimark-Saker bifurcations. Consequently, the model trajectories can be periodic, quasiperiodic, and chaotic oscillations. Studies [51, 52] consider changes in bifurcation boundaries forming the model stability domains with variation of the parameter values. Changes in community dynamics due to interaction of prey and predator are analyzed based on the model trajectories [50–52]. This paper analyzes the influence of interspecies interaction on the dynamics of predator-prey community using dynamic mode maps [54], which has allowed obtaining new biologically meaningful conclusions.

INTERSPECIFIC INTERACTION INFLUENCE ON THE COMMUNITY DYNAMICS

To understand the mechanisms of interspecific interaction influence on each species dynamics in a community it is necessary to compare cases with and without interspecific interaction. Indeed, if food abundance does not change from year to year, then the reproductive potential can be considered as a constant value. This situation is observed in natural populations of Arctic foxes inhabiting coastal areas. Animals eat seabirds, fish, seals and marine invertebrates; the availability of these feed resources remains almost unchanged from year to year [55]. As a result, coastal arctic foxes produce small litter each reproductive season, and their birth rate is around constant. In terms of model (1), this is true when $\alpha(x_1(n)) = 1$, which is equivalent to $x_1(n) / (x^* + x_1(n)) = 1$ for system (3). The equality of coefficient u to zero in system (1) (for equations (3): $\alpha\cdot y_2(n)/(x^* + x_1(n)) = 0$) indicates that the prey population is local and not affected by predator. Note that if $x_1(n) / (x^* + x_1(n)) = 1$ and $\alpha\cdot y_2(n) / (x^* + x_1(n)) = 0$, then model (3) is a set of two uncoupled systems, each of which may be considered separately. The case corresponds to a situation without interaction between species.

Figure 2,a shows possible dynamic modes that occur in a rodent population without predator pressure. The selected parameter values correspond to the case when stability loss occurs via both the Feigenbaum scenario and the Neimark-Sacker one. With the selected values of initial condition the local rodent population can demonstrate two-year, three-year oscillations or stationary state under the different reproductive potential values (Fig. 2,a). At the same time, multistability is observed in a wide region of parametric space: the 3-year cycle area overlies the stability domain of the non-trivial fixed point and its bifurcation according to the Neimark-Saker scenario. The proposed model describing dynamics of age-structured predator population with food abundance demonstrates the emergence of quasi-periodic oscillations with growth of birth rate parameter. In the case when the coefficient values are located into periodic windows of quasi-periodic dynamics area, regular oscillations are observed (Fig. 2,b).
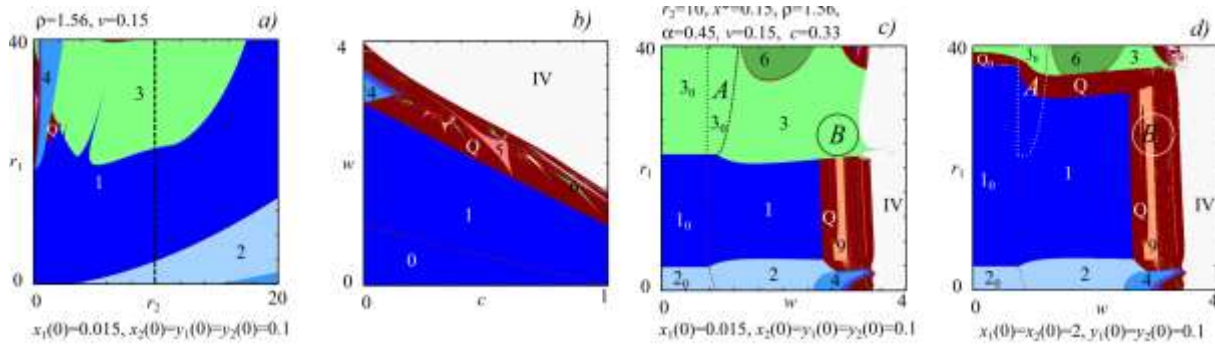
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Fig. 2. Dynamic mode maps of model (3) **a**) the dynamics of prey population with $x_1(n)/(x^* + x_1(n)) = 1$ and $\alpha \cdot y_2(n) / (x^* + x_1(n)) = 0$; **b**) the dynamics of predator population with $x_1(n) / (x^* + x_1(n)) = 1$ and $\alpha \cdot y_2(n) / (x^* + x_1(n)) = 0$; **c–d**) community dynamics with interspecific interaction under different initial conditions. The figures correspond to the period of observed cycles, Q is quasiperiodic dynamics, IV is infeasible parameter value area where the model loses its meaning. 0 (index 0) is an area with the absence of a predator.

The presence of interspecific interaction in the community leads to increasing variety of emerging dynamic modes of the predator population size. The Figure 2,c for fixed values of interaction parameters allows studying the evolution of dynamic modes in the prey population with increasing predator reproductive potential. Thus, the map 2,a for fixed value of $r_2 = 10$ with an increase in the r_1 values shows the following shifts of dynamic modes along the dotted line: 2-cycle, stable state, 3-cycle. On the map 2,c, the ordinate axis corresponds to the dotted line (the same dynamic modes are observed). Consequently, by increasing the reproductive potential of the predator, we can analyze possible changes in dynamic modes of both the prey population and the community.

In particular, the predator population goes extinct with low values of its reproductive potential. At the same time, the prey population demonstrates various dynamic modes, whose nature depends on its birth rate and self-regulation processes. Increasing in parameter w values leads to emerging dynamic modes in the predator population of the community, the nature of which is similar to the dynamic modes of the prey population in the absence of the predator. That pattern remains until the Neimark-Sacker bifurcation occurrence that forms a closed invariant curve. As a result, quasiperiodic oscillations appear and they are caused by the interaction between the predator and prey, and therefore the predator impact on the prey population results in quasiperiodic dynamics in the prey population of community (Fig. 2,c–d).

Figures 2,c,d show dynamic mode maps with multistability areas in which initial condition variation changes the 3-cycle domain that overlaps the stability area of non-zero fixed point and the regimes emerging due to its stability loss via the Neimark-Sacker scenario. Initially the 3-cycle occurs in rodent population without predator. Figures 2,c–d allows one to conclude that into the domain A the 3-cycle of the prey population in the community with extinct predator coexists with the community showing stable dynamics or quasiperiodic fluctuations of interacting populations. Accordingly, the initial condition variation can result in two opposite scenarios for the community development. The first one is the prey population size fluctuates with 3-year period, which results in predator extinction due to drops in prey number. The second scenario corresponds to the coexistence of predator and prey: the community stabilizes or quasiperiodically fluctuates, which depends on the demographic parameter values of the both species. In the case of species coexistence, the community dynamics suits to the prey dynamics. At the same time, there is a possibility of dynamic mode shift in the prey population. Therefore, if a change in the dynamics regime occurs in the prey population, then corresponding changes will occur in the dynamics of the predator population.

Figure 3,a shows the attraction basins, demonstrating coexistence of alternative attractors: the predator population extinction and the sustainable community. The model trajectories

constructed for the initial conditions from different attraction basins demonstrate that at the same parameter values the community stabilizes under some initial conditions, and the predator population goes extinct under others ones (Fig. 3,a).
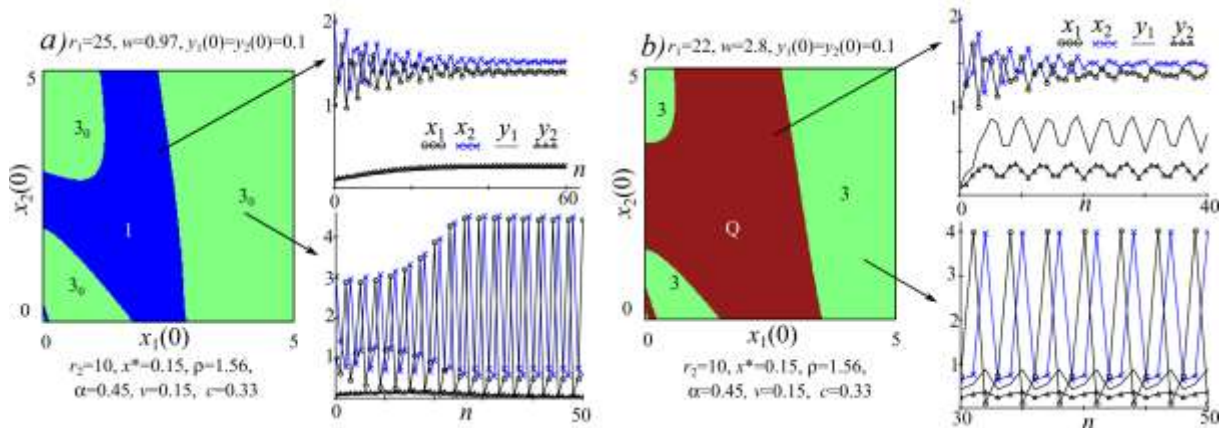

Fig. 3. Attraction basins of coexisting dynamic modes with corresponding trajectories of model (3). The figures correspond to the period of observed cycles, Q is quasiperiodic dynamics, 0 (index 0) is a case of a predator extinction.

The predator dynamics is adjusted to the prey dynamics until bifurcation value of the predator reproductive potential, at which a transition from stable state to quasi-periodic oscillations occurs (Fig. 2,a–b). In the case of multistability, if the current values of community population sizes are into the attraction basins of 3-cycle, which initially arises in the prey population, then the predator dynamics also begins to fluctuate with three-year period. As a result, if this multistability domain overlies the parametric area with the predator dynamics impacted on the prey, then current sizes of community populations will determine the species, who initiates the same dynamic behavior in the rest part of community. The maps of Figure 2,c–d show domain B that is a fragment of the area with such an "overlapping". Figure 3,b depicts the attraction basins corresponding to the phase space division by various attractive states that give various scenarios of community development, which depend on the "leading" species. Therefore, in the area with Figure 3, three-year fluctuations are observed, and the predator dynamics follows the prey dynamics. In the area of quasiperiodic dynamics, the predator initiates fluctuations in the prey population.

We use dynamic mode maps to study changes in the stability areas of System (3) fixed points and fluctuation emergence scenarios in the populations of predator and prey due to stability loss with an increase in values of both the community parameter that determine the interacting species dynamics and the interaction coefficient (half saturation constants x^*). Figure 4 shows dynamic mode maps demonstrating the "predator-prey" community evolution with variations in the parameters describing the species interaction (Fig. 4).

Consuming part of prey by a predator with a high reproductive potential can lead to irregular (quasi-periodic) fluctuations in community. The smaller the coefficient x^* value, the faster the prey population dynamics turns into irregular fluctuations with growth of the predator reproductive potential. A similar situation is observed with increasing values of parameter α. Note that dynamics of a predator with low reproductive potential values adjusts to the prey population dynamics. However, with a higher birth rate of the predator the community turns into irregular fluctuations that are initiated by the predator.
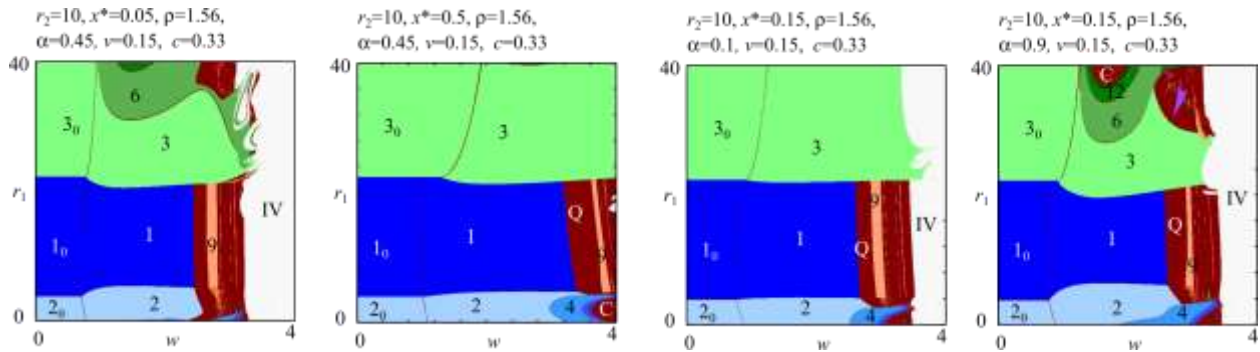
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Fig. 4. Dynamic mode maps of model (3) with different values of parameters describing interspecific interaction. The figures correspond to the period of observed cycles, 0 (index 0) is an area with the absence of a predator, Q is quasiperiodic dynamics, C is chaotic dynamics, IV is infeasible parameter value area where the model loses its meaning. Initial conditions are $x_1(0) = 0.015$, $x_2(0) = y_1(0) = y_2(0) = 0.1$.

Harvest influence on the community dynamics

Anthropogenic impact involving deratization, and some types of removal such as surveys or hunting can influence on the dynamics of predator – prey community. To consider this effect, we propose the following model modification of the community like "arctic fox – rodent" assuming removal to be proportional to the size of harvested species.

$$\begin{cases} X_1(n+1) = \left((a_1 X_1(n)\left(1 - \dfrac{\alpha_0 \cdot Y_2(n)}{X*+X_1(n)}\right) + a_2 X_2(n)\right) \cdot e^{-\beta_1 \cdot X_1(n)\left(1 - \frac{\alpha_0 \cdot Y_2(n)}{X*+X_1(n)}\right) - \beta_2 \cdot X_2(n)}\right)(1 - h_1), \\[2mm] X_2(n+1) = \left(s \cdot X_1(n)\left(1 - \dfrac{\alpha_0 \cdot Y_2(n)}{X*+X_1(n)}\right) + v \cdot X_2(n)\right)(1 - h_1), \\[2mm] Y_1(n+1) = w \cdot \dfrac{X_1(n)}{X*+X_1(n)} \cdot Y_2(n)(1 - h_2), \\[2mm] Y_2(n+1) = \left(Y_1(n)\left(1 - \dfrac{Y_1(n)}{M}\right) + c \cdot Y_2(n)\right)(1 - h_2), \end{cases} \qquad (4)$$

where h_1 and h_2 denote harvest rates of prey and predator, respectively. The meaning of the other variables and parameters does not change. Model (4) with substitution (2) takes the form:

$$\begin{cases} x_1(n+1) = (1 - h_1)\left(r_1 x_1(n)\left(1 - \dfrac{\alpha \cdot y_2(n)}{x*+x_1(n)}\right) + r_2 x_2(n)\right) \cdot e^{-\rho \cdot x_1(n)\left(1 - \frac{\alpha \cdot y_2(n)}{x*+x_1(n)}\right) - x_2(n)}, \\[2mm] x_2(n+1) = (1 - h_1)\left(x_1(n)\left(1 - \dfrac{\alpha \cdot y_2(n)}{x*+x_1(n)}\right) + v \cdot x_2(n)\right), \\[2mm] y_1(n+1) = w \cdot \dfrac{x_1(n)}{x*+x_1(n)} \cdot y_2(n)(1 - h_2), \\[2mm] y_2(n+1) = (1 - h_2)(y_1(n)(1 - y_1(n)) + c \cdot y_2(n)). \end{cases} \qquad (5)$$

This paper considers the following two cases: (i) the harvest of predator ($h_1 = 0$), and (ii) the harvest of prey ($h_2 = 0$). Each of the models has thee fixed points: a trivial, a semi-trivial, and a nontrivial solutions. Similar to the case without harvesting, the considered systems demonstrate periodic, quasiperiodic, and chaotic fluctuations as well as multimodality [30, 31, 51, 52] depending on population parameters values. Therefore, a variation of current

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population size can shift the dynamic mode of the community. Let us proceed with considering each case dynamics in more detail.

Harvest of prey population

The semi-trivial and non-trivial fixed points of Model (5) in the case of prey population harvest ($h_2 = 0$) take the form:

1) $$\{\bar{x}_1 = \frac{1-vH}{H+\rho(1-vH)}\ln\frac{H(r_1(1-vH)+r_2H)}{1-vH}, \quad \bar{x}_2 = \frac{H}{1-vH}\bar{x}_1,$$
$$\bar{y}_1 = 0, \quad \bar{y}_2 = 0\}$$
, (6)

2) $$\{\bar{x}_1(1-u) = \frac{(1-vH)}{H+\rho(1-vH)}\ln\frac{H(1-u)(r_1+H(r_2-r_1v)}{1-vH}, \quad \bar{x}_2 = \frac{\bar{x}_1(1-u)H}{1-vH},$$
$$\bar{y}_1 = W\cdot\bar{y}_2, \quad \bar{y}_2 = \frac{W+c-1}{W^2}\},$$
(7)

where $1-u = 1-\dfrac{\alpha\cdot\bar{y}_2}{x^*+\bar{x}_1}$, $W = w\dfrac{\bar{x}_1}{x^*+\bar{x}_1}$, $H = 1-h_1$.

Figure 5 shows dynamic modes of Model (5) and their shifts because of changing value of prey's harvest rate. In addition, figure 5 illustrates the typical forms of stability domains of the semi-trivial and non-trivial solutions of Model (5) as well as their changes with growth of the parameter h_1.
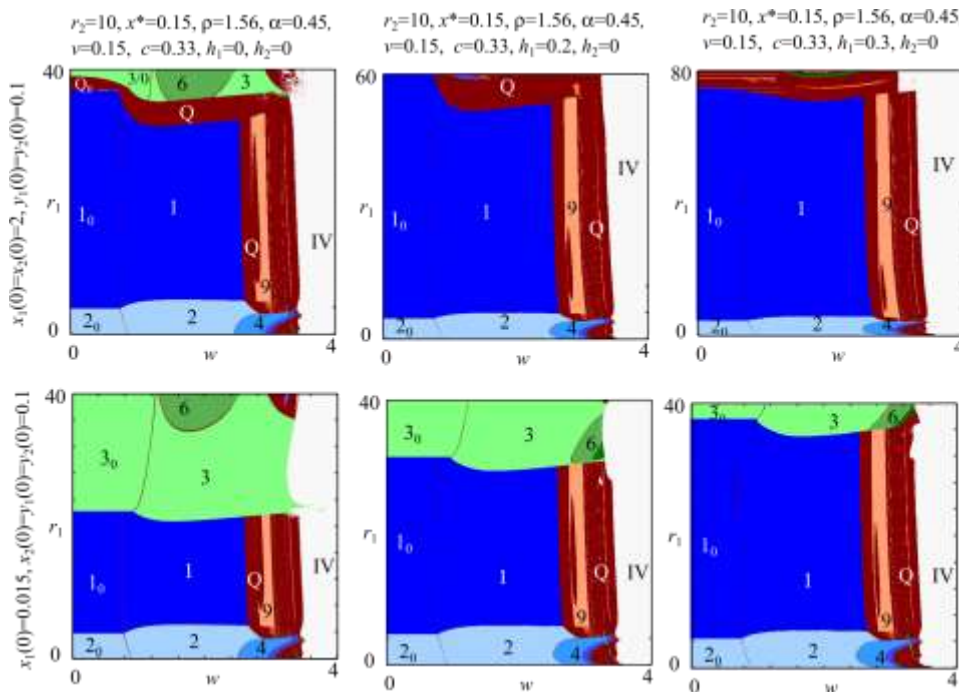

Fig. 5. Dynamic mode maps of model (5) with $h_2 = 0$, and different values of harvest rate of prey and initial conditions. The figures correspond to the period of observed cycles, Q is quasiperiodic dynamics, IV is infeasible parameter value area where Model (5) loses its meaning. Index 0 is an area with the absence of a predator.

One can see that stability domains of fixed points (6) and (7) are formed by bifurcation lines giving emergence of two-year fluctuations or quasiperiodic dynamics when crossed (Fig. 5, upper row). Harvest of a prey affects predator dynamics slightly, but changes a multistability area (Fig. 5, bottom row) where community dynamics depends on initial population sizes. In particular, multistability region with coexisting stable dynamics and

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periodic oscillations narrows, thus community behavior becomes more predictable (Fig. 5). Therefore, a prey harvest regularizes the community dynamics. On the other hand, at high values of reproductive potentials, the population sizes determines the "leading" species, whose dynamics defines the behavior of the whole system. Growth of harvest coefficient value narrows this area and results in expanding parametric space region with fluctuations of rodent population size initiated by predator. Note, the parametric area with prey's 3-year cycle and predator extinction narrows.

Note, the more prey is harvested, the smaller is the parametric space region with two-year fluctuations of the community size, initiated by rodents (Fig. 6,b). The 2-cycle area decreases up to its disappearance, which results in extending stability region of the fixed point. On the other hand, along with narrowing the 2-cycle area, the quasiperiodic fluctuations region emerges that that is between stability domains of non-trivial fixed point and 2-cycle. This region goes up with intensity of harvest rate growth (Fig. 6), which indicates destabilization of the community dynamics.
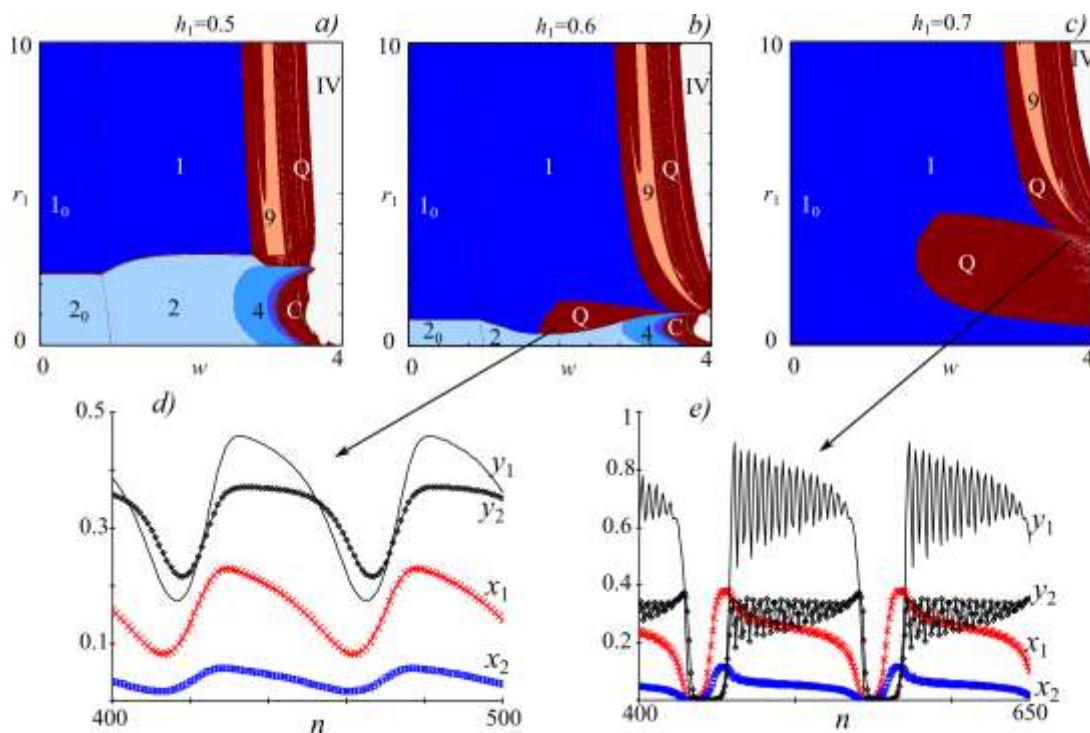

Fig. 6. Dynamic mode maps of model (5) with $h_2 = 0$, and different values of harvest coefficient of prey and initial conditions. Parameter values are $r_2 = 10$, $\rho = 1.56$, $v = 0.15$, $\alpha = 0.45$, $c = 0.33$, $x^* = 0.15$. Initial conditions are $x_1(0) = 0.015$, $x_2(0) = y_1(0) = y_2(0) = 0.1$. The maps are supplemented with examples of the model trajectories with long-period fluctuations. The figures correspond to the period of observed cycles, Q is quasiperiodic dynamics, IV is infeasible parameter value area where Model (5) loses its meaning. Index 0 is an area with the absence of a predator.

In general, an increase in prey harvest intensity when reproductive potentials of both species are sufficiently low results in situations when prey dynamics adapts to that of predator. Note, these are the areas where long-period oscillations emerge (Fig. 6,b and 6,c) like in continuous time models. However, discrete-time models produce more variety of dynamic modes due to different quasiperiodic regimes, the type of which is determined by the traversal order of closed invariant curve. In particular, long-period fluctuations, which are similar to those demonstrated by continuous time models, emerge in the case when the phase trajectory points fill an invariant curve in sequence (Fig 6,d). When the invariant curve is filled "in random manner", the model trajectory fluctuates with a small period and amplitude changing at each time, while the envelope dynamics is a long-period oscillation. Figure 6,e shows, the traversal order of limiting invariant curve on its various parts can differ.

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Harvest of predator population

Semi-trivial solution of System (5) at $h_1 = 0$ coincides with semi-trivial one of Model (3). In case of predator harvest, non-trivial fixed point of System (5) takes the following form:

$$\bar{x}_1(1-u) = \frac{1-v}{1+\rho(1-v)} \ln \frac{(1-u)(r_1(1-v)+r_2)}{1-v}, \quad \bar{x}_2 = \frac{\bar{x}_1(1-u)}{1-v},$$

$$\bar{y}_1 = HW \cdot \bar{y}_2, \quad \bar{y}_2 = \frac{H^2W + Hc - 1}{H^3W^2}, \tag{8}$$

where $1-u = 1 - \dfrac{\alpha \cdot \bar{y}_2}{x^* + \bar{x}_1}$, $W = w \dfrac{\bar{x}_1}{x^* + \bar{x}_1}$, $H = 1 - h_2$.

Figure 7 shows dynamic mode maps of Model (5) at $h_1 = 0$ and their changing because of increase in predator harvest rate.
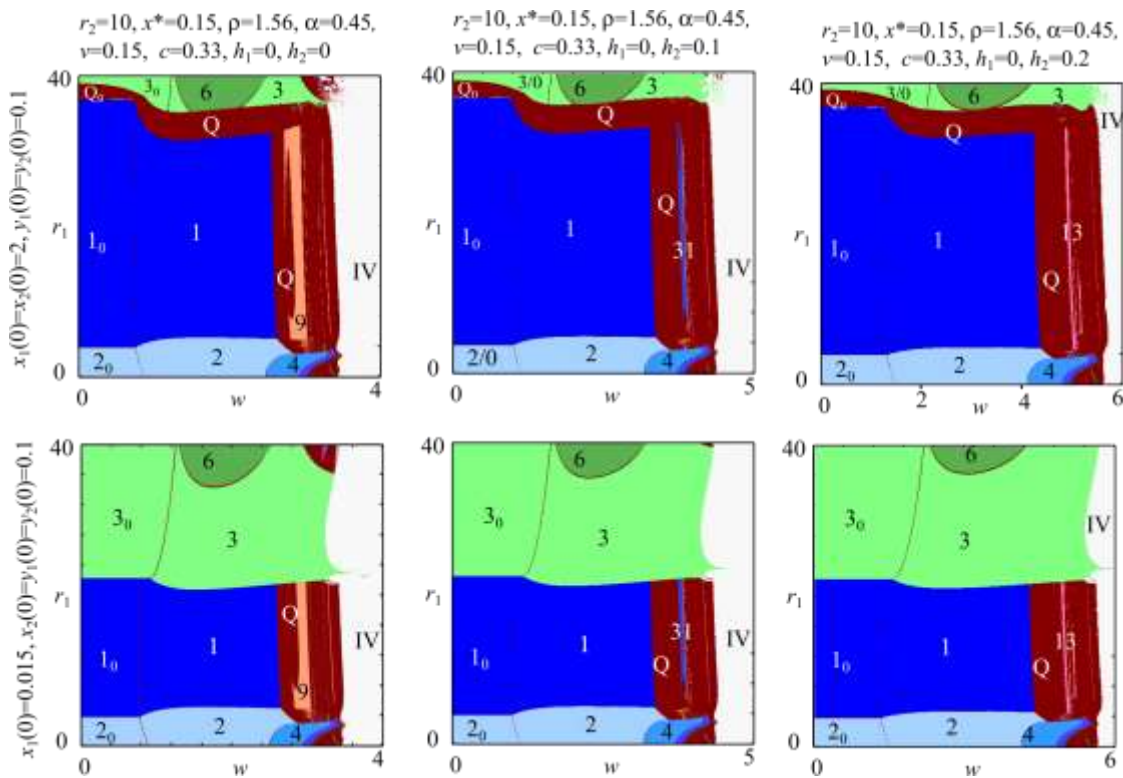

Fig. 7. Dynamic mode maps of model (5) with $h_1 = 0$, and different values of harvest rate of predator and initial conditions. The figures correspond to the period of observed cycles, Q is quasiperiodic dynamics, IV is infeasible parameter value area where Model (5) loses its meaning. Index 0 is an area with the absence of a predator.

A growth of predator harvest rate that is proportional to the predator population size extends the stability area of non-trivial fixed point of Model (5) with an increase in reproductive potential of predator (Fig. 7), i.e. in the line of abscise. Dynamic mode maps show, with a moderate rate of prey population grow, harvest of predator population regularizes community dynamics because of Neimark-Sacker bifurcation occurs latter. Consequently, quasiperiodic fluctuations resulting from prey–predator interaction with leading role of predator are observed only at high values of the predator reproductive potential. The area of quasiperiodic dynamics changes also demonstrating appearance of periodicity windows with different cycles. Similar to the previous case, at $h_1 = 0$ Model (5) has multistability areas that extend with growth of harvest rate value. As shown on Figure 7, if the community demonstrates 3-year fluctuations, then harvest does not remove the system from the attraction region of 3-cycle, i.e. the community dynamics is defined by that of prey.

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When dynamics of community is quasiperiodic, predator harvest stabilizes community dynamics, and it leaded by prey dynamics again. Note, growth of h_2 changes slightly the parametric areas where a variation of current population numbers alters leading species. At that, the parametric region with predator extinction due to emergence of 3-year oscillation of prey extends.

Let us consider the effect of harvest on the structure of the phase space Model (5) in the multistability regions. Figure 8 shows attraction basins from multistability area with predator population extinction (Fig. 8, row A) and where current population numbers of predator and prey defines the leading species that defines dynamics of community (Fig. 8, row B).
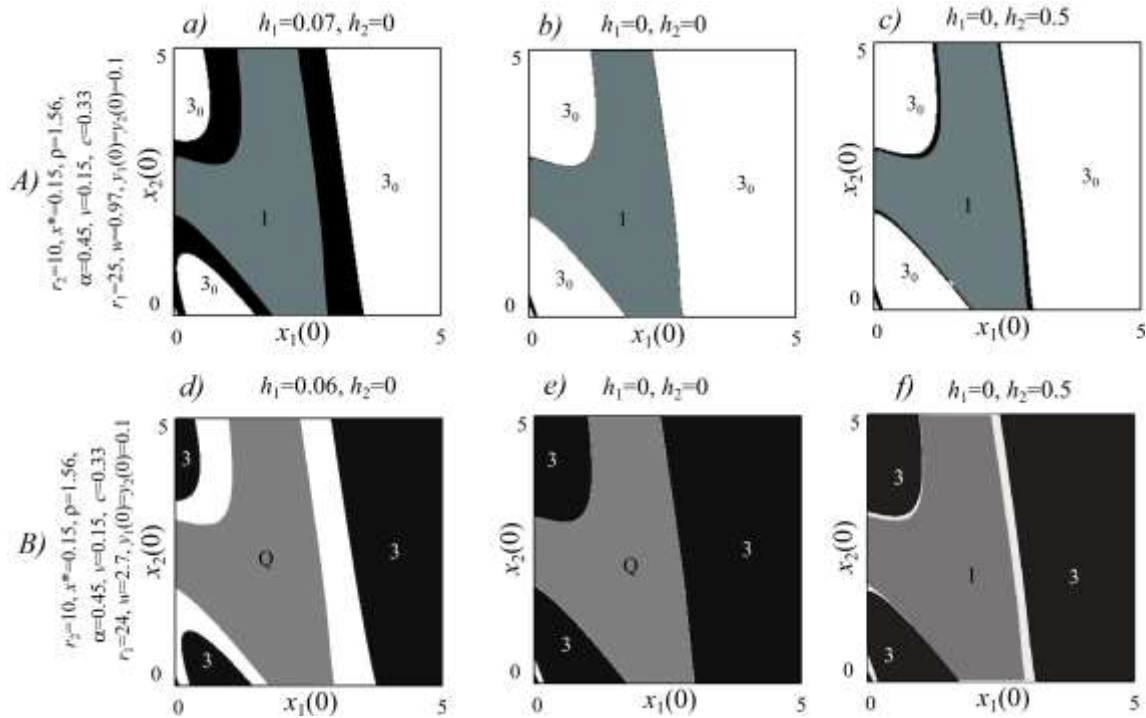

Fig. 8. Attraction basins of dynamic modes for the community with and without harvest. The area dividing dynamic modes corresponds to 3-cycle in the case without harvest and fixed point (or quasiperiodic dynamics) in the community with harvest. The figures correspond to the period of observed cycles, Q is quasiperiodic dynamics, and index 0 is an area with the absence of a predator.

One can see growth of prey harvest rate narrows attraction basin of 3-cycle, thus emergence probability of three-year fluctuations in rodent population followed by predator extinction goes down. Further increase in prey harvest rate results in the situation where attraction basin of fixed point captures the entire phase space. On the contrary, predator harvest slightly changes attraction basins, which allows to conclude the prey population defines the development scenario of predator population and of all community, as emergence of three-year fluctuations followed by predator extinction and prey dynamics stabilization do not depend on either predator population nor interaction. In multistability area where current population numbers define the leading species (i.e. the species which dynamics defines that of all community), prey harvest rapidly extends attraction basin of quasiperiodic dynamics up to its capture of all phase space. Accordingly, prey harvest leads to the fact that its dynamics adapts to the predator dynamics. In turn, predator harvest stabilizes the community dynamics and expands the attraction basin of the stationary state slightly. Thus, predator and, consequently, community dynamics adapts to that of prey in 3-cycle area as well as in the stationary state one.

CONCLUSION

Basing on the discrete-time dynamics model of prey-predator community like "arctic fox – rodent" proposed earlier [50–52], the paper analyses interspecific interaction on the community dynamics by means of construction and study of dynamic mode maps. Periodic, quasiperiodic and chaotic fluctuations are shown to emerge in the system. The dynamic mode is also revealed to depend on the initial population numbers in the community. Types of dynamic modes of the proposed model and possibility of their change are investigated. Interspecific interaction in a community is shown to expand the variety of dynamic modes emerging in predator population essentially. Quasiperiodic oscillations emerging with high values of the predator reproductive potential turned out to be the result of interaction between predator and prey and thus, one could conclude the predator influence on prey population results in fluctuation appearance. Note, that dynamics of predator with low values of its reproductive potential adapts to that of prey, but higher birth rate of predator changes the situation essentially and then the community demonstrates irregular fluctuations initiated by predator.

The model reveals multistability when a variation of initial condition changes a scenario of the community development. In particular, 3-cycle and modes emerged by its bifurcation coexist with both the equilibrium and the modes appeared due to its stability loss. Depending on the system parameter values and current population numbers in the community, various scenarios of community development are possible. The first one is that the prey population demonstrates three-year fluctuations, which results in extinction of the predator because of drops in prey number. The second scenario occurs with coexistence of predator and prey populations, and their current sizes determine the leading species whose dynamics defines that of community. The third case is also characterized by species coexistence, however, community dynamics always adapts to that of prey, and dynamics mode shift is possible in the prey population, which changes predator dynamics in the same way.

To study an anthropogenic effect on the community dynamics we proposed a modification of discrete-time model describing populations' number dynamics in the community like "arctic fox – rodent" that allows considering the anthropogenic effect as a harvest of prey or predator population.

Harvest of prey population proportionally its size is shown to extend the stability area of fixed point corresponding to stable species coexistence. It is interesting that generally harvest of a prey population does not influence on predator dynamics considerably, the changes are mainly visible in areas of multistability, where the community dynamics depends on the initial values of the population numbers. In particular, one can observe narrowing the multistability region, where transition from stable dynamics to periodic fluctuations and vice versa is possible, thus, and the community behavior becomes more predictable. As a result, prey harvest regularizes the community dynamics. Dynamics of prey population is shown to be sensitive to its harvest. Even a small rate of harvest dampens fluctuations in its numbers; in multistability areas the equilibrium captures all phase space. Harvest is shown to stabilize the community dynamics in most cases. However, in some situations a high of prey harvest rate initiates fluctuations in a stable community.

Predator harvest extends stability area of equilibrium along the parameter characterizing reproductive potential of predator. Accordingly, only predator having high values of its reproductive potential can determine prey dynamics. Consequently, at a medium growth rate of the prey population, harvest of the predator population regularizes the community dynamics, and multistability areas extending with harvest rate goes up continue to persist. A change of the community dynamics mode is possible as a result of shift in the dynamic mode of prey population, which initiates oscillations of the same type in the predator population.

Note, the conducted study of selective harvest effect on the community dynamics confirms our concepts of the leading species that determines the community dynamics. In

particular, prey harvest dampens fluctuations in its numbers, and the more the harvest rate, the wider the stability area of system fixed point along the parameter characterizing reproductive potential of rodents. At that, fluctuation emergence in the community depends on the values of predator reproductive potential, and transition from stable dynamics to quasi-periodic one depends on predator influence on the rodent population provided that predator has high birth rate. In turn, this fact also confirms the shift of Neimark-Sacker bifurcation line along the axis of the parameter *w* with an increase in predator harvest rate. Indeed, predator harvest reduces its population size, and, consequently, the pressure of the predator impact on the prey population decreases. As a result, dynamics of a community with a predator having high reproductive potential is stabilized by harvest, adapting to prey population dynamics.

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================= ПЕРЕВОДЫ ОПУБЛИКОВАННЫХ СТАТЕЙ =================

Динамические режимы структурированного сообщества «хищник-жертва» и их изменение в результате антропогенного изъятия особей

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Аннотация. В работе изучаются режимы динамики, которые возникают в результате взаимодействия видов в дискретной во времени модели «хищник - жертва», ориентированной на описание динамики сообщества «мышевидные грызуны-песец» с учетом возрастной структуры. Особое внимание уделяется анализу ситуаций, при которых возможна смена динамического режима. В частности, оказалось, что 3-цикл, возникающий в динамике жертвы, может приводить к гибели хищника. При этом сценарий развития, соответствующий неполному сообществу, сосуществует с возможностью развития полного сообщества, которое может быть, как устойчивым, так и неустойчивым. Изучается влияние антропогенного изъятия особей на режимы динамики сообщества. Рассмотрено 2 случая, когда реализуется изъятие жертвы, и когда осуществляется избирательный промысел хищника. Показано, что изъятие жертвы приводит к расширению области значений параметров, при которых численности взаимодействующих видов стремятся к устойчивому нетривиальному равновесию. При этом изъятие жертвы практически не сказывается на характере динамики хищника, изменения преимущественно касаются областей мультистабильности. В частности, наблюдается сужение области мультистабильности, в которой в зависимости от начальных условий могут реализовываться разные динамические режимы: переход к устойчивому равновесию или установление периодических колебаний, т.е. поведение сообщества становится более предсказуемым. Показано, что динамика популяции жертвы чувствительна к ее изъятию: в областях мультистабильности устойчивое равновесие захватывает все фазовое пространство. В случае, изъятия хищника, наблюдается расширение области устойчивости равновесия, и как результат хищник определяет динамику жертвы только при высоких значениях его репродуктивного потенциала. Показано, что здесь смена динамического режима в сообществе возможна в результате смены динамического режима в популяции жертвы, которая инициирует колебания такого же характера в популяции хищника. Проведено сравнение динамических режимов, возникающих в модели сообщества, когда оно свободно от изъятия и когда оно подвергается избирательному изъятию.

Ключевые слова: математическая модель с дискретным временем, сообщество, хищник-жертва, устойчивость, динамические режимы, возрастная структура, изъятие.