

Article

## About a modification of May model of parasite-host system dynamics

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### Abstract

Current publication is devoted to the construction of modification of well-known May model of parasite – host system dynamics and its analysis. In basic model and in modified model there is one and the same assumption that under the determined values of sizes of interacting populations number of attacked hosts is determined by binomial law. In modified model it was took into account that hosts, which were attacked two or more times by parasites, die, and it doesn't lead to the increase of parasite population size. For modified model population dynamic regimes and structure of the space of model parameters are analyzed.

**Keywords** parasite–host system dynamics; May model.

### 1 Introduction

Big number of publications are devoted to construction of models and analysis of population dynamics of predator – prey (or parasite – host) system (see, for example, Brauer, Castillo-Chavez, 2001; Kolmogoroff, 1936; Kostitzin, 1937; Turchin, 2003; Lotka, 1920, 1925; Volterra, 1931; Nedorezov, 1986; Nedorezov, Utyupin, 2003, 2011; Isaev et al., 1984, 2001, 2009; Nedorezov, Sadykov, 2004 and many others). Some publications are devoted to methodological problems: to pure theoretical analysis of possible variants of population size fluctuations at various types of interaction between populations and influence of self-regulative mechanisms etc. (see, for example, Berezovskaya, Karev, Snell, 2005; Logofet, 1993; May, 1974, 1975; May, Oster, 1976; Nedorezov, 1995, 1997; Nedorezov, Nazarov, 1996; Nedorezov, Nedorezova, 1995 and others).

Other part of publications is devoted to the problem of comparison of theoretical (model) results with real datasets (Berryman, 1981, 1991, 1992, 1995; Tonnang et al., 2009, 2010; Varley et al., 1978; Golubev, Insarov, Strakhov, 1980; Bjornstad et al., 1999; Falck et al., 1995; Fromentin et al., 2001 and others). One more part of publications is devoted to the use of discrete time mathematical models as a base for various ecological theories (see, for example, Isaev and Khlebopros, 1973, 1977; Isaev et al., 1984, 2001, 2009; Nedorezov and Utyupin, 2011).

Before the comparison of theoretical and empirical datasets (and before the use of one or other model as the base of various biological theories) we have to be sure, that selected mathematical model corresponds to observed process (on quantitative and qualitative levels). If model doesn't correspond to observed phenomenon a priori, it can lead to unrealistic results (Gilpin, 1973). Thus, solutions of methodological problems in modeling of population processes are of extreme interest and important stage in analysis of every biological species.

In current publication we analyze one of possible modifications of well-known discrete time mathematical model of parasite – host system dynamics by R.M. May (1978). This model is a modification of Nicholson – Bailey model (Nicholson, Bailey, 1935). Within the framework of this model it was assumed that for the fixed values of hosts and parasitoids the quota of non-attacked hosts (which produce the next generation) is equal to the probability  $P$  of the event, that stochastic variable with binomial distribution is equal to zero. Respectively, the quota of attacked hosts in population is equal to  $1 - P$ . It was also assumed that number of parasites of new generation is equal to the number of infected hosts multiplied by constant, which is less than one. It is obvious assumption: not every attacked host transforms into viable parasite of new generation.

One more assumption in the model (May, 1978) is following: the quota of attacked hosts depends on number of parasites only. Obviously, in general case this quota must depend on the relation of numbers of interacting populations. In current publication we follow the first author's assumption. But we have to note, that this assumption correlates with additional limits for the domain of applicability of the model to the description of interaction of species: model doesn't work in the domain of phase space where number of hosts is much bigger than number of parasites (multiplied on the number of hosts which can be attacked by one parasite).

## 2 Description of Model

Let  $x_k$  be the number of hosts,  $y_k$  be the number of parasites at time moment  $k$ . Let's assume that host population dynamics is described by the Moran – Ricker model (Moran, 1950; Ricker, 1954) when number of parasites is equal to zero:

$$x_{k+1} = Ax_k e^{-\alpha x_k}. \quad (1)$$

Coefficient  $A$  is maximum birth rate of population,  $\alpha$  is a coefficient of self-regulation. It is possible to point out a huge number of publications which are devoted to analysis of model (1) and its application to various species (see, for example, May, 1974, 1975; May and Oster, 1974; Tonnang et al., 2009, 2010; Nedorezov et al., 2008; Nedorezov and Sadykova, 2008, 2010).

Influence of parasites on host population dynamics can be taken into account by various ways. For example, for fixed values  $x_k$  and  $y_k$  the quota  $q$  of uninfected hosts (and these hosts can only produce individuals of the next generation) increases with decrease of number of parasites. If number of parasites is equal to zero the quota  $q$  is equal to one. With unlimited growth of parasites  $q$  converges to zero asymptotically. In particular case  $q$  can be presented in the following form:

$$q = \left( \frac{1}{1 + ay} \right)^r. \quad (2)$$

In expression (2)  $y$  is the number of parasites;  $a$ ,  $a = const > 0$ , is a coefficient of efficiency of parasitism. Parameter  $r > 0$  corresponds to efficiency of parasitism too: for every fixed values of  $a$  and  $y$  increase of value of parameter  $r$  leads to decrease of quota  $q$ , and it means that efficiency of parasites decreases. Amounts of these coefficients depend on various factors and conditions, and in particular, it depends on the type of parasite's strategy in finding hosts.

Expression (2) can be explained in other way. Namely, it is assumed a priori that probability of every separated host to be infected by parasites is determined by binomial law. Thus, expression (2) is the probability

of event that one host will not be infected. In such a situation parameter  $r$  must be integer, and real biological sense of this parameter is following:  $r$  is equal to maximum number of attacks (by parasites) for every host.

Taking into account expression (2) the equation (1) can be transformed into the form:

$$x_{k+1} = Ax_k e^{-\alpha x_k} \left( \frac{1}{1 + ay_k} \right)^r. \quad (3)$$

Respectively, we have that expression  $1 - q$  is the probability of event that every host will be attacked by one parasite or *several parasites* (note, that this number of parasites is unlimited with positive probability). If we *additionally* assume that every attacked host can potentially produce one viable parasite, we have the following equation for changing of number of parasites in time:

$$y_{k+1} = Acx_k e^{-\alpha x_k} \left( 1 - \left( \frac{1}{1 + ay_k} \right)^r \right). \quad (4)$$

Non-negative coefficient  $c$ ,  $c = \text{const} < 1$ , allows to take into account in the model the event that not every attacked host transforms into viable parasite. Part of individuals can die in a result of impacts of various stochastic factors, part of individuals can die in a result of effect of over-infection etc. Thus, combination of equations (3) and (4) gives us the May' model of parasite – host system dynamics (May, 1978).

It is important to note that for various natural populations (for example, for insects; Isaev et al., 1984, 2001, 2009; Nedorezov, 1986) model (3)-(4) gives unrealistic description of interaction between two species. Hosts which were attacked two or more times die – and it doesn't lead to increase of number of parasites (over-infection effect; victim's body doesn't contain enough volume of nutrient matter for normal development of two or more parasite's larvae).

Let's consider the following modification of model (3)-(4) when successive development of parasite's larva is possible if and only if host was attacked one time only. Within the limits of assumptions, which were used for the construction of May' model, the probability  $q_1$  that host was attacked by one parasite only is determined by the expression:

$$q_1 = C_r^1 \left( \frac{1}{1 + ay_k} \right)^{r-1} \frac{ay_k}{1 + ay_k} = \frac{ray_k}{(1 + ay_k)^r}.$$

Taking it into account, we have the following equation for parasites dynamics:

$$y_{k+1} = Acx_k e^{-\alpha x_k} \frac{ray_k}{(1 + ay_k)^r}. \quad (5)$$

Combination of equations (3) and (5) gives us modified the May' model with over-infection effect. We have to note that similar idea was used in our previous publication (Ivanchikov and Nedorezov, 2011) for constructing of the modification of well-known Beddington – Free – Lawton model of parasite – host system dynamics.

Below we'll assume that coefficient of self-regulation in host population  $\alpha$  is greater than zero, and coefficient of parasite's efficiency  $a$  is positive too. Thus, without losing the generality of analysis we can put  $a = 1$  and  $\alpha = 1$ . Finally, the modified May model has the following form:

$$x_{k+1} = \frac{Ax_k e^{-x_k}}{(1 + y_k)^r},$$

$$y_{k+1} = \frac{Bx_k y_k e^{-x_k}}{(1 + y_k)^r}. \quad (6)$$

Parameter  $B = Acr > 0$ .

### 3 Properties of Model

Initial values of population sizes must be non-negative,  $x_0, y_0 \geq 0$ . Model (6) has the following properties:

1. If  $x_0 = 0$  and  $y_0 > 0$  then  $x_k \equiv 0$ ,  $y_k \equiv 0$  for all  $k > 0$ . If  $x_0 > 0$  and  $y_0 = 0$  then  $y_k \equiv 0$  for all  $k > 0$ ; in this case host dynamics describes by the Moran – Ricker model (Moran, 1950; Ricker, 1954).
2. Stable invariant compact  $\Delta$  exists in  $R_+^2$ :

$$\Delta \subset R_+^2 = \{(x, y) : x \geq 0, y \geq 0\}.$$

If  $(x_0, y_0) \in \Delta$  then for all  $k > 0$   $(x_k, y_k) \in \Delta$ . If  $(x_0, y_0) \notin \Delta$  then trajectory of model (6) converges to  $\Delta$  asymptotically (for  $r > 1$ ):

$$\Delta = \left[ Ae^{-1}, \frac{Be^{-1}(r-1)^{r-1}}{r^r} \right].$$

3. Coordinates of stationary states of system (6) can be found with the following system of algebraic equations:

$$x = \frac{Axe^{-x}}{(1+y)^r}, \quad y = \frac{Bxye^{-x}}{(1+y)^r}.$$

Stationary states have the following coordinates:

$$(0,0), (\ln A, 0), \left( \frac{A}{B}, \left( Ae^{-\frac{A}{B}} \right)^{\frac{1}{r}} - 1 \right).$$

Thus, within the framework of model (6) regimes of population mass outbreaks cannot be realized (Isaev et al., 1984, 2001, 2009).

4. Stationary state  $(0,0)$  is complex equilibrium. If  $A < 1$  this point is global stable equilibrium. In this case we have a regime of non-conditional extinction of both interacting populations. Intersection of bifurcation line  $A = 1$  at  $A > 1$  equilibrium  $(0,0)$  becomes a saddle type point with characteristic values  $\lambda_1 = A$  and  $\lambda_2 = 0$  (axis  $y$  is incoming trajectory, and axis  $x$  is out-coming trajectory). This intersection leads also to appearance of stationary state  $(\ln A, 0)$ .

5. Jacoby matrix determined in point  $(\ln A, 0)$  is following:

$$J(\ln A, 0) = \begin{pmatrix} 1 - \ln A & -r \ln A \\ 0 & \frac{B \ln A}{A} \end{pmatrix}.$$

Thus, characteristic numbers are following:

$$\lambda_1 = 1 - \ln A, \quad \lambda_2 = \frac{B \ln A}{A}.$$

Consequently, if the following inequalities are truthful the stationary state  $(\ln A, 0)$  is global stable equilibrium:

$$1 < A < e^2, B < \frac{A}{\ln A}, \quad (7)$$

If first inequality in (7) isn't truthful,  $A > e^2$ , and the second inequality in (7) is truthful, then stationary state  $(\ln A, 0)$  becomes unstable, and there appears global stable (in  $R_+^2$ ) attractor (cycle) on  $x$  axis.

6. The bifurcation curve which corresponds to appearance of third non-trivial stationary state in the phase space of system is determined by the equation:

$$Ae^{-\frac{A}{B}} = 1.$$

7. Dividing second equation of the system (6) onto the first equation we obtain the following relation:

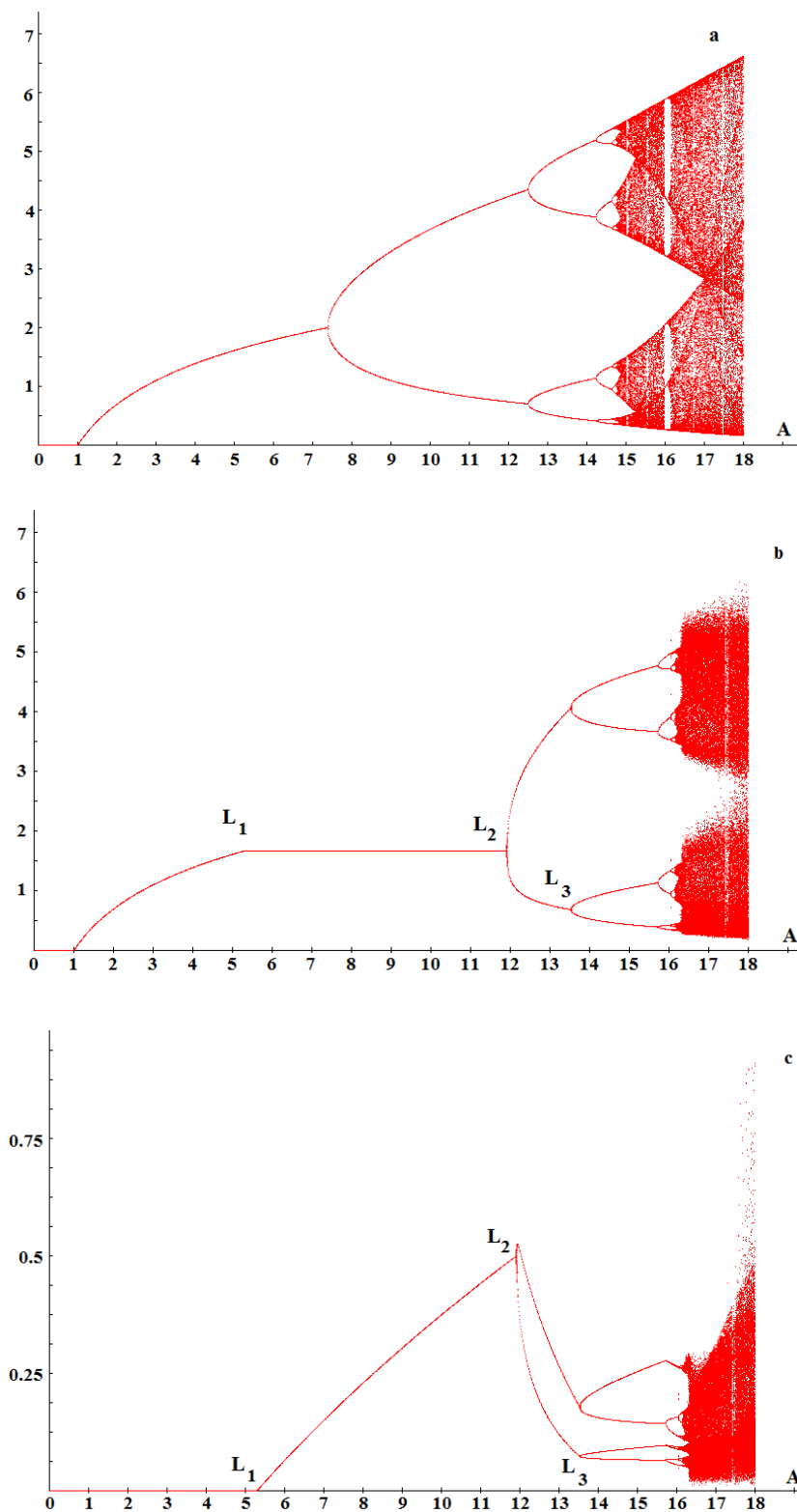
$$\frac{y_{k+1}}{x_{k+1}} = \frac{B}{A} y_k. \quad (8)$$

This relation is unrealistic equation from the standpoint of ecology: from this relation we have that fraction of two population sizes of the next generation is determined by current parasite population size. This formula (8) is direct result of unrealistic assumption in May model that number of attacked hosts is determined by size of parasite population only. Equation (8) can be presented in the form:

$$\frac{y_{k+1}}{x_{k+1}} = \frac{B^{k+1}}{A^{k+1}} y_0 \prod_{i=1}^k x_i.$$

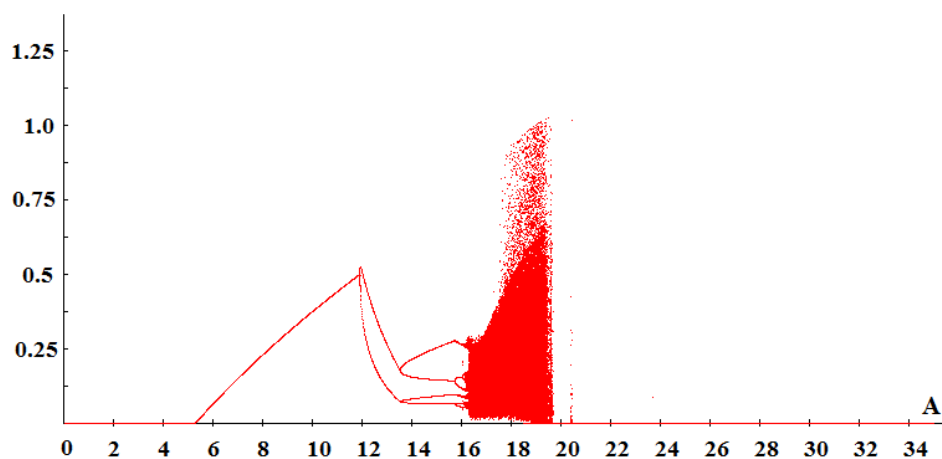
On figure 1 bifurcation diagrams are presented. Parameter  $A \in [0, 18]$ ,  $r = 2$ ,  $c = 0.3$ . The first bifurcation diagram describes the changing of stable dynamic regimes for host population fluctuations without parasites (in this situation bifurcation diagram of Moran – Ricker model is presented on fig. 1a; presentation of this diagram is important for comparison with diagram on fig. 1b and estimation of real role of parasites in population dynamics). On fig. 1c there is the diagram which describes the changing of stable dynamic regimes for parasite population. For obtaining all diagrams we used 400 initial points in  $\Delta$  (these points belong to plane lattice with constant step and cover domain  $\Delta$ ), and for every initial point (initial values of population sizes) we made 5000 “empty steps” (for stabilization of population fluctuations).

As we can see on these diagrams, parasites can play the role of stabilizer of ecological system: intersection of bifurcation value  $A \approx 5.2945$  (it is denoted as critical point  $L_1$  on fig. 1b and 1c) leads to the situation when increase of population birth rate (it can be a result of increase of productivity of individuals or increase of surviving) doesn't lead to increase of stationary level of population. Note that such a zone (it was called as zone of strong control of population by parasites; Isaev et al., 1984, 2001, 2009) is observed in natural conditions. For example, it was observed in interaction of *Ips subelongatus* Motsch. with its parasites in Siberian forests (Isaev et al., 1984).



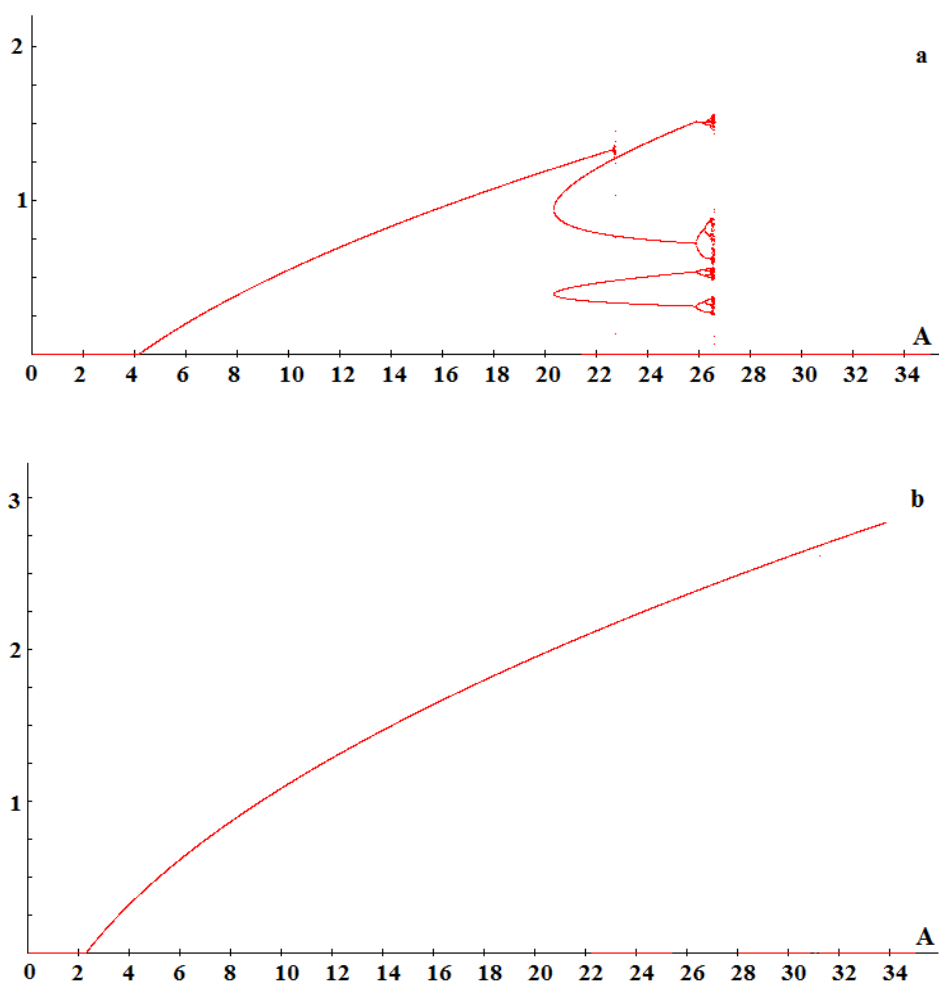
**Fig. 1** Bifurcation diagrams for model (6) for  $r = 2$ ,  $c = 0.3$ . a – diagram for Moran – Ricker model. b – changing of coordinates of stable attractors for host population size; c – changing of stable attractors for parasite population size. Coordinates of stable attractors are of the red color.

Further increasing of birth rate leads to loosing of the control role of parasites: after the intersection of critical point  $L_2$  (Fig. 1b and 1c) we can observe the cyclic regime for interacting populations (with the length 2). It is interesting to note that increasing of the range of host population fluctuations leads to decreasing of both coordinates of the cycle 2 for parasites. After the intersection of critical level  $L_3$  the cycle of the length 4 appears in phase space (Fig. 1b and 1c). After this intersection we can observe increasing of maximum of parasite population size in ecosystem. Further increasing of the value of parameter  $A$  leads to strong increasing of the range of parasite population fluctuations.



**Fig. 2** Bifurcation diagrams for model (6) under the same conditions (changing of stable attractors for parasite population size). Coordinates of stable attractors are of the red color.

On Fig. 2 there is the same diagram like on Fig. 1c but the interval of changing of parameter  $A$  is bigger. As we can see on this figure, further increasing of the value of parameter  $A$  leads to the realization of a situation when parasites eliminate for every positive initial values of their size. Such (rather strange) effect was also observed in a modification of Beddington – Free – Lawton model of parasite – host system dynamics (Ivanchikov, Nedorezov, 2011). We cannot exclude the hypothesis that this effect appears in a result of incorrect assumptions in the base of May model and Beddington – Free – Lawton model pointed out above. On the other hand, it can be pure dynamic effect – elimination of parasites is determined by the cyclic fluctuations of hosts with sufficient big number of values with low population size.



**Fig. 3** Bifurcation diagrams for model (6) for  $r = 2$ . a –  $c = 0.35$ , b –  $c = 0.6$ .

Further increasing of value of parameter  $c$  (Fig. 3) leads to the increase of the domain where parasites play the role of strong stabilizer of ecosystem, interval  $[L_1, L_2]$ . For some values of model parameters we can see interesting dynamic regimes (Fig. 3a) when we have three stable attractors in the phase space: non-trivial stationary state, origin, and stable cycle with the length 4. Existing in positive part of phase plane of two stable attractors allows us to assume that within the limits of discrete models we may have analogs of fixed outbreaks. And these analogs have one non-trivial stationary state in the phase space. Note that analogs of various types of outbreaks with one stationary state we may also have in models with continuous time when hosts or parasites are the fast variables with respect to another one (Nedorezov, 1986; Nedorezov and Khlebopros, 1985).

On Fig. 3b we can also observe the realization of trigger dynamic regimes with two stable stationary states in phase space. Such kind of regimes can be identified as fixed outbreak, and can be realized in natural conditions for *Xylotrechus altaicus* Gebl. In Siberian forests (Isaev et al., 1984, 2001, 2009).



#### 4 Conclusion

Analysis of modified May model of parasite – host system dynamics shows that in model can be realized complicated dynamical regimes, and, in particular, cycles of various length (Fig. 1 and 2). Numerical analysis of model allows us to conclude that in most cases parasites play the role of stabilizer of the system: without the parasites we can observe cyclic fluctuations of hosts (with increase of its unstable stationary state; Fig. 1a), and stable behavior of hosts when parasites appear in the system (Fig. 1b).

Increase of surviving of parasites can lead to the transformation of initially complicated dynamical regime to much simpler regime. Sometimes it can lead to the regime with one global stable equilibrium in positive part of phase space, sometimes we can observe trigger regimes with two stable attractors (see Fig. 3b). Such kind of regimes can be identified as direct analogs of fixed outbreak regime, which can be observed for some species of forest insects.

It is also important to point out very interesting dynamical regime which can be observed in model at increase of productivity of hosts. Increase of the value of the respective parameter at fixed value of other parameters of the model leads to asymptotic extinction of parasites for all positive initial values of interacting populations (Fig. 2 and 3a).

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