Article

Continuous-discrete model of parasite-host system dynamics: Trigger regime at simplest assumptions

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Abstract
In paper continuous-discrete model of parasite-host system dynamics is analyzed. Within the framework of model it is assumed that appearance of individuals of new generations of both populations is realized at fixed time moments $t_k = hk$, $t_0 = 0$, $k = 1,2,...$, $h = const > 0$; it means that several processes are compressed together: producing of eggs by hosts, attack of eggs by parasites (with respective transformation of host's eggs into parasite's eggs), staying of hosts and parasites in phase "egg", and appearance of new individuals. It is also assumed that death process of individuals has a continuous nature, but developments of both populations are realized independently between fixed time moments. Dynamic regimes of model are analyzed. In particular, it was obtained that with simplest assumptions about birth process in host population and numbers of attacked hosts regime with two non-trivial stable attractors in phase space of system can be realized.

Keywords parasite-host system dynamics, mathematical model.

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1 Introduction

Dynamics of parasite-host system is analyzed in a lot of various publications (Nicholson and Bailey, 1935; Kostitzin, 1937; Maynard, 1968, 1974; Beddington et al., 1975; Isaev et al., 1984, 2001, 2009; Kot, 2001; Brauer and Castillo-Chavez, 2001; Nedorezov, 1986, 1997, 2012; Elhassanein, 2014; Nedorezo and Sadykov, 2012; Elsadany et al., 2012; Ivanchikov and Nedorezov, 2012 and many others). Dynamics of this system can be described with the help of ordinary differential equations or recurrence equations, and in most cases there are no differences between parasite-host and predator-prey systems. It depends on the level of generality of description of a process of interaction between species. But in the case of use of continuous-discrete models (Kostitzin, 1937; Nedorezov, 1986, 1997, 2012) we have to divide between these qualitatively different cases.
As it was demonstrated in our previous publications (Nedorezov, 2012; Nedorezov and Utyupin, 2011) rather

realistic description of predator-prey system dynamics leads to necessity in introduction of one more variable into model which corresponds to volume of consumed food or level of saturation of predators. Productivity process in population of predators may depend on average of level of saturation during a certain time interval. At the same time for some particular cases (for example, for forest insects with one-year generations in boreal zone; Isaev et al., 1984, 2001, 2009) process of interaction between species is realized during short time interval, and it can be described as a “jump” of model trajectory. Between these time moments (moments of “jumps”) there are no interactions between species, and their dynamics can be described independently. It allows integrating of differential equations and deducing of model to system of recurrence equations.

2 Model

Let $x(t)$ and $y(t)$ be the numbers of hosts and parasites respectively at time t. We’ll assume that developments of both populations are realized in one-year generations at fixed time moments $t_k = hk$, $k = 0,1,2...$, $h = const > 0$. Respectively, appearance of individuals of new generation correlates with death of all individuals of previous generation. Let $x(t_k - 0)$ be a number of hosts survived to moment t_k, and $y(t_k - 0)$ be a number of parasites at the same time moment.

We will also assume that at moments t_k survived hosts produce eggs with a certain rate. Let Y be an average of number of eggs produced by one survived host. Thus number of produced eggs E_k will be determined by the following expression:

$$E_k = Yx(t_k - 0).$$

Below we’ll analyze a situation when $Y \equiv const > 1$. It is obvious if the inverse inequality is truthful both populations extinct for all initial values of populations.

Let’s also assume that at moments t_k parasites attack host’s eggs, and denote as P a quota of infected eggs. Thus, $Yx(t_k - 0)P$ is equal to total number of infected eggs. Additional assumption is following: every infected egg was attacked by only parasite, and every infected egg can be transformed into one parasite at moment t_k.

We have to assume that P is determined on numbers of hosts and parasites survived to moment t_k: $P = P(u,v)$ where $u = x(t_k - 0)$, $v = y(t_k - 0)$. Following the biological sense of function P next conditions must be truthful:

1. For fixed value of hosts increase of number of parasites $v = y(t_k - 0)$ leads to monotonic increase of function P, and P is equal to one asymptotically:

$$\frac{dP}{dv} > 0, \ \lim_{v\to\infty} P(u,v) = 1.$$

2. If $y(t_k - 0) = 0$ quota of infected hosts P is equal to zero too:

$$P(u,0) = 0.$$

3. For fixed number of parasites increase of number of hosts leads to monotonic decreasing of quota of infected hosts P, and under unlimited growth of amount u function P converges to zero asymptotically. At these conditions number of infected hosts is determined by a number of survived parasites and their potential activity:

$$\frac{dP}{du} < 0, \ \lim_{u\to\infty} P(u,v) = 0, \ \lim_{u\to\infty} YuP(u,v) = \mu v.$$

Parameter $\mu > 1$ describes potential possibilities of parasites to infection of host’s eggs, and it is equal to maximum number of eggs which can be infected by one parasite. It is obvious, if $\mu < 1$ for all values of other model parameters number of parasites converges to zero asymptotically for all initial values of populations.

In simplest case P can be presented in the following form:

$$P(u,v) = \frac{\mu v}{q + Yu + \mu v}.$$

Amount of parameter $q = const > 0$ depends on conditions for parasites in their search of host's eggs. Increase of value of this parameter q leads to decrease of number of attacked hosts.

We have to note that assumption about monotonic behavior of function P isn't obligatory. In general case we have to assume that for every fixed number of hosts it is possible to point out a certain number of parasites when function P has its maximum. Further increasing of parasites leads to decrease of this function that can be explained as a result of influence of over-infection effect.

We'll also assume that sojourn time of individuals in phase "egg" and "infected egg" is rather small, and there is no necessity to consider respective processes in model. Thus, we'll assume that transformation of eggs into adults of new generation is realized at moment t_k. Finally, we'll assume that at moments t_k we have following relations for adults for hosts and parasites:

$$x_k = Yx(t_k - 0)(1 - P(x(t_k - 0), y(t_k - 0))),$$

$$y_k = cYx(t_k - 0)P(x(t_k - 0), y(t_k - 0)). \qquad (1)$$

In (1) coefficient c, $0 < c \le 1$, is equal to quota of successfully transformed eggs from all infected host's eggs.

It is naturally to assume that between selected time moments t_k there are no interactions between hosts and parasites: this is one of basic differences between parasite-host and predator-prey systems. Moreover, on time intervals $[t_k, t_{k+1})$ we can observe monotonic decreasing of population's sizes which we'll correspond to Verhulst' law (Verhulst, 1838):

$$\frac{dx}{dt} = -\alpha_1 x - \beta_1 x^2;$$

$$\frac{dy}{dt} = -\alpha_2 y - \beta_2 y^2. \qquad (2)$$

Conditions (1) are initial values for system (2) for every interval $[t_k, t_{k+1})$. Integration of system (2) on interval $[t_k, t_{k+1})$ with initial conditions (1), $x(t_k) = x_k$, $y(t_k) = y_k$, gives the following results:

$$x(t_{k+1} - 0) = \frac{x_k}{a_1 + b_1 x_k}, \quad y(t_{k+1} - 0) = \frac{y_k}{a_2 + b_2 y_k}.$$

New parameters are determined by the following relations:

$$a_i = e^{\alpha_i h}, \; b_i = \frac{\beta_i}{\alpha_i}(e^{\alpha_i h} - 1).$$

Taking into account expressions (1) and expression for function P we obtain the following system of recurrence equations:

$$x_{k+1} = \frac{Yx_k}{a_1 + b_1 x_k} - \frac{Y\mu x_k y_k}{q(a_1 + b_1 x_k)(a_2 + b_2 y_k) + Yx_k(a_2 + b_2 y_k) + \mu y_k(a_1 + b_1 x_k)},$$

$$y_{k+1} = \frac{cY\mu x_k y_k}{q(a_1 + b_1 x_k)(a_2 + b_2 y_k) + Yx_k(a_2 + b_2 y_k) + \mu y_k(a_1 + b_1 x_k)} . \quad (3)$$

3 Properties of Model

3.1 For non-negative and finite initial values of populations x_0 and y_0 trajectories of model (3) are non-negative and bounded.

3.2 If initial number of parasites is equal to zero, $y_0 = 0$, number of hosts changes with respect to Kostitzin' law (Kostitzin, 1937): if $x_0 > 0$ and $Y > a_1$ population size stabilizes at non-zero level $(Y - a_1)/b_1$; if $Y < a_1$ then population extinct for all initial values of population size. Note, if inequality $Y < a_1$ is truthful origin is global stable equilibrium of system (3).

3.3 If inequality $Y > a_1$ is truthful system (3) has stationary state on x-line $(D,0)$ where D can be found from equation

$$D = \frac{YD}{a_1 + b_1 D}.$$

Thus $D = (Y - a_1)/b_1$. Jacobi matrix calculated for point $(D,0)$ has the following form:

$$J(D,0) = \begin{pmatrix} \frac{a_1}{Y} & \frac{\mu D}{a_2(q+D)} \\ 0 & \frac{c\mu D}{a_2(q+D)} \end{pmatrix}.$$

Eigenvalues of matrix $J(D,0)$ are following:

$$\lambda_1 = \frac{a_1}{Y}, \quad \lambda_2 = \frac{c\mu D}{a_2(q+D)}.$$

Consequently, $\lambda_1 < 1$. If the following inequality is truthful $(D,0)$ is stable stationary state:

$$c\mu D < a_2(q+D).$$

If the inverse inequality is truthful in last expression there are one or three non-trivial stationary states in phase space of system (3).

3.4 Numerical analysis of model (3) shows that in spite of simplest assumptions about self-regulations, birth processes, and interaction between populations complicated dynamic regimes can be realized. On figure 1 bifurcation diagram calculated for $a_1 = 92$, $b_1 = 1.1$, $a_2 = 1.2$, $b_2 = 8$, $\mu = 100$, $c = 0.5$, $q = 0.01$ (ordinate line corresponds to coordinates of stable attractors for number of hosts; before printing of 200 points model had 1500 steps of free work) is presented.

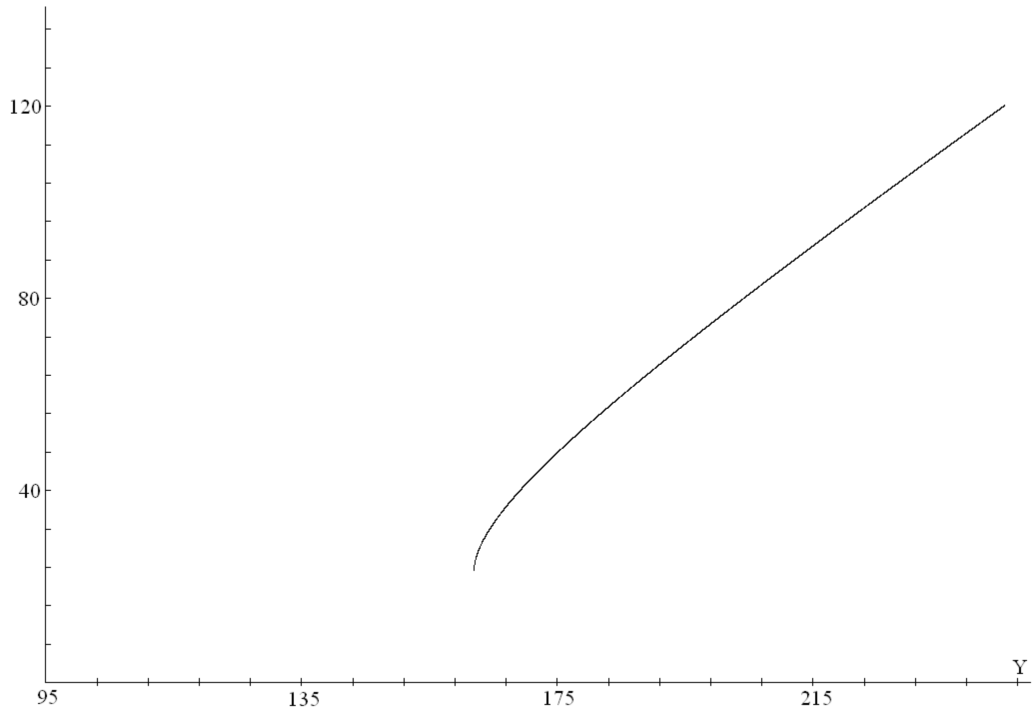

Fig. 1 Bifurcation diagram for model (3): $a_1 = 92$, $b_1 = 1.1$, $a_2 = 1.2$, $b_2 = 8$, $\mu = 100$, $c = 0.5$, $q = 0.01$.

Scale on Fig. 1 doesn't allow seeing part of bifurcation diagram (see Fig. 2) corresponding to rather small values of stable attractors. As we can see on these pictures 1 and 2 increase of productivity of hosts Y can lead to appearance in phase space one more stable attractor – trigger regime. It corresponds to situation when productivity Y becomes bigger than threshold level, and under these condition parasites can lose their regulative role. It is also determined by initial values of population sizes. Such effects are observed for some species of forest insects (Isaev et al., 1984, 2001, 2009).

Numerical analysis of structure of lower attractor (1500000000 steps of free work of model) for the same model parameters shows (see Fig. 3) that in this part of phase plane we observe periodic fluctuations of populations. It is interesting to note that this attractor looks like stable cycle for two-dimensional system of ordinary differential equations. In a result of it down part of bifurcation diagram has specific structure (black color only). Values of autocorrelation function (calculated for 20000 steps) are close to one (but these values don't equal to one), and maximum values are observed after 21-23 steps of function argument.

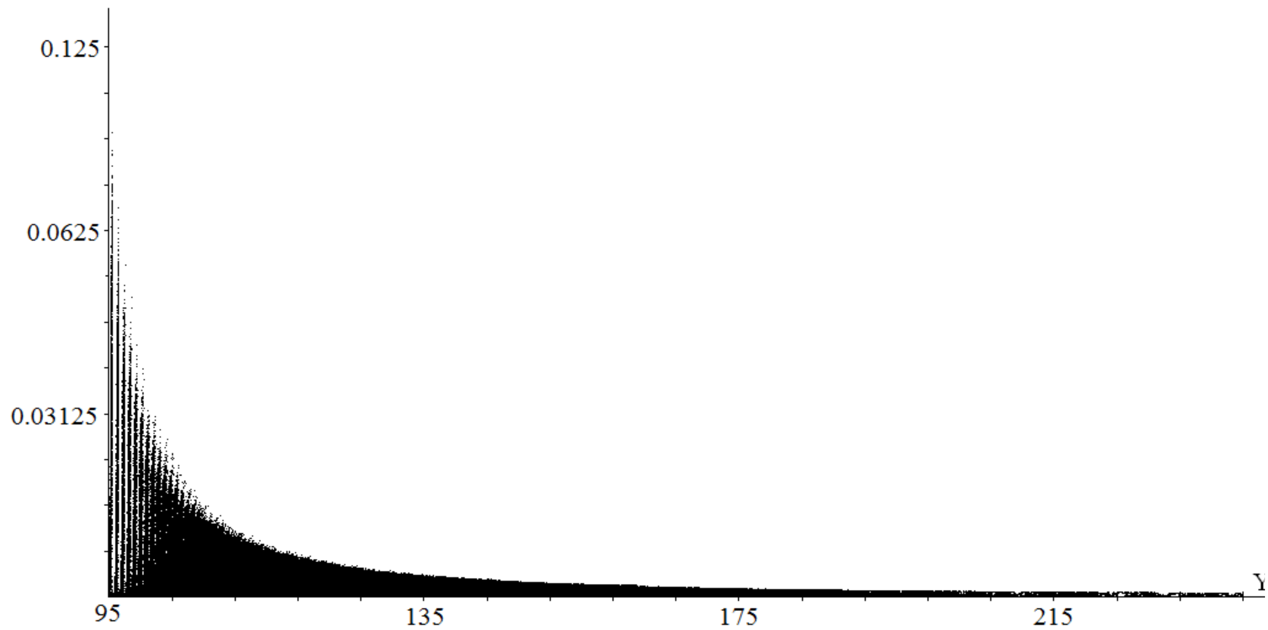

Fig. 2 Part of bifurcation diagram obtained for the same values of model parameters.

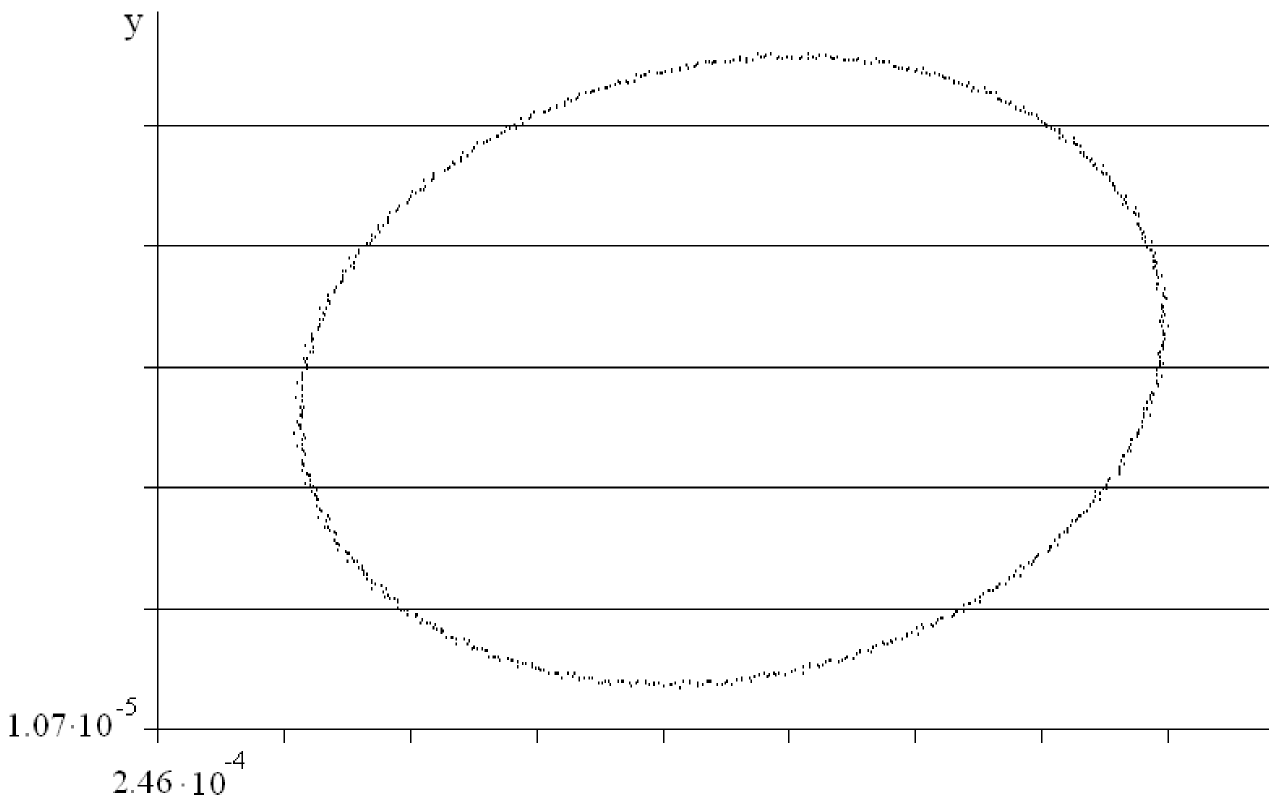

Fig. 3 Cyclic fluctuations of both populations on plane (x, y). Step along abscissa is equal to $5.0 \cdot 10^{-17}$. Step along ordinate line is equal to 10^{-18}. On picture there are 20000 points of model trajectory.

4 Conclusion

Analysis of model shows that influence of parasites can lead to realization of complicated dynamic regimes in phase space which can contain, for example, two stable attractors. Realization of these dynamic regimes is a result of influence of parasites: if initial number of parasites is equal to zero number of hosts stabilizes monotonously at determined finite level. It is very important to note that realization of these dynamic regimes was observed under very simple assumptions about acting of self-regulative mechanisms in both population, about productivity of hosts (it was assumed to be a constant), and process of interaction between species. We have also to note that close dynamic regimes are observed for some species of forest insects in boreal zone (Isaev et al., 1984, 2001).

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