About a model of population dynamics with time lag in birth process

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Key words: mathematical model of isolated population dynamics, differential equation with time lag

Abstract. In current publication mathematical model of isolated population dynamics is considered. It is assumed that birth process and death process have continuous nature but appearance of new individuals depends on population size at previous time moments. Dynamics regimes of model are analyzed. It is proved that within the framework of model oscillation regimes are absent.

Introduction

One of interesting and important questions in modern mathematical ecology concerns the problem of creating of philosophical background for one of very popular models. This is the Hutchinson' model (Hutchinson, 1947, 1948):

$$\frac{dx}{dt} = r\left[1 - \frac{x(t-h)}{K}\right]x(t).\qquad(1)$$

In model (1) t is continuous variable (time), $x(t)$ is population size at moment t, r, h and K are non-negative parameters of model. It is assumed that r is Malthusian parameter, K is non-trivial stationary state, and h is time lag argument. Sometimes K is announced as carrying capacity but it looks incorrect: within the framework of model (1) population size can intersect this level and save positive derivative for certain time. Creating of philosophical background for Hutchinson' model is important because in modern literature it is possible to find a lot of various models (modifications of model (1), predator – prey systems etc.) which are based on model (1).

When we are talking about philosophical background we think, first of all, about correct biological interpretation of model parameters and biological sense of functions in right-hand side of considering equation (Wangersky, Canningham, 1957; Cooke, van der Driessche, Zou, 1999; Kolesov, 1980, 1981; Baker, 2000; Brauer, 1977 and others). But before discussing problems of interpretations of model parameters it is important to say some words about time lag itself. Partly "time lag" is a *stone of misunderstanding* between mathematicians and ecologists.

Biggest part of researches assume that time lag is dependence of speed of changing of population size in time on own population sizes at previous time moments (Volterra, 1931; Kolesov,

1980, 1981; Berryman, 2002, 2003; Kendall et al., 1999 and many others). At the same time it is possible to point out other opinion on time lag in reaction of biological mechanisms (Isaev et al., 1984, 2001, 2009). We can talk about time lag like about a time of returning back (to previous stationary state after disturbance) of population system under influence of regulative mechanisms. Both groups of researches assume that time lag in reaction of population regulative mechanisms plays most important role in population dynamics. This property of regulative mechanism (time lag in reaction on population size changing) is in bases of some ecological theories.

Let's note that two approaches to understanding of reaction of regulative mechanisms are not equal to each other. In the first case, for example, for description of population size dynamics ordinary differential equations with lumped-lag and distributed-lag arguments can be used (Hutchinson, 1947, 1948; Volterra, 1931; MacDonald, 1976; Nedorezov, 1997, 2012; Nedorezov, Utyupin, 2003, 2004, 2005, 2011). It has also direct relation to recurrence equations with time lag (Gonzales-Andujar, Hughes, 2000; Kipnis, Nigmatulin, 2003; Bjornstad et al., 1999, 2001; Stenseth et al., 1998, 1999; Sadykova, Nedorezov, 2013). But in the second case we *can use* ordinary differential equations without time lags.

Let's assume that dynamic of population system is described by ordinary differential equations, and let's consider a situation when population system was pushed out from ε-neighborhood of stable stationary state (for example, by influence of modifying factors). It is obvious that regulative mechanisms cannot return system back to ε-neighborhood immediately, and they need in certain time to do it. Time of returning back will depend on amount of ε, on amount of deviation etc. In all cases it will not be a constant.

We have to note that both types of time lag can be observed in one and the same model. But it leads to problem in understanding of various situations – what's type of time lag we are talking about? And does it correctly to take into account within the framework of mathematical model?

Let's try to discuss real biological sense of components of the equation (1). Increase of amount of $x(t-h)$ leads to decrease of relative speed of population size changing $\dot{x}/x$. Thus, it allows concluding that this component describes an influence of self-regulative mechanisms on population dynamics. In a situation when $x(t-h)$ describes the lag in a process of appearance of new individuals and equals to number of individuals which can produce these individuals, then increase of amount of $x(t-h)$ must lead to respective increase of birth rate. Consequently, very popular interpretation that this component of equation corresponds to lag in reproduction process, must be marked as incorrect explanation from biological point of view.

After opening the brackets in (1) we can see that Hutchinson' model is a direct modification of Verhulst' model (Verhulst, 1838):

$$\frac{dx}{dt} = rx(t) - \frac{r}{K} x(t)x(t-h).$$

Non-negative parameter r is equal to difference between intensity of birth rate and intensity of death rate. Within the framework of original Verhulst' model this parameter can be negative – if it is truthful population eliminates for all non-negative initial values of population size. In Hutchinson' model this parameter must be positive – relation r/K is coefficient of self-regulation. Process of self-regulation is described by the expression $x(t)x(t-h)$ - it leads to appearance of natural question: what kind of real biological process can be described by this expression?

Within the framework of Verhulst' model respective expression is equal to x^2 and this amount is proportional to speed of interactions between individuals. Within the framework of Hutchinson model (1) this component of equation describes interaction of existing individuals with individuals lived $t-h$ time moments ago (it looks like Hutchinson's horror film – individuals interact with dead individuals, and it determines population dynamics). It is obvious that such interpretation and explanation of components of equation (1) are not acceptable. Individuals can interact with survived individuals only. New question is following: what is the amount of survived individuals? Does it proportional to $x(t-h)$? What's a background for this conclusion?

Let's note that number of survived individuals doesn't equal to $x(t-h)$ because for death process we have a non-linear law. But if we assume (or postulate) that number of survived individuals is equal to this amount $x(t-h)$ it means that we assume that individuals in population live with two qualitatively different laws at one and the same time.

In literature it is possible to find one more variant of explanation of applicability of Hutchinson equation (1) to description of population dynamics (Svirezhev, Logofet, 1978). Author's assumption is following: component with time lag describes influence of previous generation on a current generation. In particular, it can be competition between "young" and "old" individuals – if it is true, h can be a time of living of one generation.

But we cannot say that presented view on considering problem is a satisfactory explanation. If $x(t)$ is total population size at moment t, $x(t-h)$ is the same total size at moment $t-h$, how we can conclude that product $x(t)x(t-h)$ describes a process of interaction of pointed out subgroups in population at moment t? Thus, this discussed assumption leads to appearance to one more problem: before we had a problem with number of survived individuals (which isn't proportional to $x(t-h)$), and now we get a problem with determination of sizes of subgroups of young and old individuals in population. We have no reasons to assume that model (1) is rather universal and describes population dynamics *for all variants of dividing* of population on subgroups. If it is true model (1) can be simply

deduced from von Voerster' model (von Voerster, 1959) of population dynamics with continuous age structure. But up to now nobody presented these results.

There exists one more important question: what is a background for assumption about dependence of population speed growth on fixed time moment $t - h$? If model (1) describes an influence of individuals of previous generation on dynamics of current generation it is naturally to assume that it has a direct relation to accumulation of poisons in system, to influence of previous generation on volume of suitable food during a certain time interval and so on. But it will lead to necessity to use a model with *distributed lag*.

J. Maynard Smith (1968, 1974) presented the following explanation for expressions in model (1). If volume of resources decreases monotonously at increasing of population size, such a situation can be described by Verhulst' model; but in real population system resources can be restored, thus real level of resources must depend on population size at time moment $t - h$. In this occasion h is time of species' development which is play a role of resource.

For obtaining a good background for this explanation of model components, first of all, we have to construct a respective model of resource – consumer system dynamics. The next step is following: we have to deduce Hutchinson' model from this constructed model. This is unobvious situation: existing models of predator – prey system dynamics (based on systems of ordinary differential equations) don't allow obtaining of Hutchinson' equation (for example, in a result of decreasing of order of system assuming that one of variables is fast or slow). Thus, the question about respective model of resource – consumer system dynamics which allows deducing of Hutchinson' model is open.

Now we can conclude that Hutchinson' model hasn't simple, obvious and concrete biological interpretation of its components (like Malthus' model or Verhulst' model). May be, the following interpretation is the best one: model (1) is non-balanced model and separated components haven't biological interpretations. At the same time we cannot exclude hypothesis that models of (1) type are not applicable to the description of population dynamics at all. At the same time models with distributed lags (Volterra, 1931 and many others) are effective instruments in analysis of population dynamics.

Discussion of problem of biological interpretation of components of Hutchinson' model (1) showed that there is a lot of serious problems without obvious answers. It allows concluding that up to current moment this scientific direction (Cooke, van der Driessche, Zou, 1999; Baker, 2000; Brauer, 1977; Guckenheimer, Oster, Ipaktchi, 1977; Blythe, Nisbet, Gurney, 1982 and many others) hasn't a serious biological background. Existence of big number of possible interpretations isn't a characteristics of variety of applications of models of (1) type – this is indicator of absence of serious biological interpretations.

It doesn't mean that models of (1) type are not interesting for theory of population dynamics. Models with distributed lags can be reduced to ordinary differential equations with time lag after transformation of variables. Moreover, it is possible to point out equations with time lag with obvious biological interpretation. For example, it is the following equation with lag in birth process:

$$\frac{dx}{dt} = f(x(t-\tau)) - g(x(t)). \tag{2}$$

In model (2) $x(t)$ is population size at time moment t; function f describes a process of population size increasing; function g describes a process of death of individuals in population. Time lag in equation (2) corresponds to following population process. In population at every time moment we have individuals of two various types (or phases of development). For example, we have adults (and their number is denoted as $x(t)$) and eggs. Adults permanently produce eggs, and living process and transformation of eggs into adults don't depend on amount $x(t)$. It allows us concluding that staying of individuals in phase "egg" is finite, fixed, and equal to τ. Moreover, number of survived eggs and transformed into adults is proportional to number of produced eggs, but number of produced eggs is proportional to respective number of adults.

Non-negative functions f and g in (2) must correspond to following obvious conditions:

$$f(0) = g(0) = 0, \ \frac{dg}{dx} \geq 0, \ f(x) \xrightarrow[x \to \infty]{} 0.$$

In particular case function g can be linear. Function f can be non-monotonic function, for example, in a case when Allee' effect is observed in population (Allee, 1931).

Equation (2) with different functions f and g was used many times for description of various population processes (see, for example, Guckenheimer, Oster, Ipaktchi, 1977; Blythe, Nisbet, Gurney, 1982; Levin, Goodycar, 1980). It was also used for description of dynamics of bloody red cells, various physiological processes, forest dynamics and so on (Chow, 1974; Mackey, Glass, 1977; Glass, Mackey, 1979; Mackey, 1979; Heiden, Mackey, 1982; Dzhanseitov K.K., Kuzmichev V.V., Kibardin Yu.V., 1976).

Model

Let's consider the following model of isolated population dynamics. It will be assumed that birth process and death process of individuals in population have continuous nature. Additionally we'll assume that birth rate depends on population size it was τ moments ago and survived to current time moment. Let's assume that that population dynamics is described by the following equation (Verhulst' model; Verhulst, 1838):

$$\frac{dx}{dt} = (\alpha_1 - \alpha_2)x - \beta x^2. \tag{3}$$

In equation (3) $x(t)$ is population size at moment t; coefficient α_1 is an intensity of birth rate; coefficient α_2 is an intensity of death rate; parameter β is coefficient of self-regulation. Let's assume that coefficients α_2 and β are constants, $\alpha_2, \beta = const > 0$, and death speed is described by the following equation:

$$\frac{dx}{dt} = -\alpha_2 x - \beta x^2. \tag{4}$$

Let's $\xi(t)$ be a number of individuals at moment t which lived τ moments ago and survived to considering time moment. Let

$$x(t-\tau) = \xi(t-\tau) = \xi_0. \tag{5}$$

On time interval $[t-\tau, t]$ dynamics of variable $\xi(t)$ must correspond to general law (4) because it is truthful for all individuals. Thus, we have the following equation:

$$\frac{d\xi}{dt} = -\xi(\alpha_2 + \beta x). \tag{6}$$

For Cauchy problem (5)-(6) we have the following solution which gives us the number of survived individuals to moment t:

$$\xi(t) = \xi_0 e^{-\alpha_2 \tau - \beta \int_{t-\tau}^{t} x(s)ds} = x(t-\tau)e^{-\alpha_2 \tau - \beta \int_{t-\tau}^{t} x(s)ds}. \tag{7}$$

Now we can put expression (7) into equation (3) and obtain model of population dynamics with finite time of development of birth process:

$$\frac{dx}{dt} = \alpha_1 x(t-\tau)e^{-\alpha_2 \tau - \beta \int_{t-\tau}^{t} x(s)ds} - \alpha_2 x - \beta x^2. \tag{8}$$

For correct presentation of mathematical problem we have to point out initial conditions: $x(t) = \phi(t) > 0$ for $t \in [-\tau, 0]$, $\phi(t) \in C_{[-\tau, 0]}$. We'll assume that there are no immigration of emigration processes in system. Thus, on time interval $[-\tau, 0]$ we cannot have values of argument t when population size is equal to zero, $x(t) = \phi(t) = 0$: inverse assumption is in contradiction with absent of migration processes in system.

After transformation of variables in (8), $t = \tau t'$, $y = \beta \tau x$, we obtain the model with smaller number of parameters:

$$\frac{dy}{dt'} = Ay(t'-1)e^{-B - \int_{t'-1}^{t'} y(s)ds} - By - y^2. \tag{9}$$

Initial conditions for (9) will change too:

$$y(t') = \rho(t') > 0 \text{ for } t' \in [-1,0], \ \rho(t') \in C_{[-1,0]}. \tag{10}$$

Below we'll write t instead of t' for equation (9) and conditions (10).

Properties of model (9)-(10)

For all values of model (9) parameters stationary state $y = 0$ exists. If the following inequality is truthful

$$A > Be^B \tag{11}$$

non-trivial stationary state $y \equiv \overline{y}$ exists in phase space; $\overline{y}$ is a solution of the following algebraic equation:

$$Ae^{-B-y} - B - y = 0.$$

Note that following relation is truthful:

$$\left. \frac{dy}{dt} \right|_{y=0} = Ay(t-1)e^{-B-\int_{t-1}^{t} y(s)ds}.$$

It follows from conditions (10) (initial function must be positive), and from obvious property: function in right-hand side is non-negative at $y = 0$. Thus, solutions of equation (9) are non-negative for positive initial functions.

Let's prove the following property of solutions of model (9)-(10): all solutions are limited. For this reason let's consider the following equation:

$$\frac{dy}{dt} = Ay(t-1) - By - y^2. \tag{12}$$

We'll assume that equation (12) has the same initial conditions (10). It is obvious that solutions of equation (12) majorize solutions of equation (9). Thus, we have to prove that solutions of equation (12) are bounded.

Equation (12) has two stationary states $y = 0$ and $y = A - B$. Second stationary state exists if the following inequality is truthful $A > B$. If inequality $A \leq B$ is truthful it is easy to show that $y \to 0$ at $t \to \infty$. Thus, we can observe a regime of population extinction for all initial values if inequality $A \leq B$ is realized for model parameters. Let

$$r_0 = \max_{t \in [-1,0]} \rho(t).$$

Solutions of the following Cauchy problem

$$\frac{dy}{dt} = Ar_0 - By - y^2, \ y(0) = r_0 \tag{13}$$

majorize solutions of Cauchy problem (12), (10). Solutions of equation (13) converge asymptotically to level r_1. For this amount r_1 next inequality is truthful:

$$r_1 = -\frac{B}{2} + \sqrt{\frac{B^2}{4} + Ar_0} < r_0.$$

For sufficient big value of t we can consider following Cauchy problem:

$$\frac{dy}{dt} = Ar_1 - By - y^2, \ y(0) = r_1.$$

Thus, we can get a sequence of values r_0, r_1,..., which converges to zero:

$$\lim_{k \to \infty} r_k = 0.$$

It allows concluding that all solutions of equation (9) converge to zero if inequality $A \le B$ is observed for model parameters.

Let $A > B$. If for initial function the following inequality is truthful $\rho(t) \le A - B$ then

$$\left.\frac{dy}{dt}\right|_{y=A-B} = A(y(t-1) - (A-B)) \le 0.$$

It allows concluding that all solutions with initial functions from the band $(0, A-B]$ cannot intersect boundaries of this band. Let

$$R_0 = \max_{t \in [-1,0]} \rho(t) > A - B.$$

With the help of method described above it is possible to prove that solution converges to $A - B$. It gives requirement result that solutions are limited.

Let's introduce a new variable:

$$I = B + \int_{t-1}^{t} y(s)ds.$$

Taking into account this new variable equation (9) transforms into following system of ordinary differential equations with time lag:

$$\frac{dy}{dt} = Ay(t-1)e^{-I} - By - y^2,$$

$$\frac{dI}{dt} = y(t) - y(t-1). \tag{14}$$

Initial conditions will have the following forms:

$$y(t) = \rho(t) > 0 \text{ at } t \in [-1,0], \ \rho(t) \in C_{[-1,0]}, \ I(0) = B + \int_{t-1}^{t} \rho(s)ds. \tag{15}$$

System (14) is standard system of ordinary differential equations with time lag. It was proved above that solutions are limited and, respectively, solutions of problem (14)-(15) exist and unique for

all $t > 0$. System (14) has stationary state $(0, B)$ (it corresponds to origin of equation (9)) and $(\bar{y}, \bar{I})$ (it corresponds to non-trivial stationary state of equation (9)). Point $(0, B)$ is stable if the inequality $A \leq B \exp(B)$ is truthful. And this point is unstable if the inverse inequality is realized for model parameters.

Characteristic equation for system (14) near stationary state $(0, B)$ is following:

$$Ae^{-B-\lambda} - B - \lambda = 0.$$

If inequality $A > B \exp(B)$ is truthful this characteristic equation has real positive root. If $A \leq B \exp(B)$ is realized for model parameters characteristic equation hasn't roots with positive real parts.

System (14) near stationary state $(\bar{y}, \bar{I})$ has the form:

$$\frac{dy}{dt} = (-B - 2\bar{y})y + Ae^{-\bar{I}} y(t-1) - A\bar{y}e^{-\bar{I}} I,$$

$$\frac{dI}{dt} = y(t) - y(t-1).$$

This system can be presented in other form:

$$\frac{dy}{dt} = (-B - 2\bar{y})y + (B + \bar{y})y(t-\tau) - A\bar{y}(B + \bar{y})I,$$

$$\frac{dI}{dt} = y(t) - y(t-\tau). \tag{16}$$

Taking into account that $\bar{I} = B + \bar{y}$ we obtain the following characteristic equation for the system (16):

$$e^{\lambda}(\lambda + \bar{I}) - \bar{I} = 0. \tag{17}$$

Quasi-polynomial function (17) has zero root: this root appeared when equation (9) was transformed into system (14). Thus, we can shift the imaginary axis, $\lambda = \mu + \delta$, and in result we have the following quasi-polynomial function:

$$e^{\mu}e^{\delta}(\mu + \delta + \bar{I}) - \bar{I} = 0.$$

Re-writing this quasi-polynomial function we get

$$-(\delta + \bar{I})e^{\mu} + \frac{\bar{I}}{e^{\delta}} - \mu e^{\mu} = 0. \tag{18}$$

Theorem (Bellman, Cook, 1967): If the following conditions are truthful

1. $p < 1$,

2. $p < -q < \sqrt{a_1^2 + p^2}$, where a_1 is root of equation $a = p \mathrm{tg} a$, $0 < a < \pi$,

all roots of equation

$$pe^z + q - ze^z = 0$$

are in left side with respect to imaginary line.

For sufficient small values of δ, $\delta > 0$, the following inequalities for (18) are truthful:

1. $-\delta - \bar{I} < 1$,

2. $-\delta - \bar{I} < -\dfrac{\bar{I}}{e^\delta} < \sqrt{a_1^2 + (\delta + \bar{I})^2}$.

It means that quasi-polynomial function (18) for small $\delta > 0$ has roots with negative real parts only. Note, that quasi-polynomial function (18) hasn't pure imaginary roots. Consequently, equilibrium point $(\bar{y}, \bar{I})$ of system (14), and respectively equilibrium point $y = \bar{y}$ of equation (9) is stable stationary state (if it exists).

Finally, it was proved that solutions of equation (9) are non-negative and bounded; if inequality $A \le B\exp(B)$ is truthful all solutions converge to zero point; if $A > B\exp(B)$ is truthful non-trivial stationary state exists in phase space, and this equilibrium is asymptotically stable.

Conclusion

Considered in current publication model of isolated population dynamics contains the set of dynamic regimes which is close to set of regimes we can observe within the framework of original Verhulst' model (Verhulst, 1838). Like in original model regime of population extinction and regime of asymptotic stabilization at non-zero level can be observed in new model. At the same time we can observe regimes which cannot be realized within the framework of Verhulst' model: for example, it is the regime of fading fluctuations.

But it is very important to note that backgrounds for these models are qualitatively different. Within the framework of considered model it was took into account that speed of population size increasing depends on population size at previous time moment, and, the second, it was took into account that birth process has fixed finite time for development τ. Note, that analyzed model can be as a good base for constructing other models of population and ecosystem dynamics.

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