About a continuous-discrete model of fish population dynamics

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Abstract

In current publication the detailed description of continuous-discrete model of fish population dynamics is presented. It is assumed that in population there are non-overlapping generations, and there exist fixed time moments t_k, $k = 0,1,2...$, $t_{k+1} - t_k = const > 0$, of appearance of individuals of new generations. It is also assumed that rate of decreasing of population size between fixed time moments depends on natural death rate, influence of self-regulative mechanisms, speed of exploitation, and average biomass of individuals. For particular cases basic properties of model are pointed out. It is also presented a way for comparison of theoretical (model) trajectories with real time series, and determination of values of model parameters.

Key words: model of fish population dynamics, continuous-discrete model, dynamic regimes, estimation of model parameters

Introduction

Discrete time mathematical models are often used for the description of fish population dynamics (see, for example, Ricker, 1954, 1973, 1979; Beverton, Holt, 1957; Frisman, 1980; Frisman et al., 1982, 2006 and others). In simplest variant such a model can be presented in the following form:

$$x_{k+1} = x_k F(a, x_k). \tag{1}$$

In (1) x_k is population size of the generation number k (or k th year), F is a birth rate of population, and a is a vector of model parameters. Function F describes a combined influence of birth process, death process, influence of self-regulative mechanisms, weather factors etc. Within the limits of various models it is assumed that F is monotonic decreasing function with respect to population size (negative feedback; Nedorezov, 1997, 2012 a):

$$\frac{dF}{dx} < 0. \tag{2}$$

This property (2) is truthful for Kostitzin model (Kostitzin, 1937; Skellam, 1951; Beverton, Holt, 1957), Moran – Ricker model (Moran, 1950; Ricker, 1954) and some other models. It is possible to point out discrete models where Alley effect was taken into account (see, for example, Berezovskaya, Karev, Snell, 2005; Nedorezov, 1997, 2012 a; Nedorezov, Utyupin, 2011), and function F has extreme point on the domain $\{x: \quad x > 0\}$.

Use of models of (1) type leads to appearance of several serious problems in description of real population dynamics. First of all, within the framework of model (1) we have discrete time moments only, and we have no time in between these moments. It means that there are no possibilities to take into account (in model of (1) type) in correct manner an influence of fishing time interval (start moment and length of this interval) onto the next generation. Moreover, these important parameters are out of the set of regulative parameters. The second, absence of real time leads to impossibility to give a correct description of average weight of individuals onto final result. At the same time results of fishing are normally presented in tons (but not in numbers of individuals). Respectively, it leads to the necessity of recalculation of tons into numbers of individuals: model (1) describes dynamics of individuals but not tons in time. It is obvious, that this recalculation leads to appearance of unpredictable errors in datasets.

This list of problems in application of discrete time mathematical models to the description of fish population dynamics can easily be continued. But it is important to note that these problems cannot be correctly solved within the framework of models of (1) type. Correct solution of pointed out problems can be provided with other mathematical apparatus – ordinary differential equations with impulses (Kostitzin, 1937; Aagard-Hansen, Yeo, 1984; Poulsen, 1979; Nedorezov, 1986; Il'ichev, 2004; Mailleret, Lemesle, 2009).

In our publications (Nedorezov, 1986, 1989, 1997, 2012 a; Nedorezov, Nedorezova, 1994, 1995; Nedorezov, Utyupin, 2011) this apparatus was developed and applied to the description of dynamics of various biological species. For example, insect populations in boreal zone have two impulses per year: for the first time it is observed at moment of appearance of new generation, the second time is observed at the beginning of winter conditions (it is not necessary to have additional equation for the description of decreasing of population size during the winter time – it can be described as "jump down" because every individual can die with any probability p, and can survive with probability $1 - p$). Fish populations have "impulse" at moment of appearance of new generation and death of the previous one.

In current publication we give a description of a continuous-discrete model of fish population dynamics, and point out some basic properties of model. We give also a description of

the way to determination of model parameters for existing time series, and description of model of fish population dynamics under the discrete management.

Description of model

Let $x(t)$ be a population size at time t. In model we'll assume that at fixed time moments t_k, $k = 0,1,2...$, $t_{k+1} - t_k = h = const > 0$, there are the spawning in population (appearance of individuals of new generation and death of individuals of the previous one). Between these time moments (see fig. 1) there is the monotonic decreasing of population size $x(t)$ in a result of influence of natural death of individuals, influence of intra-population self-regulative mechanisms (first of all, intra-population competition for food), and fishing.

Let x_k be the population size after spawning (fig. 1), $x_k = x(t_k)$, and $x(t_k - 0)$ be the population size before spawning. Let Y be a mean productivity of individuals survived to moment of spawning, $Y = const > 0$. In general case amount of Y depends on food conditions, and in simplest case it can be taken into account as dependence of Y on population average on the interval $[t_k, t_{k+1})$: $Y = Y(\bar{x})$, where

$$\bar{x} = \frac{1}{h} \int_{t_k}^{t_{k+1}} x(s)ds .$$

For all time moments t_k we have the following relation:

$$x_k = x(t_k) = Yx(_k - 0).$$

Changing of number of individuals on the time interval $[t_k, t_{k+1})$ can be described with the following Verhulst' equation (Verhulst, 1838):

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

In (3) coefficient α is an intensity of natural death rate (Malthusian parameter), β is a coefficient of self regulation, $R(x)$ is an intensity of general death rate. Within the framework of model it is assumed that $\alpha, \beta = const > 0$. For equation (3) $x_k = x(t_k)$ is initial condition.

We'll assume that for every time interval $[t_k, t_{k+1})$ there exists subinterval $[u_k, v_k]$, $[u_k, v_k] \subset [t_k, t_{k+1})$, when the catch of population is allowed. Denote as c the intensity of catch. In the model we'll assume that $c = const > 0$ (the real value of this parameter depends on the power of fishing fleet): for every $t \in [t_k, t_{k+1})$ we have the following relation for speed of catching

$$g(x) = \begin{cases} cx(t), \, t \in [u_k, v_k], \\ 0, \, t \notin [u_k, v_k]. \end{cases}$$

Taking it into account, we have to modify equation (3):

$$\frac{dx}{dt} = -\alpha x - \beta x^2 - g(x)I(K,W). \qquad (4)$$
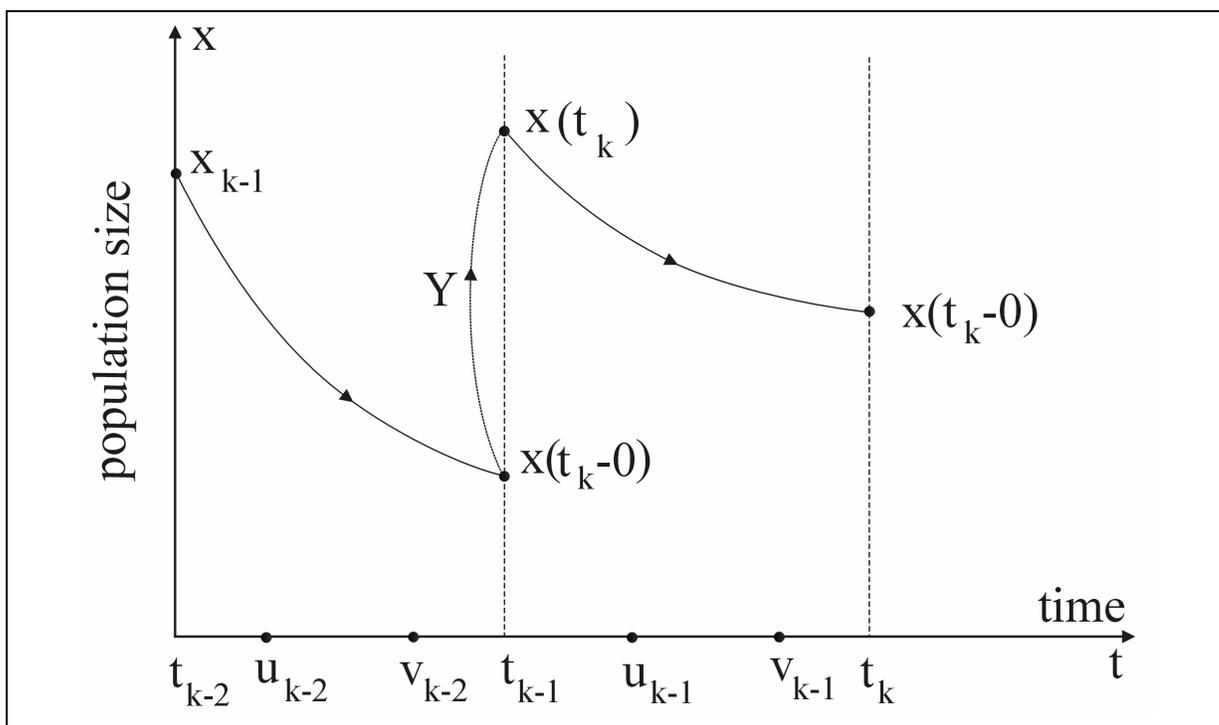
Fig. 1. Changing of population size $x(t)$ in time t. All notifications are in the text.

In equation (4) function I depends on variable W and parameter K: if $W < K$ then $I = 1$ and $I = 0$ if we have inverse inequality. Parameter K corresponds to maximum amount of biomass which can be obtained during time interval $[u_k, v_k]$. Note, K is one of most important managerial parameters of considering system. Respectively, $W(t)$ is a total biomass which is obtained to moment t. Dynamics of this variable can be described with the following equation:

$$\frac{dW}{dt} = g(x)m(t)I(W,K). \qquad (5)$$

In (5) variable $m(t)$ corresponds to average weight of individuals at moment t. Additionally we'll assume that for every time moment u_k variable $W_0 = W(u_k) = 0$. On the right boundary of interval $[u_k, v_k]$ we have the inequality $W(v_k) \le K$. In most cases these values $\{W_k = W(v_k)\}$ form time

series which can be used for prognoses of population size changing, estimation of model parameters, determination of quotas for fishing etc.

Dynamics of variable $m(t)$ can be described, for example, with Bertalanffy equation (Bertalanffy, 1957; Zaika, Makarova, 1971):

$$\frac{dm}{dt} = am^\gamma - bm. \tag{6}$$

In equation (6) a is a coefficient of anabolism, b is a coefficient of catabolism. Parameter $\gamma < 1$. In simplest case we can assume that $a, b, \gamma = const > 0$. But in more realistic situation at least one coefficient must depend on population size: $a = a(x)$. Increasing of population size leads to the respective decreasing of rate of average biomass increase:

$$\forall x \ a(x) \geq 0, \ a(\infty) = 0, \ \frac{da}{dx} < 0.$$

It is obvious, that for initial condition for equation (6) $m(t_k) \equiv m_0 > 0$ and $a, b, \gamma = const > 0$ we have the following inequality:

$$m_0 << \left(\frac{a}{b}\right)^{\frac{1}{1-\gamma}}.$$

Additionally we have to assume that $m_0 = m_0(x(t_k - 0))$: if $x(t_k - 0) \neq 0$ then $m_0(x(t_k - 0)) = const > 0$. If $x(t_k - 0) = 0$ then $m_0(x(t_k - 0)) = 0$ (if population size is equal to zero there are no reasons to talk about average weight of individuals). Combining all equations and relations (3)-(6) together with initial conditions we get the model of fish population dynamics under exploitation.

Some properties of model

1. For all non-negative initial values of variables: $x_0 \geq 0$, $m_0 \geq 0$, $W_0 = 0$, - solutions of system of differential equations are non-negative: for all $t > 0$ we have $x(t) \geq 0$, $m(t) \geq 0$, $W(t) \geq 0$.

2. In non-negative part of phase space R_+^3 there exists stable invariant compact Δ: if for any t_0 point $(x(t_0), W(t_0), m(t_0)) \in \Delta$ then for all $t \geq t_0$ we have $(x(t), W(t), m(t)) \in \Delta$.

Under the construction of model it was assumed that for all time moments $0 \leq W(t) \leq K$. If $a, b, \gamma = const > 0$ then for all moments t the following inequality is truthful (it follows from the equation (6)):

$$m_0 < m(t) < \left(\frac{a}{b}\right)^{\frac{1}{1-\gamma}} = m_{max} \, .$$

As it was proved in our publications (Nedorezov, Nedorezova, 1994, 1995) solutions of equation (3) with periodic "jumps up" are limited, and there exists value x_{max} : if $x_0 \le x_{max}$ then for all $t > 0$ we have the inequality $x(t) \le x_{max}$. Thus, stable invariant compact Δ has the following form:

$$\Delta = [0, x_{max}] \times [0, K] \times [0, m_{max}] \, .$$

3. Origin (0,0,0) is stationary state of considering system of differential equations. If the following inequality is truthful

$$Y_{max} < e^{hR(0)} \, ,$$

where Y_{max} is maximum value of productivity, population eliminates for all possible initial values (even without fishing; sufficient condition). If the inverse inequality is truthful elimination of population depends on intensity of fishing.

Estimation of model parameters

In the end of certain time period of fishing we get a total yield – values of variable W at determined time moments v_k: $\{W_k = W(v_k)\}$, $k = 1,2,...,n$, where n is sample size. Let's assume that we have no other information, and we have to estimate model parameters using this information only. First serious problem is following: if for every time moment j we have $W_j = K$ (this value can change from year to year), there are no possibilities to find estimations of model parameters. These possibilities will be saved if together with values $W_j = K$ we have respective time moments t_j^* , $u_j < t_j^* < v_j$, when the respective amount was achieved.

If for every time moment j we have $W_j < K$ least square method can be applied for estimation of model parameters:

$$Q(\vec{c}) = \sum_{k=1}^{n} (W(\vec{c}, k) - W_k)^2 \rightarrow \min_{\vec{c}} \, . \tag{7}$$

In expression (7) $\vec{c}$ is vector of unknown model parameters. Note, that initial population size x_0 and average initial biomass m_0 are unknown parameters too. $W(\vec{c}, k)$ are the values at fixed time moments which were obtained as solutions of considering model (global fitting; Wood, 2001).

Respective functional form (like (7)) can be pointed out in a situation when sample contains time moments $\{t_k^*\}$ only. In this situation least square method can be applied for estimation of model parameters too:

$$Q(\vec{c}) = \sum_{k=1}^{n} (t^*(\vec{c},k) - t_k^*)^2 \to \min_{\vec{c}} . \qquad (8)$$

In (8) $t^*(\vec{c},k)$ are theoretical (model) values which can be obtained in the model for fixed values of model parameters, t_k^* are empirical (observed) time moments.

Criterions (7) and (8) cannot be applied for model parameters estimations in a situation when we have mixed variant – when part of values $W_j = K$, and we have to use as amounts $\{W_k\}$, as time moments $\{t_k^*\}$. In this rather complicated situation it is much better to use approach which is developed in our publications (Nedorezov, 2012 a, b; Nedorezov, Utyupin, 2011). Basic idea of this approach is following. At the beginning we don't need to estimate model parameters (like using least square method or maximum likelihood) or tried to find distributions of model parameters (Bayesian approach). First of all we have to determine a suitable domain in space of parameters where considering model and empirical dataset are not in contradiction.

It means that at the very beginning we have to point out a set of statistical criterions which we are assuming to use for analysis of correspondence of empirical datasets and theoretical values (and we have to choose one and the same significance level for all criterions). For every criterion we have to find a set of points where model trajectories and empirical dataset are not in contradiction. After that we have to find an intersection of these domains. If obtained set is empty it means that considering model has no relation to observed biological process. Thus, we have to reject initial hypothesis that considering model can be applied for the description of existing datasets. If set isn't empty formally we can use every point from this domain. But it is much better to find a mid point of this stochastic set of points.

Choosing of group of statistical tests is very important point in analysis of suitability of model for description of existing datasets. Standard set of tests contains the following criterions for analysis of deviations between theoretical and empirical datasets: checking of hypothesis about equivalence of average to zero, testing for Normality (Shapiro, Wilk, Chen, 1968; Lilliefors, 1967; Lakin, 1990), and testing for existence/absence of serial correlation (with Durbin – Watson test, analysis of behavior of auto-correlation function etc.) (McCallum, 2000; Wood, 2001; Draper, Smith, 1986, 1987).

It is very important to note that assumption about Normality of deviations has no background. Numerical analysis of simplest mathematical model of migrations with Alley effect shows that this assumption isn't truthful with big probability (Nedorezov, 2012 b, 2013). For set of deviations we have to check a symmetry of density function with respect to origin with nonparametric methods (Bolshev, Smirnov, 1983; Hollander, Wolfe, 1973) and monotonic behavior of branches of this function. Analysis of existence/absence of serial correlation in sequence of residuals must be provided too using respective methods.

Model with discrete management

Let's assume that real population dynamics can be effectively described by the system (3)-(6). In most cases we have no total information about real dynamics, and for management of population size changing we try to use (much more) simpler models. For example, it can be Kostitzin model (Kostitzin, 1937; this model is also known as Beverton – Holt model; Beverton, Holt, 1957; Kovalev, 2006):

$$x_{k+1} = \frac{Ax_k}{1 + Bx_k}, \; A, B = const > 0.$$
(9)

If we are sure that equation (9) gives good description of population size changing in time under the exploitation, we have to be careful in estimation of value of parameter A: if $A < 1$ then origin is global stable state, and it corresponds to regime of population extinction. This coefficient is equal to maximum of productivity multiplied onto probability of surviving (formally, quota of survived individuals) of individuals to moment of appearance of individuals of the next generation. Value of this coefficient depends on living conditions (temperature, salinity etc.), food conditions, and fishing. We have to note that some of these characteristics are stochastic variables. Thus, every year we have to control the value of parameter A. It means that we have to have a procedure for estimating of total population size (before time moment u_k), for estimating of final population size (at moment $t_{k+1} - 0$), and we have to choose number of years N which must be used for obtaining confident estimations of parameter A.

Let $\{x_k^* = x(u_k)\}$ and $\{x_k^{**} = x(t_k - 0)\}$ be sets of the respective values of population size. Taking into account that average productivity Y^* can be estimated too, we can estimate initial population size of the next generation: $x_{k+1}^{***} = Y^* x_{k+1}^{**} = Y^* x(t_{k+1} - 0)$. After that we can find estimations of model (9) parameters:

$$Q(x_{k+1-N}^{***}, A, B) = \sum_{j=1}^{N} \left(x_{k+1-N+j}^{***} - \frac{Ax_{k-N+j}^{***}}{1 + Bx_{k-N+j}^{***}} \right)^2 \rightarrow \min_{A,B,x_{k+1-N}^{***}} .$$

Obtained estimations allowed constructing forecast of population size changing for one or more years. If estimation $A < 1$ it means that during N time moments (years) we have asymptotic elimination of population. It can be like a signal to decreasing of quotas for the next year. If $A > 1$ it can be used as indicator that population size will increase and, thus, quotas can be increased. Changing of amounts of quotas must depend on sample $\{x_k^* = x(u_k)\}$.

Conclusion

Within the limits of considering model of fish population dynamics it is assumed that population has one-year generations only. Appearance of individuals of the next generation correlates with death of the previous one. But in combination with Leslie matrix model (Leslie, 1945, 1948) it can be easily modified for more complicated situations.

For all possible modifications of model (3)-(6) we'll have one and the same problem – this is a problem of finding (estimation) of confident model parameters. Modern statistical approaches to this problem are not correct: for the first time we estimate model parameters, and after that we check properties of set of deviations between theoretical and empirical datasets. If set of deviations doesn't satisfy to any criterion, we may conclude that model cannot be applied for fitting of existing datasets. Taking into account one set of deviations we formulate a final conclusion about total properties of model.

First of all, estimations of model parameters which can be obtained with the help of criterions, for example, (7) or (8), are the best from the standpoint of statistics. But these "best" properties (like effectiveness) have no relation to biology. And assumption that best estimations of parameters correspond to minimum of variation of deviations hasn't a biological background. This is pure statistical assumption without any real background. But use this assumption leads to appearance of unsolved situations when we have several time series with different units: tons, time moments, numbers etc.

This important problem can be solved if we choose other way. At the beginning we select group of statistical criterions for deviations between theoretical and empirical datasets. For every criterion we determine a set of points in space of model parameters which gives positive result: if parameters belong to this set respective statistical criterion doesn't allow rejecting its Null hypothesis (for example, about equivalence of average to zero, about symmetry of distribution etc.). Intersection of all sets gives a new set in the same space: if parameters of model belong to this final

set deviations satisfy to all statistical criterions. We can call this final set as *set of suitable values* of parameters for model. This set can be empty – it means that from the standpoint of selected criterions model cannot be applied for fitting of empirical datasets.

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