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Population Dynamics of Bithynia Tentaculata *

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Abstract

Dynamics of snail populations are analyzed both qualitatively and quantitatively. Starting from the concrete measured data in the form of tables, the modelling logistic-type equations have been determined at first. These are then examined as deterministic and random dynamical systems under various constraints. Finally, the results obtained from such a mathematical analysis are interpreted in biological terms.

Key words: Logistic-type equations, asymptotic behaviour, bifurcations, random affects, functional dependence.

1991 Mathematics Subject Classification: 34D05, 46N60, 58F40

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1 Introduction

First of all, let us introduce those facts consisting with previous biological knowledge, which have arisen during the construction of the models (see [6]).

- The life time of an individual is estimated at one to three years. The majority of population is biennial.
- Individuals of species *B.t.* are gonochorists. The ratio of males to females in the population during year is not precisely known. We suppose that it is 1 : 1.
- Both mating and egg laying time are dependent on water temperature. Individuals begin to mate sporadically as soon as the water temperature is about 10°C, the biggest part of population reproduce when the water temperature increases (about 18–20°C). Embryonal evolution of individuals takes from two to four weeks and depends mainly on a water temperature. Egg capsules appear from the beginning of May until the end of August, mostly in July. Usually there are 10–35 eggs in an egg capsule.
- Individuals do not reach maturity in the year they are born and only reproduce the next year. This fact is essential for following introduced models.
- Species *B.t.* frequently occur in beta-mezosaprobic waters (waters with a mean measure of organic pollution).
- There is no macrovegetation in the study site. Snails prefer a bottom with stones sized 250–500 cm².
- Individuals feed on detritus (remains of vegetable and animal bodies deposited on the bottom as soft silt) and are able to obtain food by water filtering and thus are relatively resistant to food shortage. This ability enables individuals to live in high concentrations in a small area.

Exact data for predation pressure, migration and intraspecific competition are not known at present. We do not pay attention to the following two factors:

- Predation pressure. It is true that snails have natural enemies at any given locality. The smallest individuals, those which are not yet reproducing in a given year, are more vulnerable to exposed to predation pressure. That is why the predation is mostly projected into large values of mortality of young individuals.
- Migration. Large movement on the part of individuals were not observed.

We present measured numbers of individuals in size categories at each sample and water temperature $T^{\circ}\text{C}$. These data describe the situation in the riffle and respond to the $\frac{1}{3}$ m² bottom area (see [6]).

No.	date	T	number of individuals in size class							Total
			I	II	III	IV	V	VI	VII	
1	29/6/1992	19	0	1	2	3	9	8	0	23
2	23/7/1992	21	270	92	3	1	34	38	2	440
3	2/9/1992	19	54	116	39	13	11	19	0	252
4	5/10/1992	13	12	72	22	11	17	12	0	146
5	10/11/1992	4	0	35	18	8	7	6	3	77
6	16/12/1992	2	1	1	0	2	0	0	0	4
7	20/1/1993	2.5	4	7	2	1	6	5	0	25
8	26/2/1993	1	0	1	1	0	1	1	0	4
9	1/4/1993	3.5	0	2	0	0	1	1	0	4
10	3/5/1993	13	0	8	10	7	15	5	1	46
11	7/6/1993	18	250	1	6	8	4	11	0	280
12	19/7/1993	19	252	253	14	3	10	44	0	576
13	31/8/1993	17	81	200	81	41	15	14	0	432

Let us introduce the employed terminology:

- **Density of the population.** *Number of individuals on the unit of area. In this case it is $\frac{1}{3}m^2$.*
- **Fertility of the population.** *Ability of population to increase. It is occurrence count of new individuals. Relative fertility b is defined as the ratio of the number of new individuals ΔN^b over time Δt to the number of all individuals N , consequently $b = \frac{\Delta N^b}{N\Delta t}$.*
- **Mortality of the population.** *Mortality of individuals in population. Relative mortality is defined in a similar way: $d = \frac{\Delta N^d}{N\Delta t}$.*

The ratio of males to females in the population is not known at present. Therefore, we are working with average values related to one individual in the population.

The following three models are valid to periodic environments.

2 1st model

We present this model mainly to analyse the random influences affecting the population which is possible in this case. As we see in the 2nd model, which is rather more complicated, it is nearly impossible to perform such an analysis. We introduce numerical simulations of spreading these influences for that reason.

2.1 Model construction and its analysis

We add the following hypotheses to the basic assumptions:

- We do not distinguish individuals from different size classes.
- Number of adult individuals will not change during the breeding period.

The second assumption, although not applicable in the first case, is acceptable, because the number of adult individuals is essential only during the breeding period (when their deaths on high numbers are not observed). Young do not mature in the same year (that is why they do not reproduce) and most of population borne in the previous year reach adult age during the winter and spring before the beginning of the reproduction period.

For random influence analysis, we separate birth and death of individuals. This is possible because young individuals do not reproduce and have no effect on the population dynamics at the year, when they were born and since adult individuals do not die during the reproduction period.

Notation:

- t is the variable indicating time (years),
- $x(t)$ is the number of all individuals in time t ,
- $x'(t)$ is the change of individuals number in time t ,
- $k > 0$ is the constant corresponding to the average eggs number of the egg capsule,
- $r(t)$ is the continuous 1-periodic function of environmental “suitability”. The function $kr(t)$ determines an increase (real size egg capsules) in time t ,
- $x_0 > 0$ is the constant corresponding to the number of adult individuals, which begin to mate,
- the continuous function $l(t)$, defined over the reference interval $[0, 1]$, is the function describing a survival over time t (in %).

The appropriate model looks as follows

$$x(t) = l(t) x_0 \left(1 + k \int_0^t r(\tau) d\tau \right), \quad t \in [0, 1].$$

One can readily check that the function $x_0 + kx_0 \int_0^t r(t) dt$ solves the initial value problem

$$x'(t) = x_0 k r(t), \quad x(0) = x_0, \quad t \in [0, 1].$$

This means, that the change of individuals number is proportional to the function defining an increase, the number of individuals which begin to mate and to the egg capsules size.

The solution in time $t > 0$ takes the form

$$x(t) = x_0 \left[l(1) \left(1 + k \int_0^1 r(t) dt \right) \right]^{[t]} l(t - [t]) \left(1 + k \int_0^{t-[t]} r(t) dt \right).$$

The symbol $[t]$ means an integer part of t . From this we can see that *the solution $x(t)$ is 1-periodic if and only if*

$$c = l(1) \left(1 + k \int_0^1 r(t) dt \right) = 1.$$

Moreover, it is stable, but not asymptotically stable. If $c > 1$, then $x(t) \rightarrow \infty$ as $t \rightarrow \infty$, if $c < 1$, then $x(t) \rightarrow 0$ as $t \rightarrow \infty$.

2.2 Numerical modelling

2.2.1 Estimation of function $r(t)$

Let R denote the percentage of eggs hatched (≈ 0.9). Function

$$\frac{r(t)}{R}$$

describes the intensity of egg capsules laid by one adult individual at time t . Number

$$\frac{1}{R} \int_{t_i}^{t_{i+1}} r(t) dt = \frac{1}{R} r_i$$

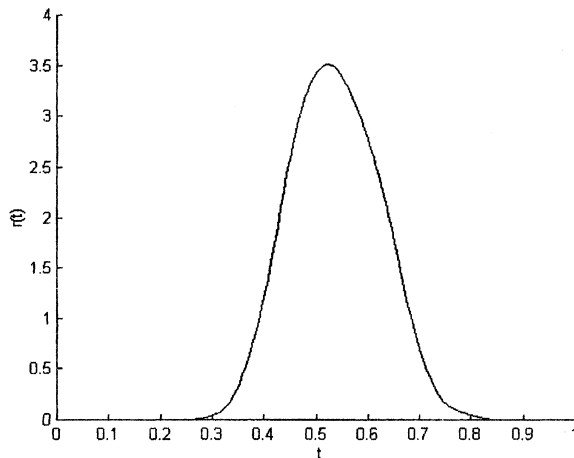
is the average number of egg capsules laid by one individual during the time $[t_i, t_{i+1}]$.

We compute values r_i , $i = 1, \dots, n - 1$ in the following way: the number of new individuals (in the first size class I, see exordial table) divided by R corresponds to the sum of all eggs laid during the time interval $[t_i, t_{i+1}]$. We divide this number by the number of adult individuals and by the average egg capsule size to obtain r_i . Then we use Histosplines (see Appendix) for the data r_i , $i = 1, \dots, n - 1$. The eventual function $r(t)$ is from the C^1 -class and

$$\int_{t_i}^{t_{i+1}} r(t) dt = r_i, \quad i = 1, \dots, n - 1.$$

The values t_i , $i = 1, \dots, n$ are the sampling instants. The actual values have to be a bit higher than the measured data, because some small individuals would have died before the sampling took place. These values were obtained by extrapolation.

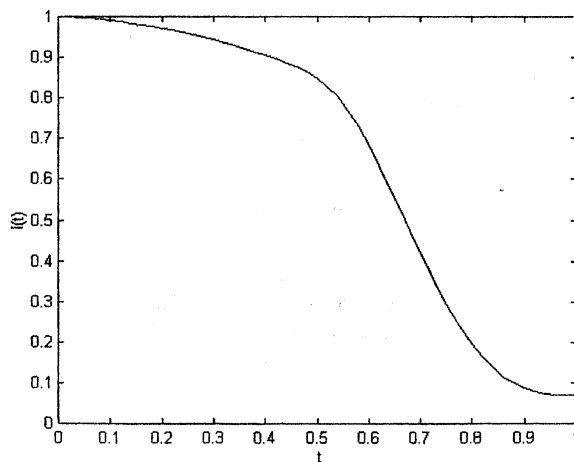
The graph of function $r(t)$:



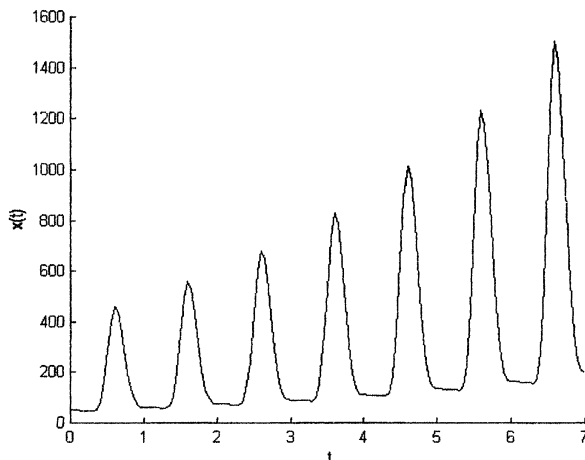
2.2.2 Estimation of function $l(t)$

We have at our disposal the numbers x_{t_i} of individuals in samples, which will be used to construct the function $l(t)$. Let s_i be the ratio of the number of individuals which survive to another sample $i + 1$ to the number of individuals in sample i . Values s_i can be approximated by the ratio of the numbers at column "Total" (rows $i, i + 1$). Thus $l(t_{i+1}) = s_1 s_2 \dots s_i$, $l(t_1) = 1$.

So, we obtain the values of function $l(t)$ at several points. These points are fitted by a cubic spline (see Appendix), which already gives rise to the desired function $l(t)$:



Letting, e.g. $x_0 = 50$, $k = 20$, the mollusc population would evolve in the following way (vertical axis: number of individuals, horizontal axis: time in years):



2.3 Random influences

Various accidental influences affect the population. For example, changes in seasonal water temperature are not same every year, but move in a certain interval. Population mortality and fertility $l(t)$, $kr(t)$ may also be influenced. Moreover, the initial state of population x_0 is not defined accurately. In such a case, there is not one, but a whole set of possible solutions.

Assume that the initial value number of individuals x_0 , the average egg number in egg capsules k , the suitability function $r(t)$ at each time t and the mortality function $l(t)$ at each time t are all normally distributed random variables with a certain mean value and variance.

Denote

$$F(t, x_0, k, l_1, \dots, l_n, r_1, \dots, r_{n-1}) = x(t),$$

and

$$f(x_0, k, l_n, r_1, \dots, r_{n-1}) = F(1, x_0, k, l_1, \dots, l_n, r_1, \dots, r_{n-1}) = x(1).$$

To determine the dynamics of our model, it is sufficient to observe value $x(1)$, i.e. the initial state of the population for the next year. The mean value is $f(\mu)$. We take into account both the bias and the variance of this random variable (see e.g. [3]).

Definition 1 Denoting by \otimes the Kronecker product, we can define

$$a^{j\otimes} = \underbrace{a \otimes a \otimes \dots \otimes a}_{j\text{-times}}.$$

Denoting still (observe that x is a column vector)

$$\left(\frac{\partial}{\partial x}\right)^{1\otimes} f(\mu) = \frac{\partial f(x)}{\partial x} \Big|_{x=\mu},$$

$$\left(\frac{\partial}{\partial x}\right)^{2\otimes} f(\mu) = \left[\left(\frac{\partial^2 f(x)}{\partial x_1 \partial x'}, \frac{\partial^2 f(x)}{\partial x_2 \partial x'}, \dots, \frac{\partial^2 f(x)}{\partial x_n \partial x'} \right) \Big|_{x=\mu} \right]',$$

(' denotes the transposition) it will be very useful to recall the following theorems.

Theorem 1 ([3]) *Let $f(x) : R^n \rightarrow R^1$ be a function which can be represented by an infinite Taylor series on some domain D and $\mu, \mu + e \in D$. Then*

$$f(\mu + e) = f(\mu) + \sum_{j=1}^{\infty} \frac{1}{j!} \left[\left(\frac{\partial}{\partial x'}\right)^{j\otimes} f(\mu) \right] e^{j\otimes}.$$

Now, let either (i) or (ii) be satisfied:

- (i) A function $f(\cdot) : R^n \rightarrow R^1$ can be represented by a Taylor series on a domain D . Let $S_j \subset [a_j, b_j]$, where $-\infty < a_j < b_j < \infty$, $j = 1, \dots, n$ and $S = \prod_{j=1}^n S_j \subset D$, where S_j is the support of the probability measure, given by the distribution function $F_j(\cdot) : R^1 \rightarrow R^1$ of the j th component of random vector $\epsilon = \hat{\mu} - \mu$.
- (ii) A function $f(\cdot) : R^n \rightarrow R^1$ is a polynomial of an arbitrary (finite) degree and all statistical moments of the random vector $\hat{\mu} = \mu + \epsilon$ exist (in this case S can be even R^n).

As a consequence of conditions (i) or (ii) the random variable $f(\hat{\mu})$ possesses all statistical moments and the series

$$\sum_{j=1}^{\infty} \frac{1}{j!} \left[\left(\frac{\partial}{\partial x'}\right)^{j\otimes} f(\mu) \right] e^{j\otimes}$$

converges uniformly on S and absolutely for any $e \in S$ (in detail cf. [3]).

In the sequel, let the symbol E express the mean value under the probability measure considered. Let

$$E(\epsilon) = 0, \quad E(\epsilon\epsilon') = \Sigma, \quad E[\epsilon \otimes (\epsilon\epsilon')] = \phi, \quad E[(\epsilon\epsilon') \otimes (\epsilon\epsilon')] = \psi.$$

Denote $\delta_2 = \text{vec}(\Sigma)$, $\delta_3 = \text{vec}(\phi)$, $\delta_4 = \text{vec}(\psi)$, where $\text{vec}(A)$ means the (mn) -dimensional column vector given by the columns of the $m \times n$ matrix A ordered one under another.

If $\epsilon \sim N_n(0, \Sigma)$, then $E(\epsilon) = 0$, $E(\epsilon\epsilon') = \Sigma$. Letting $\{\Sigma\}_{i,j} = \sigma_{i,j}$, then $\delta_3 = 0$ and $\{\delta_4\}_{i,j,k,l} = \sigma_{i,j}\sigma_{k,l} + \sigma_{i,k}\sigma_{j,l} + \sigma_{i,l}\sigma_{j,k}$.

Theorem 2 ([3]) Under the assumptions (i) or (ii),

$$b = \sum_{j=2}^{\infty} a'_j \delta_j, \quad V = \sum_{r=1}^{\infty} \sum_{j=1}^{\infty} (a'_r \otimes a'_j) (\delta_{j+r} - \delta_j \otimes \delta_r),$$

where b is the bias and V is the variance of $f(\hat{\mu})$ and

$$a'_j = \frac{1}{j!} \left(\frac{\partial}{\partial x'} \right)^{j \otimes} f(x) \Big|_{x=\mu}.$$

To compute the bias and the variance of $x(1)$, the function $r(t)$ is piece-wise approximated by lines. If $h_i = t_{i+1} - t_i$, $i = 1, \dots, n-1$, where t_i are the sampling instants, then

$$r(t)|_{[t_i, t_{i+1}]} = r_i + \frac{r_{i+1} - r_i}{h_i} t, \quad t \in [0, h_i].$$

After an arrangement, we get

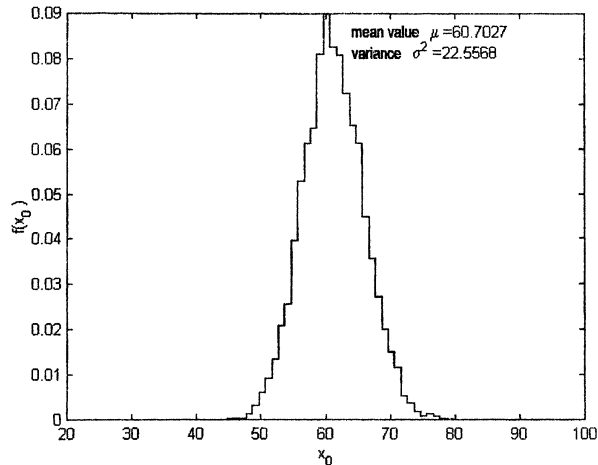
$$x(1) = x_0 l_n \left[1 + \frac{k}{2} \left(r_1 h_1 + \sum_{i=2}^{n-1} r_i (h_{i-1} + h_i) + r_n h_{n-1} \right) \right].$$

We know from the measured data, used in a numerical modelling, that $h = (0.156, 0.09, 0.063, 0.123, 0.115, 0.115, 0.1, 0.093, 0.145)$, $x_0 = 50$, $l_n = 0.07$, $k = 20$, $r = (0, 0, 0.007, 0.6, 2.07, 3.42, 1.5, 0.11, 0.001, 0)$. Value l_n is the value $l(1)$.

Suppose, that x_0 , l_n , k , r_i are mutually independent normally distributed random variables with the above cited mean values and standard deviations $\sigma_{x_0} = 2$, $\sigma_{l_n} = 0.003$, $\sigma_k = 1$ and $\Sigma_r = \text{diag}(0, 0, 0, 0.002, 0.08, 0.14, 0.06, 0.004, 0, 0)$, for example.

Under these assumptions, the mean value of $x(1)$ is $\mu = 60.3461$ and the variance of $x(1)$ is $V = 22.8405$. The bias b is zero because of the form of $x(1)$ and the assumptions of independence of random variables. The calculation was performed by means of the software **Mathematica 2.2**.

Another possible method consists in a numerical simulation. This was done by means of the software **Matlab 5.0**. After 10000 realizations, we obtain that the mean value is $\mu = 60.7007$ and the variance is $V = 22.4525$, which corresponds well with the values detected analytically. In the following graph, we can see experimentally estimated density of the random variable $x(1)$, which gives a new initial state, i.e. $x(1) = x_0$:



3 2nd model

We do not separate mortality and fertility in this model. For that reason, this model is more accurate than the previous one.

3.1 Model construction and its analysis

Let us take the same assumptions as for the 1st model, but understand survivability (or mortality) by another way.

We can also use the same notation, but

- $l(t)$ this time represents the continuous 1-periodic function describing a decrease in time t .

The appropriate model reads as

$$x'(t) = k x_0 r(t) - l(t) x(t), \quad x(0) = x_0, \quad t \in [0, 1]. \quad (1)$$

The change in the number of individuals in time t is defined by the product of the function describing an increase, the number of individuals which begin to mate and by the egg capsule size, reduced by the number of perished individuals.

Theorem 3 *The initial value problem (1) has a unique solution $x(t)$. If $l(t)$, $r(t)$ are C^2 -functions, then $x(t)$ is continuous on the interval $[0, \infty)$ and $x(t) \in C^3([j, j+1])$, $j \in \mathbb{N}$.*

Proof The solution takes the form

$$x(t) = x_0 \left(\int_0^t e^{\int_0^\tau l(z) dz} k r(\tau) d\tau + 1 \right) e^{-\int_0^t l(\tau) d\tau}, \quad t \in [0, 1].$$

Denoting

$$c = e^{-\int_0^1 l(\tau) d\tau} \left(\int_0^1 e^{\int_0^\tau l(z) dz} k r(\tau) d\tau + 1 \right), \quad (2)$$

we have for $t > 0$ that

$$x(t) = x_0 c^{[t]} e^{-\int_0^{t-[t]} l(\tau) d\tau} \left(\int_0^{t-[t]} e^{\int_0^\tau l(z) dz} k r(\tau) d\tau + 1 \right).$$

The symbol $[t]$ means, as usual, the integer part of t . It can be seen from here that again $x(t)$ is 1-periodic if and only if $c = 1$. Moreover, $x(t)$ is stable, but not asymptotically stable. If $c > 1$, then $x(t) \rightarrow \infty$ as $t \rightarrow \infty$, if $c < 1$, then $x(t) \rightarrow 0$ as $t \rightarrow \infty$.

3.2 Numerical modelling

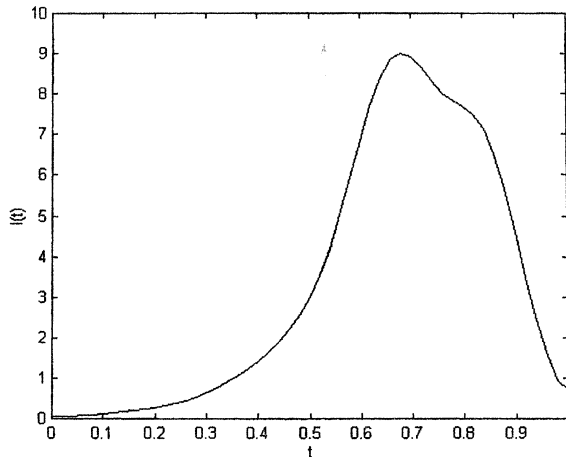
3.2.1 Estimation of function $l(t)$

The function $r(t)$ has the same meaning as in the 1st model, but $l(t)$ is different. To estimate $l(t)$, we need the exact knowledge of population evolution $x(t)$ in the course of at least one year. It follows immediately from (1) that

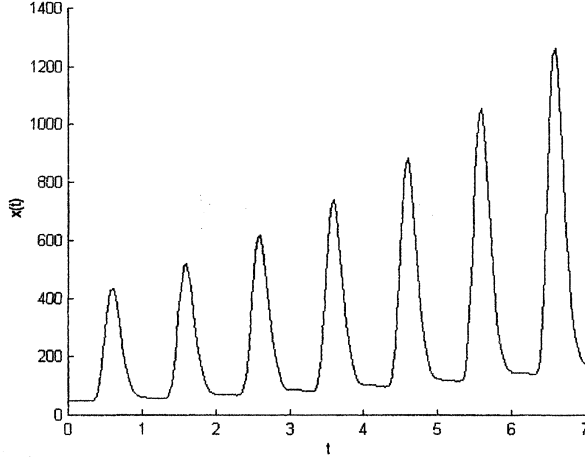
$$l(t) = \frac{k x_0 r(t)}{x(t)} - \frac{x'(t)}{x(t)}.$$

In view of $x(t)$, $x'(t)$ and previously estimated function $r(t)$, the desired $l(t)$ can be then computed.

Nevertheless, since we have not at our disposal suitable $x(t)$, we use the one from the first model. In this case the result is the following:



If, e.g. $x_0 = 50$, $k = 20$, then the mollusc population evolves as follows (vertical axis: number of individuals, horizontal axis: time in years)



3.3 Random influences

Assume that the functions $r(t)$, $l(t)$ are piece-wise linear, i.e.

$$r(t)|_{[t_i, t_{i+1}]} = r_i + \frac{r_{i+1} - r_i}{h_i} t, \quad t \in [0, h_i],$$

$$l(t)|_{[t_i, t_{i+1}]} = l_i + \frac{l_{i+1} - l_i}{h_i} t, \quad t \in [0, h_i],$$

where $r_i, l_i, i = 1, \dots, n$ are given values.

Under the given assumptions,

$$\int_0^1 l(\tau) d\tau = \frac{1}{2} \left(l_1 h_1 + \sum_{i=2}^{n-1} l_i (h_{i-1} + h_i) + l_n h_{n-1} \right),$$

$$\int_0^1 e^{\int_0^\tau l(z) dz} r(\tau) d\tau = \sum_{i=1}^{n-1} \int_0^{h_i} e^{\int_0^{t_i+\tau} l(z) dz} \left[r_i + \frac{r_{i+1} - r_i}{h_i} \tau \right] d\tau,$$

where

$$\begin{aligned} \int_0^{t_i+\tau} l(z) dz &= \int_0^{t_i} l(z) dz + \int_{t_i}^{t_i+\tau} l(z) dz \\ &= \frac{1}{2} \left(l_1 h_1 + \sum_{j=2}^{i-1} l_j (h_{j-1} + h_j) + l_i h_{i-1} \right) + l_i \tau + \frac{1}{2h_i} (l_{i+1} - l_i) \tau^2. \end{aligned}$$

Thus, we obtain the final form of $x(1)$:

$$x(1) = x_0 e^{-\frac{1}{2} \left(l_1 h_1 + \sum_{i=2}^{n-1} l_i (h_{i-1} + h_i) + l_n h_{n-1} \right)} \times \left(1 + k \sum_{i=1}^{n-1} \int_0^{h_i} e^{c_i + l_i \tau + \frac{1}{2h_i} (l_{i+1} - l_i) \tau^2} \left[r_i + \frac{r_{i+1} - r_i}{h_i} \tau \right] d\tau \right),$$

where

$$c_i = \frac{1}{2} \left(l_1 h_1 + \sum_{j=2}^{i-1} l_j (h_{j-1} + h_j) + l_i h_{i-1} \right), \quad c_1 = 0.$$

We know that $t = (0, 0.156, 0.246, 0.31, 0.43, 0.548, 0.663, 0.762, 0.855, 1)$, $x_0 = 50$, $k = 20$, $r = (0, 0, 0.007, 0.6, 2.07, 3.42, 1.5, 0.11, 0.001, 0)$, $l = (0.05, 0.2, 0.4, 0.7, 1.8, 4.5, 8.9, 8, 6.7, 0.7)$. Values x_0, k, r_i are the same as in the 1st model. Vector t contains the sampling instants, $h_i = t_{i+1} - t_i$, $i = 1, \dots, 9$, and vector l contains the function values of $l(t)$ at time t , i.e. $l_i = l(t_i)$. Let x_0, l_i, k, r_i be mutually independent normally distributed random variables with the above cited mean values and the standard deviations $\sigma_{x_0} = 2$, $\sigma_k = 1$, $\Sigma_r = \text{diag}(0, 0, 0, 0.002, 0.08, 0.14, 0.06, 0.004, 0, 0)$, and $\Sigma_l = \text{diag}(0, 0.001, 0.016, 0.028, 0.072, 0.18, 0.35, 0.32, 0.27, 0.028)$, for example.

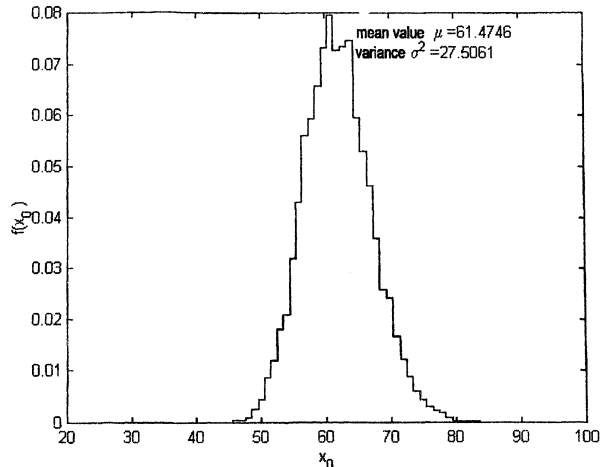
The analytical way of computing both the bias and the variance is already at this elementary stage (see the form of $x(1)$ above) complicated.

After 10000 realizations, we obtain numerically that the mean value of $x(1)$ is $\mu = 61.7700$ and the variance of $x(1)$ is $V = 27.0644$. The bias of random variable $x(1)$ is defined as

$$b = E[f(\hat{\mu})] - f(\mu),$$

and its value is 2.0244.

The values of density $f(x_0)$ can be sketched as follows:



Applying this model, the population may increase permanently. Therefore, we make the correction in the 3rd model.

4 3rd model

We will consider three modifications in this section. They will differ in their interpretation of intraspecific competition, which has been neglected until now.

4.1 Model construction and its analysis

We add the following hypotheses to the basic assumptions:

- There is an intraspecific competition among the individuals.

Let the used symbols have the same meaning as in the 2nd model and let

- $f > 0$ be a constant proportional to intraspecific competition,
- $f(v)$ be a continuous function describing the intensity of competition caused by one individual living at time $t - v$, where t is the current time.

The appropriate models follow

$$x'(t) = k x_0 r(t) - l(t)x(t) - f x^2(t), \quad x(0) = x_0, \quad (3)$$

$$x'(t) = k x_0 r(t) - l(t)x(t) - f x(t)x(t - \tau), \quad x(t) = g(t), \quad t \in [-\tau, 0], \quad (4)$$

$$x'(t) = k x_0 r(t) - x(t) \left(l(t) + f \int_0^\infty f(s)x(t-s) ds \right), \quad x(t) = g(t), \quad t \in (-\infty, 0], \quad (5)$$

where $g(t), f(s)$ are given functions.

The related theorems about the uniqueness of solutions for the initial state value problems hold quite analogously to Theorem 3.

Setting $f(s) = \delta(s - \tau)$ in integro-differential equation (5), where $\delta(t)$ is the Dirac δ -function, we obtain model (4) and, in particular for $\tau = 0$, model (3). Frequently, function $f(s)$ is taken in the form $f(s) = a e^{-as}$ (so-called exponential forgetting of the model).

Letting

$$y(t) = \int_{-\infty}^t x(s) a e^{-a(t-s)} ds,$$

we get

$$y'(t) = a(x(t) - y(t)),$$

by which equation (5) can be rewritten into

$$\begin{aligned} x'(t) &= k x_0 r(t) - x(t)l(t) - f x(t)y(t), \\ y'(t) &= a(x(t) - y(t)). \end{aligned} \quad (6)$$

The initial conditions are

$$x(0) = g(0) = x_0, \quad (7)$$

$$y(0) = \int_{-\infty}^0 g(s) a e^{as} ds = y_0. \quad (8)$$

Now let us study the behaviour of (3). Problem

$$x'(t) = kx_0r(t) - l(t)x(t) - fx^2(t), \quad x(0) = x_0,$$

can be transformed to the integral form

$$x(t) = x_0 + \int_0^t (kx_0r(\tau) - l(\tau)x(\tau) - fx^2(\tau))d\tau,$$

and for $t = 1$, we arrive at

$$x(1) = x_0 + \int_0^1 (kx_0r(\tau) - l(\tau)x(\tau))d\tau - \int_0^1 fx^2(\tau) d\tau. \quad (9)$$

By the Mean Value Theorem there exists a constant \tilde{x} such that

$$\int_0^1 fx(\tau)x(\tau) d\tau = \tilde{x} \int_0^1 x(\tau)d\tau.$$

Since $fx(t) > 0$ for all $t \in [0, 1]$, we have $\tilde{x} > 0$. Therefore, equality (9) simplifies into

$$x(1) = x_0 + \int_0^1 (kx_0r(\tau) - (l(\tau) + \tilde{x})x(\tau))d\tau,$$

which corresponds to the value of a solution of problem

$$x'(t) = kx_0r(t) - (l(t) + \tilde{x})x(t), \quad x(0) = x_0, \quad (10)$$

at time $t = 1$.

We can express the solution of (10) at time $t = 1$ explicitly (see 2nd model), namely

$$x(1) = x_0\tilde{c},$$

where

$$\tilde{c} = e^{-\int_0^1 (l(\tau) + \tilde{x}) d\tau} \left(\int_0^1 e^{\int_0^\tau (l(z) + \tilde{x}) dz} k r(\tau) d\tau + 1 \right).$$

Because of $\tilde{x} > 0$, we have that $e^{\tilde{x}} > 1$ and

$$\begin{aligned} \tilde{c} &= e^{-\tilde{x}} e^{-\int_0^1 l(\tau) d\tau} \left(\int_0^1 e^{\tilde{x}\tau} e^{\int_0^\tau l(z) dz} k r(\tau) d\tau + 1 \right) \\ &< e^{-\tilde{x}} e^{-\int_0^1 l(\tau) d\tau} \left(\int_0^1 e^{\tilde{x}} e^{\int_0^\tau l(z) dz} k r(\tau) d\tau + e^{\tilde{x}} \right) = c, \end{aligned}$$

where c is defined in (2).

For a perishing population ($c < 1$), we have that $\tilde{c} < c$ and this population extincts faster than in the 2nd model.

For a stable population ($c = 1$), we have that $\tilde{c} < 1$ and such a population approaches to extinct.

For a growing population ($c > 1$), there are three states possible:

- Population extincts for $\tilde{c} < 1$.
- Population becomes stable for $\tilde{c} = 1$.
- Population increases for $\tilde{c} > 1$, but not so quickly.

Since \tilde{x} is such that

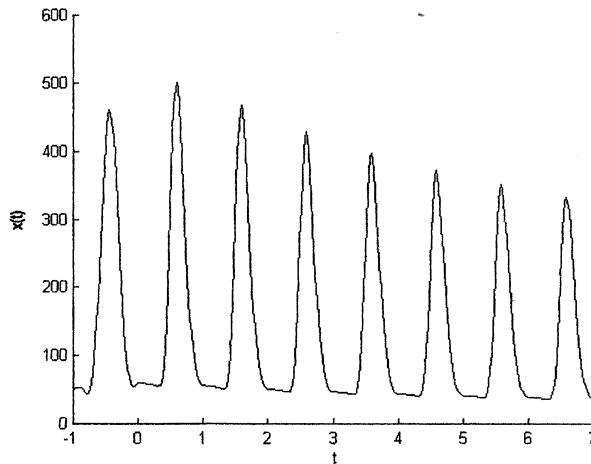
$$\int_0^1 f x(t) x(t) dt = \tilde{x} \int_0^1 x(t) dt,$$

we have that if $x_1(t) < x_2(t)$ for all $t \in [0, 1]$, then the corresponding constants \tilde{c}_1, \tilde{c}_2 satisfy $\tilde{c}_1 < \tilde{c}_2$. This means that *each population is bounded*.

It is possible to perform (in a more complicated way) a similar analysis for models (4) and (5).

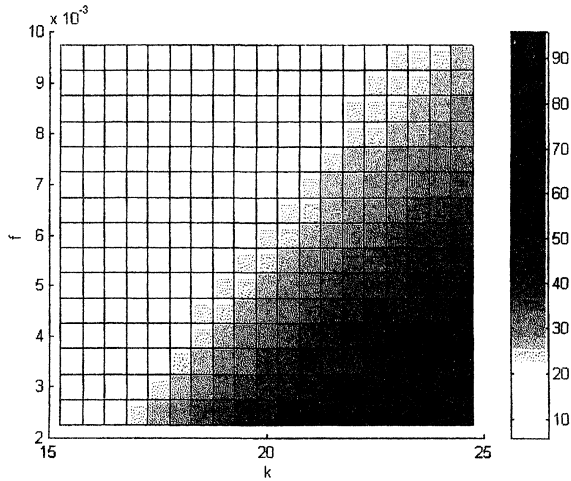
4.2 Numerical modelling

Consider equation (4) with delay $\tau = 1$. Letting $x_0 = 50$, $k = 20$, $f = 0.0015$, the mollusc population evolves in the following manner (vertical axis: number of individuals, horizontal axis: time in years):

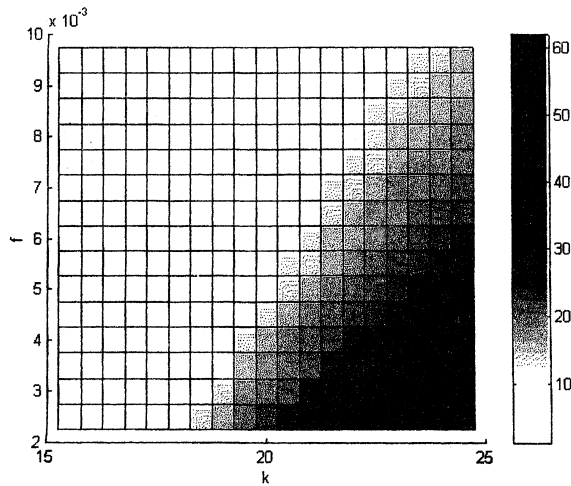


Now, we can introduce the diagrams showing the number of individuals in the population after eight years with the initial state $x_0 = 50$ in dependence on f, k . The lowest value of intraspecific competition is $f = 0.0025$ and the highest one is $f = 0.01$.

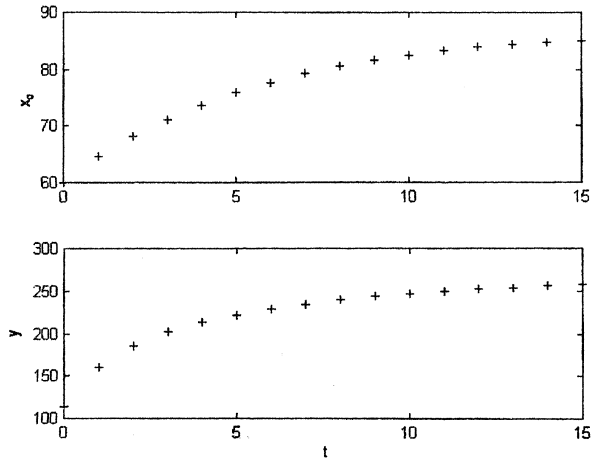
- For equation (3):



- For equation (4):



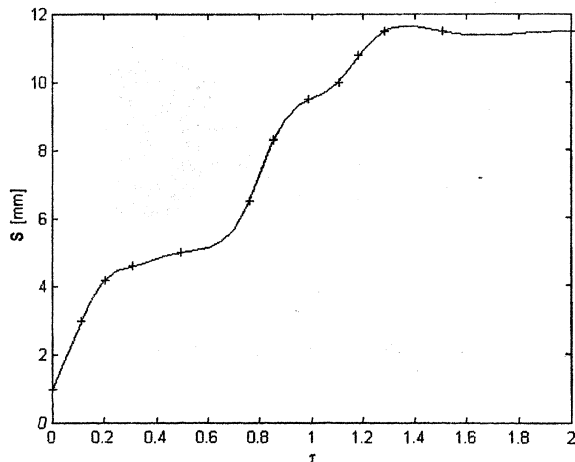
For the model (6)–(8), we set $x_0 = 50$, $a = 1$ and the initial state is a known function $g(t)$, $t \in [-1, 0]$, where $g(t) = 0$ for $t < -1$. The population then evolves in the following manner (first picture: number of individuals at the beginning of the year, second one: intensity of intraspecific competition at the same time):



5 Generalized McKendrick–von Foerster's model

At all former models, the population age structure is neglected. The model constructed in this section enables us to obtain the information about the population age structure throughout the year. So this model distinguishes individuals of different ages, and consequently individuals of different size classes.

In our modelled population, the dependence between age τ and size class S can be sketched as follows (the size class I contains the individuals of shell size 0–2 mm, the size class II contains the individuals of shell size 2–4 mm, etc.):



Notation:

- τ is the variable denoting an age of an individual,
- t is the variable denoting time,
- $x(\tau, t)$ is the number of individuals at age τ in time t ,
- $U(\tau, t)$ is the change of the mortality coefficient of an individual at age τ in time t ,
- $V(\tau, t)$ is the change of the fertility coefficient of an individual at age τ in time t ,
- $d(\tau, t, U)$ is the mortality of an individual at age τ in time t ,
- $b(\tau, t, V)$ is the fertility of an individual at age τ in time t ,
- $\phi(\tau)$ is the initial condition $\phi(\tau) = x(\tau, 0)$,
- $\bar{\tau}$ is the maximal age.

The form of functions U, V is necessary to be determined. We often take

$$U(\tau, t) = \int_0^{\bar{\tau}} u(\tau, \eta)x(\eta, t)d\eta \quad \text{and} \quad V(\tau, t) = \int_0^{\bar{\tau}} v(\tau, \eta)x(\eta, t)d\eta.$$

The function $u(\tau, \eta)$ characterizes the mortality change of an individual at age τ influenced by the natural activities of an individual at age η . The function $v(\tau, \eta)$ characterizes fertility change of an individual at age τ influenced by the natural activities of an individual at age η . The functions $b(\tau, t, V) \geq 0$, $d(\tau, t, U) \geq 0$ are defined for $0 \leq \tau \leq \bar{\tau}$, $t \geq 0$. Let $U, V \in C([0, \bar{\tau}] \times R_+^1)$, $b, d \in C([0, \bar{\tau}] \times R_+^1 \times R_+^1)$.

5.1 Model construction and its analysis (cf. [4])

In time t , the number of individuals at age $0 \leq \tau \leq \bar{\tau}$ is equal to $x(\tau, t)$. During the time since t to $t + h$, the age of individuals increases to $\tau + h$. This means that the relation

$$dx(\tau, t) = \lim_{h \rightarrow 0^+} \frac{x(\tau + h, t + h) - x(\tau, t)}{h}$$

corresponds to the speed of the change of individuals number in the class. Assuming that $x(\tau, t)$ is differentiable, we obtain

$$dx(\tau, t) = \frac{\partial x(\tau, t)}{\partial \tau} + \frac{\partial x(\tau, t)}{\partial t}.$$

Obviously, the change of individuals number in the class is caused by mortality

$$dx(\tau, t) = -d(\tau, t, U)x(\tau, t).$$

After all, we get the following model which is generalization of the McKendrick–von Foerster one:

$$\frac{\partial x(\tau, t)}{\partial \tau} + \frac{\partial x(\tau, t)}{\partial t} = -d(\tau, t, U) x(\tau, t), \quad (11)$$

$$U(\tau, t) = \int_0^{\bar{\tau}} u(\tau, \eta) x(\eta, t) d\eta, \quad (12)$$

$$V(\tau, t) = \int_0^{\bar{\tau}} v(\tau, \eta) x(\eta, t) d\eta, \quad (13)$$

with the initial condition

$$x(\tau, 0) = \phi(\tau), \quad \phi(\tau) \geq 0, \quad \phi(\bar{\tau}) = 0, \quad (14)$$

and with the boundary conditions

$$x(0, t) = \int_0^{\bar{\tau}} b(\tau, t, V) x(\tau, t) d\tau, \quad (15)$$

$$x(\tau, t) = 0, \quad \text{for } \forall \tau \geq \bar{\tau}, t \geq 0.$$

To solve this problem, we require obeying the consistence condition at point $(0, 0)$:

$$\phi(0) = \int_0^{\bar{\tau}} b(\tau, 0, V) \phi(\tau) d\tau.$$

The following theorem guarantees the existence of a solution to problem (11)–(15).

Theorem 4 ([1]) *Assume that $u(\tau, t) \equiv v(\tau, t) \equiv 1$. Let $b, d, \phi, \frac{\partial b}{\partial V}, \frac{\partial d}{\partial U}$ be continuous functions and let $b(\tau, t, V) < \infty$, $\tau \in [0, \bar{\tau}]$, $t \geq 0$, $V \geq 0$. Then problem (11)–(15) has a unique solution $x(\tau, t)$, for $0 \leq \tau \leq \bar{\tau}$, $t \geq 0$.*

It is possible to transform this problem into the form of integral equations (see e.g. [5]).

Let $x(\tau, t)$ be the solution of problem (11)–(15), for $0 \leq \tau \leq \bar{\tau}$, $t \geq 0$. For arbitrary $\tau_0, t_0 : (\tau_0, t_0) \in [0, \bar{\tau}] \times R_+^1$, define the following functions

$$\bar{x}(h) = x(\tau_0 + h, t_0 + h),$$

$$\bar{d}(h) = d(\tau_0 + h, t_0 + h, U(\tau_0 + h, t_0 + h)).$$

In view of (11), the function $\bar{x}(h)$ satisfies the ordinary differential equation

$$\frac{d\bar{x}(h)}{dh} + \bar{d}(h)\bar{x}(h) = 0. \quad (16)$$

This equation has a unique solution

$$\bar{x}(h) = \begin{cases} \bar{x}(0) \exp\{-\int_0^h \bar{d}(\eta) d\eta\} & \text{for } h < \bar{\tau} - \tau_0, \\ 0 & \text{for } h \geq \bar{\tau} - \tau_0 \end{cases} \quad (17)$$

generating the function $x(\tau, t)$ at all points of the characteristic, passing through (τ_0, t_0) .

Letting $(\tau_0, t_0) = (\tau - t, 0)$, $h = t$, we obtain from (17) and (14) that

$$x(\tau, t) = \phi(\tau - t) \exp\left\{-\int_0^t d(\tau - t + \eta, \eta, U(\tau - t + \eta, \eta)) d\eta\right\}, \quad (18)$$

$0 < t \leq \tau \leq \bar{\tau}$. This equation describes the dynamics of individuals living at initial time $t = 0$.

Letting, furthermore, $(\tau_0, t_0) = (0, t - \tau)$, $h = \tau$, we obtain from (17) that

$$x(\tau, t) = B(t - \tau) \exp\left\{-\int_0^\tau d(\eta, t - \tau + \eta, U(\eta, t - \tau + \eta)) d\eta\right\}, \quad (19)$$

$t > \tau$, $\tau \in [0, \bar{\tau}]$, where $B(t - \tau) = x(0, t - \tau)$. This equation describes the dynamics of individuals borne at time $t - \tau$.

The expression

$$l(\tau, t, U) = \frac{x(\tau, t)}{B(t - \tau)} = \exp\left\{-\int_0^\tau d(\eta, t - \tau + \eta, U(\eta, t - \tau + \eta)) d\eta\right\}, \quad (20)$$

$t > \tau$, represents the ratio of the number of individuals which survive until the age τ at time $t > \tau$ to those borne at the time $t - \tau$. Finally, we can put

$$l_0(\tau, t, U) = \frac{x(\tau, t)}{\phi(\tau - t)} = \exp\left\{-\int_0^t d(\tau - t + \eta, \eta, U(\tau - t + \eta, \eta)) d\eta\right\}, \quad (21)$$

$0 < t \leq \tau \leq \bar{\tau}$, which represents the ratio of individuals of age τ surviving until the time $t \leq \tau$ to those of age $\tau - t$ at time $t = 0$.

Denote by R the reproductive value of an individual, indicating the mean value of descendants of one individual at time $t > \bar{\tau}$ during life time, namely

$$R(t, U, V) = \int_0^{\bar{\tau}} b(\tau, t, V) l(\tau, t, U) d\tau, \quad t > \bar{\tau}.$$

For stable populations, it holds that $R \approx 1$ (see [4], [5]).

Now, substitute (18), (19) into (15). At first, letting $t < \bar{\tau}$, we obtain for $B(t)$ that

$$B(t) = \int_t^{\bar{\tau}} b(\tau, t, V) l_0(\tau, t, U) \phi(\tau - t) d\tau + \int_0^t b(\tau, t, V) l(\tau, t, U) B(t - \tau) d\tau. \quad (22)$$

Denote

$$B^-(t) = \int_t^{\bar{\tau}} b(\tau, t, V) l_0(\tau, t, U) \phi(\tau - t) d\tau, \quad 0 \leq t \leq \bar{\tau}. \quad (23)$$

For $t > \bar{\tau}$, (22) simplifies into

$$B(t) = \int_0^{\bar{\tau}} b(\tau, t, V) l(\tau, t, U) B(t - \tau) d\tau. \quad (24)$$

Similarly, after substituting (18), (19) into (12), (13), we obtain the expressions $U(\tau, t)$, $V(\tau, t)$. Denoting

$$U^-(\tau, t) = \int_t^{\bar{\tau}} u(\tau, \eta) l_0(\eta, t, U) \phi(\eta - t) d\eta, \quad 0 \leq t \leq \bar{\tau}, \quad (25)$$

$$V^-(\tau, t) = \int_t^{\bar{\tau}} v(\tau, \eta) l_0(\eta, t, U) \phi(\eta - t) d\eta, \quad 0 \leq t \leq \bar{\tau}, \quad (26)$$

we arrive at

$$U(\tau, t) = U^-(\tau, t) + \int_0^t u(\tau, \eta, V) l(\eta, t, U) B(t - \eta) d\eta, \quad 0 \leq t \leq \bar{\tau}, \quad (27)$$

$$U(\tau, t) = \int_0^{\bar{\tau}} u(\tau, \eta, V) l(\eta, t, U) B(t - \eta) d\eta, \quad t > \bar{\tau} \quad (28)$$

and

$$V(\tau, t) = V^-(\tau, t) + \int_0^t v(\tau, \eta, V) l(\eta, t, U) B(t - \eta) d\eta, \quad 0 \leq t \leq \bar{\tau}, \quad (29)$$

$$V(\tau, t) = \int_0^{\bar{\tau}} v(\tau, \eta, V) l(\eta, t, U) B(t - \eta) d\eta, \quad t > \bar{\tau}. \quad (30)$$

In [1], the equivalence of both systems, (11)–(15) and (20)–(30), has been proved.

In case $u(\tau, t) \equiv v(\tau, t) \equiv 0$, i.e. when we do not look at the intraspecific competition, we obtain the following system

$$B^-(t) = \int_t^{\bar{\tau}} b(\tau, t) l_0(\tau, t) \phi(\tau - t) d\tau, \quad 0 \leq t \leq \bar{\tau}, \quad (31)$$

$$B(t) = B^-(t) + \int_0^t b(\tau, t) l(\tau, t) B(t - \tau) d\tau, \quad 0 \leq t \leq \bar{\tau}, \quad (32)$$

$$B(t) = \int_0^{\bar{\tau}} b(\tau, t) l(\tau, t) B(t - \tau) d\tau, \quad t > \bar{\tau}. \quad (33)$$

Note that the functions b, d, l, l_0 do not depend on V , resp. U .

5.2 Numerical modelling

5.2.1 Estimation of function $\phi(\tau)$

We determine function $\phi(\tau)$ by means of histopolation. We know from the data that the number of individuals in the i th age class is ϕ_i , and that in the i th class the individuals are at age $[\tau_i, \tau_{i+1}]$. Thus,

$$\int_{\tau_i}^{\tau_{i+1}} \phi(\tau) d\tau = \phi_i.$$

5.2.2 Estimation of function $d(\tau, t)$

Assuming that the function $d = d(\tau, t)$ is piece-wise constant, we obtain from (20) and (21) that

$$\frac{x(\tau, t)}{x(\tau - \alpha, t - \alpha)} = \frac{x(\tau, t)}{B(t - \tau)} \bigg/ \frac{x(\tau - \alpha, t - \alpha)}{B(t - \tau)} = \exp\left\{-\int_{\tau - \alpha}^{\tau} d \, d\eta\right\}, \quad t \geq \tau,$$

$$\frac{x(\tau, t)}{x(\tau - \alpha, t - \alpha)} = \frac{x(\tau, t)}{\phi(t - \tau)} \bigg/ \frac{x(\tau - \alpha, t - \alpha)}{\phi(t - \tau)} = \exp\left\{-\int_{t - \alpha}^t d \, d\eta\right\}, \quad t < \tau.$$

For the values d , we get

$$\frac{x(\tau, t)}{x(\tau - \alpha, t - \alpha)} = e^{-d\alpha},$$

in both cases ($t \geq \tau$ and $t < \tau$).

From the biological assumptions done in this article, we have

$$\int_0^{\bar{\tau}} d \, d\eta = \infty,$$

because all individuals die before reaching the age $\bar{\tau}$. The function d defined above does not fulfil this condition, but values

$$\int_0^{\bar{\tau}} d \, d\eta$$

are sufficiently large to be in a reasonable agreement.

To obtain the function $d(\tau, t)$ which is sufficiently smooth, we use the quadratic Bezier surface defined over data d . For sufficiently small parts, the Bezier surface is close enough to the real function $d(\tau, t)$.

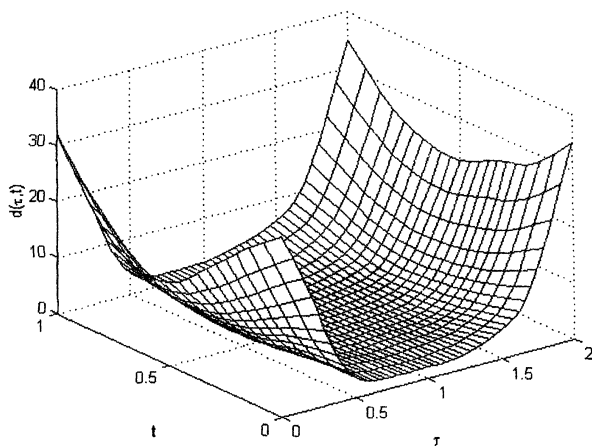
Now we determine the net of the values $d_{i,j}$ and the required Bezier surface can be spaced by these values. The idea to obtain the value $d_{i,j}$ using the table follows. The number of individuals at row $i + 1$, column $j + 1$, divided by the number at row i , column j , corresponds to the value $\exp(-d_{i,j}\alpha)$. Value $d_{i,\bar{\tau}}$, which define the values $d(\bar{\tau}, t)$, have to be infinity (i.e. sufficiently large), and the values $d_{i,j}$ at time $t = 0$ and time $t = 1$ are the same, $d(\tau, 0) = d(\tau, 1)$. We have to be careful, because some individuals at category (i, j) came over to the category $(i + 1, j)$ or $(i + 1, j + 2)$ and not to the category $(i + 1, j + 1)$.

5.2.3 Estimation of function $b(\tau, t)$

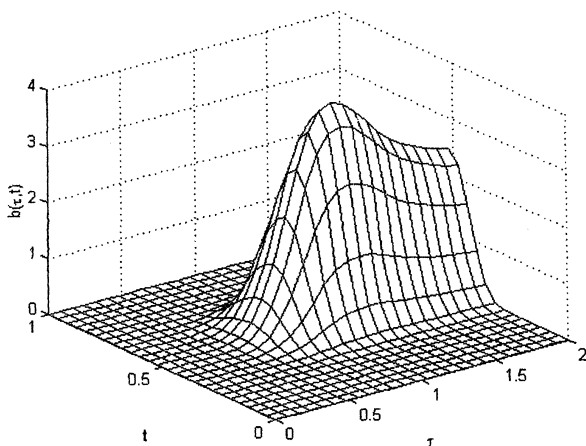
The function $b(\tau, t)$ takes the form $b(\tau, t) = b_1(\tau)r(t)$, where $b_1(\tau)$ characterizes dependence between the age and the reproduction ability, and $r(t)$ is taken from the section (2.2.1). In our case, the function $b_1(\tau)$ is guessed. For more accurate estimation we need another experiment.

The functions of fertility and mortality generated from experimental data look as follows:

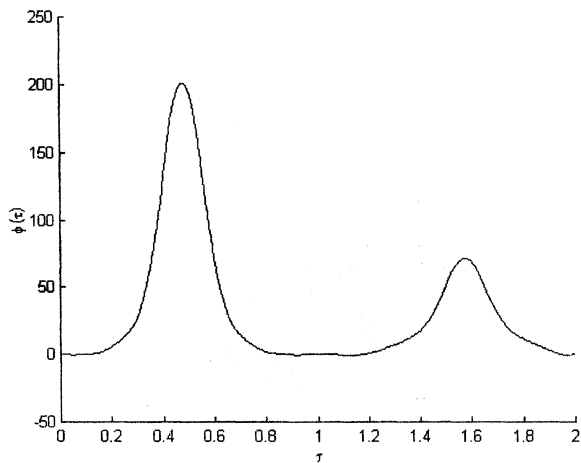
- The function $d(\tau, t)$:



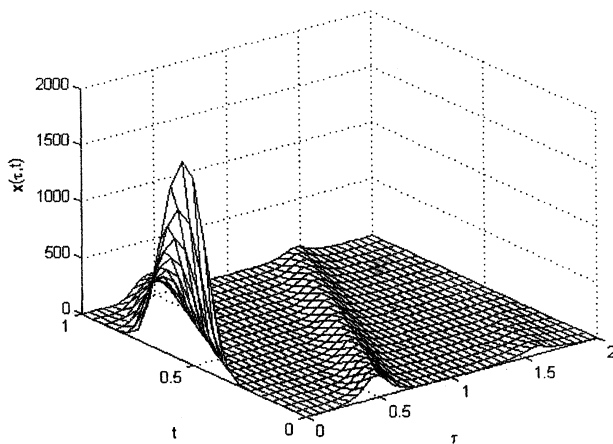
- The function $b(\tau, t)$:



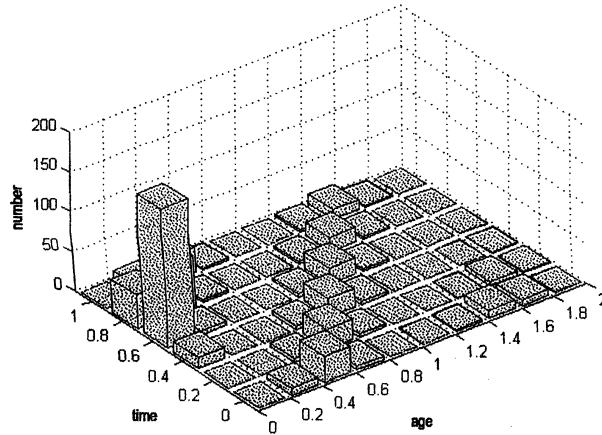
The function $\phi(\tau)$ describing the population spread in time $t = 0$ looks as follows (note that the number of individuals at age $[\tau_1, \tau_2]$ is $\int_{\tau_1}^{\tau_2} \phi(\tau) d\tau$):



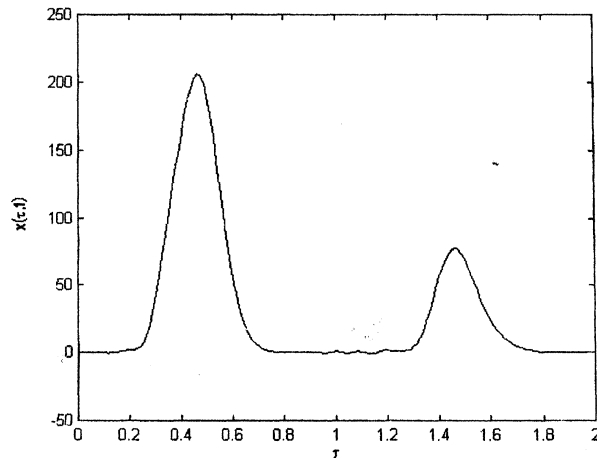
So, the evolution of the population looks as follows:



Such a function $x(\tau, t)$, as shown in the last picture, corresponds to following numbers of individuals



and the function $x(\tau, 1)$, describing the population spread in time $t = 1$, looks as follows:



6 Concluding discussion

The constant c has an essential influence on the behaviour of the first two models. It represents the rate of environmental influences on the population accumulated during one year period. If $c < 1$, the population extincts, if $c > 1$, it grows permanently and, if $c = 1$, it is stable. For the population of *Bithynia tentaculata*, which we observed for two seasons, the constant was $c > 1$. These

two models are substantially simplified as neither age structure nor intraspecific competition were considered. The simplicity of these models allows us to perform a qualitative analysis under random influences. This analysis can be used to make a prognosis of the behaviour of the population affected by random influence activities.

The 3rd model includes an intraspecific competition. Considering the intraspecific competition is one of the possible ways of stopping the continuous growth of the population. This model is more appropriate from a biological point of view. In this model, constant \tilde{c} plays the same role as constant c in the previous model. In such a case, \tilde{c} is not explicitly known, but we do know its upper estimate which is constant c from the 2nd model. Constant \tilde{c} covers, in addition to the environmental influences, the rate of intraspecific competition.

The McKendrick–von Foerster model, which is rather complicated, differs from previous models in the way that we can use it to study the age structure of the population during a year. From a biological point of view, the study of age structure is essential. Number R (the mean value of descendants of one individual during its life time) plays the same role as constant c in the first model.

In order to apply these models in biologically real sense to the prognosis of the population, it is necessary to correct them by using more extensive data sets which may describe a population as observed over a longer time frame.

The authors are indebted to the anonymous referee for careful reading of the manuscript and to Sandra Sweeney for improving the English of the paper.

Appendix

Splines

Definition 2 (cf. e.g. [2]) A function $S_{m,d}(x)$, $x \in [a, b]$, satisfying on the set of knots $(\Delta x) : a = x_0 < x_1 < \dots < x_n < x_{n+1} = b$, the following properties:

(i) $S_{m,d}(x)$ is a polynomial of degree m , at most, on each interval $[x_i, x_{i+1}]$, $i = 1, \dots, n$,

(ii) $S_{m,d}(x) \in C^{m-d}([a, b])$,

will be called the polynomial spline of degree $m \geq 0$ with defect $d \geq 0$, $m \geq d$.

In our situation, only quadratic and cubic splines with defect 1 are employed.

Histopolation

We look for a function $g(\tau)$ satisfying $\int_{\tau_i}^{\tau_{i+1}} g(\tau) d\tau = g_i$, where g_i are given values. The function $g(\tau)$ is assumed to be a quadratic polynomial $\sigma_i(\tau)$ at each interval $[\tau_i, \tau_{i+1}]$. The coefficients of each polynomial can be determined in order the desired function $g(\tau)$ to be from $C^1[0, \tau_{n+1}]$ -class, i.e. we approximate

the function g by a quadratic spline S_{21} . This procedure is usually called a *histopolation* (for more details see e.g. [2]).

Consider the set of knots $\tau_1 < \tau_2 < \dots < \tau_n < \tau_{n+1}$. At the knots τ_i , the spline value is s_i . Defining $h_i = \tau_{i+1} - \tau_i$, $i = 1, 2, \dots, n$, we can put

$$\sigma_i(\tau) = a + bq + cq^2, \quad q = \frac{\tau - \tau_i}{h_i}, \quad \tau \in [\tau_i, \tau_{i+1}].$$

The following conditions for coefficients a, b, c can be easily obtained:

$$\begin{aligned} \sigma_i(\tau_i) &= s_i, \\ \int_{\tau_i}^{\tau_{i+1}} \sigma_i(\tau) d\tau &= g_i, \\ \sigma_i(\tau_{i+1}) &= s_{i+1}, \end{aligned}$$

from which we come to

$$\begin{aligned} a &= s_i, \\ b &= \frac{6}{h_i} g_i - 4s_i - 2s_{i+1}, \\ c &= 3(s_i + s_{i+1} - \frac{2}{h_i} g_i). \end{aligned}$$

The function $g(\tau)$ constructed in this way is “only” continuous. Therefore, we are looking for values s_i to obtain C^1 -continuity.

So, we come to

$$\sigma'_{i-1}(\tau_i) = \sigma'_i(\tau_i)$$

at each knot τ_i , $i = 2, 3, \dots, n$. Furthermore, we can choose two parameters (mostly s_1, s_{n+1} , so-called boundary conditions), by which we obtain system of $n - 1$ equations for $n - 1$ unknowns:

$$\begin{aligned} 2s_2(h_1 + h_2) & \quad s_3 h_1 & & = d_2 - s_1 h_2, \\ h_i s_{i-1} & \quad 2s_i(h_{i-1} + h_i) & \quad s_{i+1} h_{i-1} & = d_i, \quad i = 3, \dots, n-1, \\ & \quad h_n s_{n-1} & \quad 2s_n(h_{n-1} + h_n) & = d_n - s_{n+1} h_{n-1}, \end{aligned}$$

where $d_i = 3(g_i \frac{h_{i-1}}{h_i} + g_{i-1} \frac{h_i}{h_{i-1}})$. Resulting values s_i generate the desired function $g(t)$.

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