On modeling of amphibious population evolution

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Abstract: We consider an evolution model of population of frogs on the aqueous stage of their development. Here we study the problem of determination of the parameters of the proposed model from the observation data, in particular, from the average times of attainment of different biological ages and from the survivability function.
Our model gives possibility to estimate the number of morphologically indistinguishable ages which is particularly interesting in the case of incomplete experimental data.

We consider a model of evolution of populations of larvae of *Rana temporaria L.* and *R. Arvalis Nills* from the stages of the fertilized spawn till the moment of outgo of young-of-the-year to land.

The number of the age stages for these populations can be rather large. For example, there are 39 age stages from that of the zero moment fertilized spawn till the free-swimming larvae stage, see [1].

The main feature of the model under consideration is the explicit description of all possible ontogenetic stages of a developing specimen till its outgo from the water to the land. This is necessary for detailed account of influence of different external and internal factors on the dynamics of the population evolution.

The modeling of this evolution is constructed in terms on the interconnected elementary processes described by the system of differential equations

$$\begin{aligned} &dI_0/dt = -(k_0 + d_0)I_0; \\ &dI_j/dt = -(k_j + d_j)I_j + k_{j-1}I_{j-1}; \quad j = 1, \dots, n; \\ &dI_{n+1}/dt = +k_n I_n. \end{aligned} \tag{1}$$

Here, the function $I_j(t)$ describes the quantity of the fertilized spawn on the age stage number j at the moment t, d_j is the mortality rate of the larvae at this age stage, k_j is the velocity of transition from the age number

j to the age number $j+1$. In general the parameters k_j, d_j can depend on the external factors (temperature, aeration etc). They are assumed to be constant in our model.

One of the main aim of construction of our model is determination of the values of these elementary processes parameters from the experimental observation data.

It is easy to verify that the solution of the system (1) has the following form

$$I_0(t) = C_0 \mathrm{e}^{-m_0 t}; \quad I_j(t) = C_j \sum_{l=0}^{n} a_{j,l} \mathrm{e}^{-m_l t}.$$

Here, $C_j = C_0 k_1 \ldots k_{j-1}$, $j = 0, \ldots, n$ and

$$a_{j,l} = \prod_{s=0, s \neq l}^{j} (m_s - m_l)^{-1}, \quad m_j = k_j + d_j,$$

As it was mentioned above, the number of morphologically distinguishable stages of the specimen development can be rather large. One can measure experimentally the length of each of these stages, the time M of the mass outgo of the larvae from the spawn, the average deviation σ of this process and the survivability S of the spawn, see [1].

Consider interconnections of the measured parameters M_j, σ_j, S_j with the coefficients k_j, d_j of our model.

It is not difficult to verify that for all values of these coefficients all the functions $I_j(t)$ and their derivatives dI_j/dt, $j = 0, \ldots, n$ have exactly one maximum. Furthermore, the kinetics of the passing of each age stage of the larvae depends on the unordered collection of the velocities of passing of the previous age stages, i.e., this kinetics will not change if any two of these velocities will be changed one to another.

If the number of the spawn which have passed from the j-th age stage to the $j+1$-th is considered as a random value with the distribution density

$$p_j(t) = m_0 \cdot \ldots m_j \sum_{l=0}^{j} a_{j,l} \exp(-m_l t),$$

then the mean time of the j-th age stage attainment and the dispersion of this process are

$$M_j = 1/m_0 + \ldots + 1/m_j, \tag{2}$$

$$D_j = (1/m_0)^2 + \ldots + (1/m_j)^2. \tag{3}$$

The part of the spawn of the age number j in the total number of the fertilized spawn has the form

$$S_j = k_0 \cdot \ldots k_j / m_0 \cdot \ldots m_j. \tag{4}$$

Here, as above $j = 0, \ldots, n$.

The relations (2) – (4) make possible determination of the parameters k_j, d_j of the elementary processes in our model from the statistical characteristics M_j, D_j, S_j.

Our model is particularly interesting in the case of incomplete experimental data, i.e., if they are known just for some of the age stages. Consider for the beginning a simple variant of this model.

Assume that the biological age number j has n_j indistinguishable sub-stages and that all these sub-stages have the same parameters k_j, d_j. Then this population has the following statistical characteristics

$$M_j = n_0/m_0 + \ldots + n_j/m_j,$$

$$D_j = n_0/(m_0)^2 + \ldots + n_j/(m_j)^2,$$

$$S_j = \prod_{s=0}^{j} (k_s/m_s)^{n_s}.$$

The numbers $j = 0, \ldots, N$ correspond to the morphologically distinguishable ages.

This system has a unique positive solution if and only if $M_j < M_{j+1}$, $D_j < D_{j+1}$, $S_j > S_{j+1}$ for all $j \geq 0$. The values of the parameters k_j, n_j, m_j can be determined from the following recurrence relations

$$m_j = \frac{(M_j - M_{j-1})}{(D_j - D_{j-1})}; \qquad n_j = (M_j - M_{j-1}) \cdot m_j;$$

$$k_j = \sqrt[n_j]{S_j/S_{j-1}} m_j.$$

1. The model dimension estimates.

Assume the mean times $\mathcal{M}_j$ of larvae sojourn in the j-th morphologically distinguishable age stage, $j = 0, \ldots, N$, and the dispersions $\mathcal{D}_j$ of this random values to be measured in the experiment. Let n_j be the number of indistinguishable age stages. In this example, we shall begin the numbering of these stages from one.

So, one has

$$\mathcal{M}_j = 1/m_1 + \ldots + 1/m_{n_j}; \tag{5}$$

$$\mathcal{D}_j = (1/m_1)^2 + \ldots + (1/m_{n_j})^2. \tag{6}$$

We need to determine here the number of indistinguishable age stages n_j and the values of the parameters $m_1, \ldots, m_{n_j}$. This problem is equivalent to determination of intersection of the positive octante of n_j-dimensional euclidean space of the variables $1/m_i$, $i = 1, \ldots, n_j$, the plane P in this space which is described by the equation (5) and the sphere S^{n_j-1} of the radius $\sqrt{\mathcal{D}_j}$ centered in the origin of this space given by the equation (6).

It is obvious that the distance between this origin and the plane P is $\mathcal{M}_j/\sqrt{n_j}$. Hence, the plane P and the sphere S^{n_j-1} do intersect only if $\mathcal{M}_j/\sqrt{n_j} \leq \sqrt{\mathcal{D}_j}$. So, we obtain a lower estimate for the integer n_j: $n_j \geq \mathcal{M}_j^2/\mathcal{D}_j$. If this inequality is strict, then this plane and this sphere have infinitely many common points in the positive octant of the space.

Additional information on relations of the unknown parameters allows to reduce this intersection. In particular, if it is known that $n_j = \lfloor \mathcal{M}_j^2/\mathcal{D}_j \rfloor + 1$ and that for some number $i_1 \leq n_j$ one has $m_i = m_{(2)}$ for all $i \neq i_1$, then the system (5), (6) has the form

$$1/m_{i_1} + (n_j - 1)/m_{(2)} = \mathcal{M}_j; \qquad (1/m_{i_1})^2 + (n_j - 1)/(m_{(2)})^2 = \mathcal{D}_j,$$

and hence,

$$m_{i_1} = \frac{n_j}{(n_j - 1)\sqrt{n_j \mathcal{D}_j - \mathcal{M}_j^2}}, \qquad m_{(2)} = \frac{n_j - 1}{\mathcal{M}_j - 1/m_{i_1}}.$$

As usual, we denote by $\lfloor z \rfloor$ the largest integer less than or equal to z.

Consider another example. Assume that the parameters $1/m_i$ corresponding to the morphologically indistinguishable age sub-stages at the stage number j compose an arithmetical progression with an unknown difference Δ.

1. Let $n_j = \lfloor \mathcal{M}_j^2/\mathcal{D}_j \rfloor + 1 = 2p + 1$ be an odd number and $\mu = 1/m_p$,

$$\frac{\mathcal{M}_j^2}{\mathcal{D}_j} = 2p + 1 - x.$$

So, $1 - x$ is the fractional part of the number $\mathcal{M}_j^2/\mathcal{D}_j$.

Then $\mathcal{M}_j = (2p + 1)\mu$, $\quad \mathcal{D}_j = (p + 1)\mu^2 + \Delta^2 p(p + 1)(2p + 1)/3$, and consequently

$$\frac{\mathcal{D}_j(2p + 1)}{\mathcal{M}_j^2} = 1 + \frac{\Delta^2 p(p + 1)}{3\mu^2},$$

hence

$$\Delta = \pm \frac{1}{2p+1}\sqrt{\frac{3\mathcal{D}_j x}{p(p+1)}}.$$

2. In the same way for an even $n_j = \lfloor \mathcal{M}_j^2/\mathcal{D}_j \rfloor + 1 = 2p$ one has

$$\Delta = \pm \frac{1}{2p}\sqrt{\frac{6\mathcal{D}_j x}{(p+1)(2p+1)}}.$$

So, for all odd and even values of n_j the sequences of the parameters m_i, $i = 1, \dots, n_j$ are determined up to the direction of their numeration, either this is an increasing arithmetical progression, or this is a decreasing arithmetical progression. The choice of the sign in the previous two formulas can be done matching the obtained results with the parameters determined for the nearby age stages with the numbers $j-1$ and $j+1$.

2. Determination of the parameters from the survivability function.

Suppose that for all values of t the total number of species in the population can be determined. Thus, one can define the function

$$X_n(t) = C_0 \sum_{i=0}^{n} k_0 \cdot \ldots \cdot k_{i-1} \left(\sum_{j=0}^{i} a_{i,j} \exp(-m_j t) \right). \tag{7}$$

We call X_n the survivability function. Corresponding random value describes the quantity of specimens whose age does not exceed n at the moment t.

Here, as above $a_{i,j} = \prod_{j=0, i\neq j}^{i} (m_i - m_j)^{-1}, \quad a_{0,0} = 1.$

Consider a distribution with the density $F_n(t) = 1 - X_n(t)/C_0$ and corresponding moments of all integer orders

$$V_{p,n} = \int_0^\infty t^p \frac{\mathrm{d}F_n}{\mathrm{d}t}\,\mathrm{d}t,$$

$p = 1, \dots, \infty$, see. [2].

Let $\alpha_i = k_i/m_i\,,\ \tau_i = 1/m_i\,,\ \beta_i = \alpha_0 \cdot \ldots \cdot \alpha_i$, where $i = 0, \dots, n$. It is obvious that $0 \le \alpha_i \le 1$, $1 \ge \beta_i \ge \beta_{i+1} \ge 0$.

We shall use in the sequel the following symmetric function

$$S_p(\tau_0, \ldots, \tau_i) = \sum \tau_0^{\alpha_0} \cdot \ldots \cdot \tau_i^{\alpha_i}$$

of the variables $\tau_0, \ldots, \tau_i$; here, we summarize over all partitions of a natural number p to non-negative summands $\alpha_0, \ldots, \alpha_i$.

Simple calculations show that

$$V_{1,n} = \tau_0 + \ldots + \beta_{n-1}\tau_n,$$

$$V_{2,n} = 2[\tau_0^2 + \beta_0\tau_1(\tau_0 + \tau_1) + \ldots + \beta_{n-1}\tau_n(\tau_0 + \ldots + \tau_n)],$$

and for $p \geq 1$

$$V_{p,n} = p!\Big(\tau_0^p + \beta_0\tau_1 S_{p-1}(\tau_0, \tau_1) + \ldots + \beta_{n-1}\tau_n S_{p-1}(\tau_0, \ldots, \tau_n)\Big).$$

Consider the problem of determination of the parameters n, β_i, τ_i, $i = 0, \ldots, n$ from the values of the moments $V_{1,n}$, $V_{2,n}, \ldots$, $V_{p,n}, \ldots$ calculated from the experimental data. Here, n denotes the number of indistinguishable age sub-stages of some morphologically distinguishable age.

Lemma 1. *Let* $k \geq 1$, $0 < \gamma_l < 1$, $l = 1, \ldots, k$, *then*

$$\lim_{i\to\infty} S_i(1, \gamma_1, \ldots, \gamma_k) = \prod_{l=1}^{k} (1 - \gamma_l)^{-1}.$$

Proof follows from induction over k.

Lemma 2. *Let* $k, q \geq 1$, *then*

$$\lim_{i\to\infty} S_i(\underbrace{1, \ldots, 1}_{q}, \gamma_1, \ldots, \gamma_k) \cdot \begin{pmatrix} i + q - 1 \\ q - 1 \end{pmatrix}^{-1} = \prod_{l=1}^{k} (1 - \gamma_l)^{-1}.$$

Proof is based on induction over k and follows from the fact that the number of partitions of an integer i to k nonnegative integer summands equals to the number of partitions of the number $i+k$ to k integer summands each of which is greater or equals 1.

Given a collection of numbers $\tau_0, \ldots, \tau_n$, we call the multiplicity of the number τ in this collection the quantity of the numbers in this collection which are equal to τ.

Next two lemmas follow from the previous statements and the definition of the moments $V_{i,n}$.

Lemma 3. *Let $\tau = \max\{\tau_0, \dots, \tau_n\}$, and let q be its multiplicity. Let m_s be the numbers for which $\tau = t_{m_s}$, $s = 1, \dots, q$. Then*

$$\lim_{i\to\infty} \frac{(q-1)! V_{i,n}}{(i+q-2)!\tau^i} = \sum_{k=m_q}^{n} \left(\beta_{k-1} \prod_{l=0,\, l\neq m_1,\dots,m_q}^{k} (1-\tau_l/\tau)^{-1} \right).$$

Lemma 4.

$$\lim_{i\to\infty} \frac{V_{i+1,n}}{iV_{i,n}} = \max\{\tau_0, \dots, \tau_n\}.$$

Let $\tau_{\{0\}} = \max\{\tau_0, \dots, \tau_n\}$. Denote by $\{\tau_0, \dots, \tau_n/\tau_{\{0\}}\}$ the set obtained from $\{\tau_0, \dots, \tau_n\}$ by eliminating this maximal number.

If the multiplicity of $\tau_{\{0\}}$ is greater than one, we eliminate this number with the maximal subscript. If the set $\{\tau_0, \dots, \tau_n/\tau_{\{0\}}, \dots, \tau_{\{k-1\}}\}$ is already constructed, then the set $\{\tau_0, \dots, \tau_n/\tau_{\{0\}}, \dots, \tau_{\{k\}}\}$ of $n-k$ numbers is constructed by the same way.

Given a sequence of positive numbers $a_0, \dots, a_n$, we introduce the following recurrent notations
$V_i^{(1)}(\tau_0, \dots, \beta_{n-1}, \tau_n; a_0) = V_{i,n} - ia_0 V_{i-1,n};$
$V_i^{(k)}(\tau_0, \dots, \beta_{n-1}, \tau_n; a_0, \dots, a_k) = V_i^{(k-1)}(\tau_0, \dots, \beta_{n-1}, \tau_n; a_0, \dots, a_{k-1}) -$
$ia_{k-1} V_{i-1}^{(k-1)}(\tau_0, \dots, \beta_{n-1}, \tau_n; a_0, \dots, a_{k-1}).$
Let σ be a permutation of the symbols $(0, 1, \dots, n)$ and $a_0 = \tau_{\sigma(0)}, \dots, a_n = \tau_{\sigma(n)}$. It is easy to verify that the function $V_{i+k+1}^{(k)}(\tau_0, \dots, \beta_{n-1}, \tau_n; a_0, \dots, a_k)$ is symmetric with respect to variables $a_0, \dots, a_k$, and that for all $i \geq 1$, $j \geq 1$

$$V_{n+j+1}^{(n+j)}(\tau_0, \dots, \beta_{n-1}, \tau_n; \tau_{\sigma(0)}, \dots, \tau_{\sigma(k-1)}) \equiv 0. \tag{8}$$

This relation allows to determine the value of parameter n from the experimental observations in our model.

Lemma 5. *Let $0 < k < n$ and σ be any permutation of the numbers $0, \dots, n$, then*

$$\lim_{i\to\infty} \frac{V_{i+1}^{(k)}(\tau_0, \dots, \beta_{n-1}, \tau_n; \tau_{\{\sigma(0)\}}, \dots, \tau_{\{\sigma(k-1)\}})}{iV_i^{(k)}(\tau_0, \dots, \beta_{n-1}, \tau_n; \tau_{\{\sigma(0)\}}, \dots, \tau_{\{\sigma(k-1)\}})} = \tau_{\{k\}}.$$

Outline of the proof: Choose k maximal numbers $\tau_{\sigma(0)}, \dots, \tau_{\sigma(k-1)}$ in the set $\{\tau_0, \dots, \tau_n\}$. Here $\sigma(0) < \dots \sigma(k-1)$ and q is the multiplicity of $\tau_{\{k\}}$ in the set $\{\tau_0, \dots, \tau_n/\tau_{\{0\}}, \dots \tau_{\{k-1\}}\}$. Comparing the maximal summands in the numerator and in the denominator in the fraction

$$\frac{V_{i+k}^{(k)}(\tau_0, \dots, \beta_{n-1}, \tau_n; \tau_{\{\sigma(0)\}}, \dots, \tau_{\{\sigma(k-1)\}})}{(i+k+q+2)!\tau_{\{k\}}^{i+k}},$$

one can verify that this fraction has a finite limit for $i \to \infty$. The statement of the lemma is verified in the same way.

Hence, the lemma 5 and the equation (8) allow to determine uniquely the values of the parameters τ_i and n from the modified values $V_i^{(k)}$ of the moments of the distribution (7) and at the same time give a simple algorithms of this determination.

However, these statements do not give possibility to reconstruct the order of the determined values $\tau_{\{0\}}, \ldots, \tau_{\{n\}}$ and the values of the numbers $\alpha_i = k_i/m_i$.

In general, this reconstruction problem has not an unique solution and the survivability function can "forget" partially or completely the order of the lengths of particular age stages.

Consider for the beginning a simple example. Assume that the ontogenesis in our model has two stages ($n = 2$), and the mean lengths of these stages are known: i.e.,

$$\frac{\mathrm{d}I_0}{\mathrm{d}t} = -m_0 I_0(t);$$
$$\frac{\mathrm{d}I_1}{\mathrm{d}t} = k_0 I_0(t) - m_1 I_1(t), \tag{9}$$

where $m_0 \geq k_0$ and the survivability function $X_1 = I_0 + I_1$

$$X_1(k_0, m_0, m_1) = C_0 \left(\mathrm{e}^{-m_0 t} + k_0 \cdot \frac{\mathrm{e}^{-m_0 t} - \mathrm{e}^{-m_1 t}}{m_1 - m_0} \right) \tag{10}$$

is known.

Now, we are going to determine the order of the numbering of the parameters $\tau_{\{i\}}$, either $\tau_{\{0\}}^{-1} = m_0$ (r) $\tau_{\{1\}}^{-1} = m_1$, or $\tau_{\{0\}}^{-1} = m_0$ (r) $\tau_{\{1\}}^{-1} = m_1$ For this purpose consider the mean for the survivability function (10).

$$M = \int_0^\infty t \, \mathrm{d}(1 - X_1/C_0) = \frac{m_1 + k_0}{m_0 m_1}.$$

If $\tau_{\{0\}}^{-1} = m_0$ and $\tau_{\{1\}}^{-1} = m_1$, then $k_0(\tau_{\{0\}}, \tau_{\{2\}}) = \frac{M - \tau_{\{0\}}}{\tau_{\{0\}} \tau_{\{1\}}}$ and in this case the survivability function has the form

$$X_1(k_0(\tau_{\{0\}}, \tau_{\{1\}}), m_0, m_1) = C_0 \left(\mathrm{e}^{-m_0 t} + k_0(\tau_{\{0\}}, \tau_{\{1\}}) \cdot \frac{\mathrm{e}^{-m_0 t} - \mathrm{e}^{-m_1 t}}{m_1 - m_0} \right).$$

In the opposite case $\tau_{\{0\}}^{-1} = m_1$ and $\tau_{\{1\}}^{-1} = m_0$, we have $k_0(\tau_{\{1\}}, \tau_{\{0\}}) = \frac{M - \tau_{\{1\}}}{\tau_{\{0\}} \tau_{\{1\}}}$, and hence,

$$X_1(k_0(\tau_{\{1\}}, \tau_{\{0\}}), m_1, m_0) = C_0 \left(\mathrm{e}^{-m_0 t} + k_0(\tau_{\{1\}}, \tau_{\{0\}}) \cdot \frac{\mathrm{e}^{-m_0 t} - \mathrm{e}^{-m_1 t}}{m_1 - m_0} \right).$$

In the case

$$0 < k_0(\tau_{\{0\}}, \tau_{\{1\}}) \le m_0, \quad 0 < k_0(\tau_{\{1\}}, \tau_{\{0\}}) \le m_1, \tag{11}$$

both variants of solution are equivalent, so the problem of ordering of the parameters $\tau_{\{i\}}$ in the model (9) has not a unique solution. If the parameters $k_0(\tau_{\{0\}}, \tau_{\{1\}}), k_0(\tau_{\{1\}}, \tau_{\{0\}})$ do not satisfy the condition (11), then only one of these ordering will be possible:

if $\tau_0 < M \le \tau_1$, then $m_0 = \tau_0^{-1}$, $m_1 = \tau_1^{-1}$;

if $\tau_1 < M \le \tau_0$, then $m_1 = \tau_0^{-1}$, $m_0 = \tau_1^{-1}$.

So, it is not possible to predict does the survivability function "remember" the ordering of the lengths of the age stages. For this purpose one needs to determine the total number of these stages and the unordered set of the values of the parameters $\{\tau_{\{i\}}\}$.

The considerations above can be extended to the cases of arbitrary $n \ge 2$. First, we shall show that the survivability function (7) is symmetric with respect to the parameters $m_0, \dots, m_n$ and to the moments $V_{p,n}$, $p = 0, \dots, n$. This symmetric form is determined as follows: Given $m_0, \dots, m_n$, $k_0 \le m_0, \dots, k_{n-1} \le m_{n-1}$, introduce the notations

$$A_{0,j,n} = 1; \quad A_{\gamma,j,n} = \sum_{\substack{0 \le j_1 < \dots < j_l \le n \\ j_1 \ne j, \dots, j_l \ne \gamma}} m_{j_1} \dots m_{j_l},$$

$$k_{i,n} = (-1)^{n-1} \left(\sum_{\gamma=0}^{n-1} \frac{A_{\gamma,i,n} V_{\gamma,n}}{\gamma!} \right) \cdot m_i^n, \quad i = 1, \dots, n.$$

Then the survivability function (7) can be represented in the following symmetric form

$$X_n = C_0 \sum_{i=0}^{n} k_{i,n} a_{n,i} \mathrm{e}^{-m_i t}. \tag{12}$$

Hence, for any positive $V_{0,n} = 1$, $V_{1,n}, \dots, V_{n-1,n}$ and positive parameters $m_0, \dots, m_n$ first n moments of the function X_n are equal to $V_{0,n}, \dots, V_{n-1,n}$, respectively.

So, the problem of determination of the number n and the set of the values $\{\tau_{\{1\}}, \dots, \tau_{\{n\}}\}$ is equivalent to determination of the symmetric form (12) of the function X_n and hence, the problem of determination of the ordering of $\{\tau_{\{1\}}, \dots, \tau_{\{n\}}\}$ is reduced to that of finding such permutation σ of the numbers $1, \dots, n$ that $\tau_{\{\sigma(1)\}} = m_1, \dots, \tau_{\{\sigma(n)\}} = m_n$.

In this case the function X_n is represented in the form

$$X_n = \sum_{j=1}^{n} C_{j-1} \sum_{l=0}^{j} a_{j,l} \mathrm{e}^{-m_l t},$$

$C_1 = C_0 k_0$, $C_2 = C_1 k_2, \ldots, C_{n-1} = C_{n-2} k_{n-1}$.

It can happen so that there are more than one permutation of the numbers for which the symmetric form (12) can be represented in the canonical form. In such cases the problem of determination of the parameters m_j for $j = 0, \ldots, n$ has several solutions.

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