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Analysis of some experimental time series by Gause: application of simple mathematical models

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Abstract

For the approximation of some of well-known time series of *Paramecia aurelia* and *Paramecia caudatum* (under the separated cultivation of both species) population size changing in time, some well-known models were used. For all considering models values of parameters were estimated with least square method (with global fitting) in two different ways: with and without additional limits for parameter's values. In the case without additional limits for model's parameters deviations between theoretical (model) trajectories and experimental time series were tested for Normality (Kolmogorov–Smirnov test, and Shapiro–Wilk test) with zero average, and for existence/absence of serial correlation (Durbin–Watson criteria). The best results were observed for Gompertz' and Verhulst' models. Under the assumption that parameter K (maximum value of population size) is greater than all elements of initial sample the best results were observed for Gompertz' model. In the last case the canonical technique for analysis of set of deviations can be applied in restricted form and needs in further development. In such a situation we cannot test the set of deviations on Normality with zero average (for big samples) because after a certain time moment all experimental points will be at one side of theoretical curve; at this situation we have to have a serial correlation in the sequence of deviations, etc.

Keywords Gause; time series; continuous time; model; approximation; test.

1 Introduction

It is difficult to point out a textbook on ecological modeling without the presentation of the results of well-known experiments by G.F. Gause (1933, 1934). Results obtained by G.F. Gause for separated and combined cultivation of *Paramecia aurelia* and *Paramecia caudatum*, are normally used for demonstration of good correspondence between theory (Verhulst' model of isolated population dynamics and Lotka–Volterra' model of competition between two species; Verhulst, 1838; Volterra, 1931; Lotka, 1920, 1925) and experiment. It is also used for demonstration of the legality of use of such mathematical models for the approximation of real datasets.

But it is important to note that in original publication by G.F. Gause (1934) there are no analyses of the correspondence of theoretical (model) results with experimental time series. Comparison of model trajectories with real datasets of population fluctuations had pure visual nature. Moreover, there are no comparisons of the results of approximations which can be obtained with Verhulst' model and other models (for example, with Gompertz' model; Gompertz, 1825). It means, that de facto Verhulst' model was postulated as a unique applicable model for the approximation of real datasets. This point of view may be truthful and can be accepted, if and only if comparisons of results of approximation of experimental time series by the group of models of one and the same class (Table 1) give a support for this point.

Table 1 Models which are used for approximation of time series

Models		Sources	Name of the model (common and/or used in current publication)
1	$\frac{dx}{dt}=\alpha x\left(1-\frac{x}{K}\right)$	Verhulst (1838)	Verhult model, logistic model
2	$\frac{dx}{dt}=\alpha x\ln\frac{K}{x}$	Gompertz (1825)	Gompertz model
3	$\frac{dx}{dt}=\alpha x^2\left(1-\frac{x}{K}\right)$	Svirezhev (1987)	Svirezhev model
4	$\frac{dx}{dt}=\alpha x\left(1-\left(\frac{x}{K}\right)^{\gamma}\right)$	Rosenzweig (1969), Rosenzweig, MacArthur (1963)	Rosenzweig model

Note: The model's ID numbers are the same in all tables

Moreover, in monograph by G.F. Gause (1934) the estimated values of Verhulst' model parameters are presented but without any explanations how these values were obtained. In a result of it there appears some misunderstanding of basic results of monograph. More precisely, if it is postulated that logistic model (Table 1) is the best model for fitting then parameter K has the following biological sense: it is the maximum population size which can be achieved asymptotically only. At the same time on various figures from Gause's monograph we can see that population sizes of considering species can intersect this level (estimations of parameter K are also presented in monograph). It allows us to conclude that Verhulst model isn't acceptable for fitting of time series (population sizes intersect the level which cannot be intersected in principle; on the other hand, the suitability of model was initially postulated), or for estimations of model parameters a non-correct statistical criteria was used.

In current publication the results of approximation of some time series from G.F. Gause's monograph by the models from Table 1 are compared in two different ways. In first case we use least square method with global fitting (approximation of time series by the trajectories of differential equations from Table 1; Wood, 2001a, b) without additional conditions on the values of model parameters. In the second case we also use global fitting under the condition that population size cannot be bigger than amount K. It is important to note that statistical methods for analyses of sequences of deviations between theoretical and experimental trajectories are qualitative different in both considering situations. For example, if in the first case it is important to check deviations on the absence/existence of serial correlation with Durbin–Watson criteria (Draper and Smith, 1986, 1987), in the second case this verification has no sense: starting with certain time moment all experimental values will be at one and the same side of theoretical curve. It means that in sequence of deviations serial correlation will be a'priori if we have sufficient big experimental sample.

One of the basic problems, we analyze in current paper, is a problem of applicability of Verhulst' model for the approximation of time series on fluctuations of *Paramecia aurelia* and *Paramecia caudatum* under the separated cultivation of both species. Results, which were obtained with the use of Verhulst' model, were compared with the results of approximations of time series, which were obtained with Gompertz' model, Svirezhev' model, and Rosenzweig' model (Gompertz, 1825; Rosenzweig, 1969; Rosenzweig and MacArthur, 1963; Svirezhev, 1987). The main goal of publication is following: it is to prove or to deny the well-known point of view that Verhulst' model gives better description of population dynamics than Gompertz' model.

2 Datasets

At present time monograph by G.F. Gause (1934) can be free downloaded in Internet, www.ggause.com. Time series on the fluctuations of *Paramecia aurelia* and *Paramecia caudatum*, which are used in current publication, can be found on the Fig. 24. Transformation of graphic information into sequences of numbers was realized with the help of graphic software, and all obtained numbers were round to nearest integer values.

In time series for *P. aurelia* there are "holes" (absent values of population size). It leads to impossibility in use of some statistical criteria for testing a correspondence between theoretical and experimental datasets.

3 Mathematical Models

In modern literature it is possible to find a big number of various models of population dynamics, which take into account only the influence of intra-population self-regulative mechanisms on birth and death rates (Isaev et al., 2009; Svirezhev, 1987; Nedorezov, 1986, 1997; Brauer and Castillo-Chavez, 2001; Turchin, 2003). In Table 1, there are simplest mathematical models of population dynamics, which can be presented in the following form:

$$\frac{dx}{dt} = F(x, \vec{\alpha}), \qquad (1)$$

where F is the respective non-linear function in the right-hand side of equations, $\vec{\alpha}$ is a vector of non-negative and unknown parameters, $x(t)$ is population size at time moment t. In G.F. Gause' experiments initial value of population size x_0 was definitely determined, hence x_0 cannot belong to the set of unknown parameters, which have to be determined with analysis of experimental time series (Nedorezov, 2010; Nedorezov and Sadykova, 2008, 2010). Thus, every considering model (Table 1) contains two unknown parameters, and only Rosenzweig' model contains three parameters.

Before applying mathematical models for the approximation of experimental time series we have to underline the biological sense of model parameters. It may have strong influence onto methodology of estimation the values of parameters. First of all, parameter α is proportional to the speed of population growth: this speed increases with growth of value of this parameter for every fixed population size. But real role of this parameter is different for various models. In particular, in Verhulst' model and Rosenzweig' model parameter α is equal to the difference between intensity of birth rate and intensity of death rate of individuals. In this case it has a dimension time^{-1}. In Gomprtz' model the product $\alpha \ln K$ has the same sense.

The second, in all considering models (table 1) parameter K is equal to limit population size, which can be achieved asymptotically if initial population size is less than K. But we may have two qualitatively different assumptions about the value of this parameter. For example, we may think a'priori that value K is stationary level of population size only. If so, in experiments we can observe values of population size which are bigger than level K.

We can also think that K is maximum limit population size. It is possible to assume that every population tries to maximize the use all accessible resources (and, in particular, accessible space), and population tries to maximize its population size. If so, it means that in experiments we cannot observe the values of population size, which is bigger than K. Thus, under the estimation of values of models we have to take into account the following inequalities:

$$K \geq \max_k x_k , \qquad (2)$$

where x_k , $k = 0,1,...,N$, are the elements of initial sample (values of population size obtained in experiments), $N+1$ is sample size.

Consequently, we have to analyze two various situations which are determined by the biological interpretation of the sense of model parameter, K. In first case, when K is a simple stationary level of population size, the following natural question arises: what are the reasons (mechanisms, conditions…) which don't allow the population to stabilize its size at maximum limit level? If parameter K is maximum limit population size then condition (2) arises, and we have to take it into account in a process of model's parameter estimations. In current publication the question about correct or incorrect biological interpretation of the sense of parameter K isn't considered. Both possible variants are used, because the main goal of publication is in comparison of models and its properties for approximation of real time series. Note, that in the first case there is the traditional problem of determination of non-linear regression, and all existing methods of analysis of deviations between theoretical and experimental datasets can be applied. In the second case there are some additional limits for the application of statistical methods for analysis of sets of deviations.

4 Statistical Criteria

Selection of statistical criterions and selection of mathematical models are most important steps in a process of finding a best model for the description of population dynamics. Results of selection process may have a strong influence on final results of analysis of population dynamics (Kendall et al., 1999; Wood, 2001a, b; Nedorezov and Sadykova, 2005, 2008, 2010).

Let $\{x_k\}$, $k = 0,1,...,N$, be an initial time series on population size changing in time, x_k is a population size at time moment k , and $N+1$ is a sample size. Denote as $x = x(t, x_0, \vec{\alpha})$ a solution of equation (1) with initial population size x_0 and defined values of model parameters. Let's note again that initial population size x_0 and first element of considering sample is one and the same number (initial population size was fixed in G.F. Gause' experiments).

For every model from the Table 1 there was one and the same problem: for existing experimental sample $\{x_k\}$ it was necessary to estimate the values of parameters of model (1). For the solution of this problem the following statistical criteria was used:

$$Q(\vec{\alpha}) = \sum_{k=1}^{N} (x_k - x(k, x_0, \vec{\alpha}))^2 \to \min_{\vec{\alpha}} , \qquad (3)$$

where $x(k, x_0, \vec{\alpha})$ are the values of the solution of equation (1) at the respective time moments. Choosing of this criterion means that a'priori it is assumed that time step in model $h = 1$ and it is equal to twenty-four hours (it is the time step between two nearest measurements of population size in G.F. Gause' experiments). It is important to note that in models of the type (1) there is no *real time*, and, respectively, it is possible to choose the amount of time step h from the standpoint of usability. Selection of criteria (3) means that in the set of model trajectories we have to find the best one, which gives a global minimum for expression (3) (*global fitting*).

Finding the minimal values of the functional (3) allows ranking considering models with these numbers, but it doesn't allow giving a final report on suitability or uselessness of one or other model for the approximation of datasets. If we follow the traditional views on mathematical models and have no additional limits for values of model parameters (in all situations we have obvious limits for parameters: K must be non-negative amount, α can be negative if intensity of death rate is bigger than intensity of birth rate in population), we have to check several hypotheses for the set of deviations between theoretical and experimental datasets (Draper and Smith, 1986, 1987; Bol'shev and Smirnov, 1983). First of all, we have to check the hypothesis that average is equal to zero (more precisely, we have to be sure that there are no reasons for rejecting the hypothesis that average is equal to zero; on the other words, we have to be sure that there are no *systematic component* in deviations between theoretical and experimental datasets).

Moreover, distribution of deviations (density function) must be symmetric and single-humped curve. At present time it is a generally accepted idea to check the set of deviations on "Normality": if we have no reasons to reject the hypothesis that deviations have Normal distribution, it gives us a certain background for statement that distribution of deviations is symmetric and single-humped curve. Thus, checking of the Normality of the distribution can be considered as sufficient condition for the respective properties of density function. For checking of the Normality of the distribution the Kolmogorov–Smirnov' test and Shapiro–Wilk' test were used (Bol'shev and Smirnov, 1983; Shapiro et al., 1968).

The sequence of deviations must also be checked for the absence/existence of serial correlation: we have to be sure that with a certain level of confidence we can consider the deviations as the values of independent stochastic variables. For these reasons the well-known Durbin–Watson criteria was used (Draper and Smith, 1986, 1987). But values of this criterion can be calculated for *P. caudatum* time series only: for *P. aurelia* there are the "holes" in the sequence of population sizes.

If we got a negative result with one or other statistical criteria, we concluded that assumption about suitability of the respective model for the approximation of real datasets isn't correct. Thus, we got the following final result: the respective model cannot be applied for fitting of time series. If all considering statistical criteria got positive results (i.e. there were no reasons for the rejecting of the hypothesis "average of deviations is equal to zero", there were no reasons for the rejecting of the hypothesis about "Normality" etc.), it allowed us to conclude that respective model can be used for the approximation of initial datasets and for the explanation of population dynamics.

In the case, when criterion (3) was used together with condition (2), some problems in comparison of theoretical and experimental datasets can be observed. It also leads to problems in comparison of various models with each other. If condition (2) is true, starting from a certain moment of time all experimental points will be at one side of theoretical curve. Consequently, if sample size is big enough, it is obvious that with small value of level of significance the hypothesis about equivalence of the average to zero will be rejected. It is also obvious that there will be a serial correlation in the sequence of residuals.

In general case the problem of testing of correspondence between model and experimental datasets is open. It is obvious, that traditional way for testing of this correspondence can be provided at the initial stages of population process when population size is sufficient small.

It is of practice interest the analysis of correspondence of theory and experiment for the tail of time series when population size is close to its saturation level K. Stochastic decreasing of population size is possible – but what are the probabilities of these events? If we follow the assumption that every system tries to restore its maximal size with maximal possible speed then bigger deviations put of the level K we have to observe with smaller probabilities. Additionally, it looks natural that mode of this distribution must be in zero (no deviations out of level K).

The following hypothesis looks rather truthful. Let ξ be the stochastic variable with integer values, and p be the probability that ξ is equal to zero, $p = P\{\xi = 0\}$ (event $\{\xi = 0\}$ corresponds to the situation when there are no deviations from the level $[K]$, where $[\cdot]$ is integer part of the number). It is obvious that stochastic variable cannot be unbounded, its values belong to the interval $[0,[K]]$ (the event $\{\xi = [K]\}$ corresponds to population extinction), and, respectively, distribution of stochastic variable ξ cannot be geometric, Poisson etc. May be, ξ has the Binomial distribution with sufficient big value of the probability p. But this idea needs in checking.

5 Results

Estimations of model' parameters for both time series and for both considering situations (with and without the additional condition (2)) are presented in Tables 2 and 3. In the first case (without additional condition (2)) the best results for *P. aurelia* and *P. caudatum* were obtained for Rosenzweig' model (Table 2). Close results were obtained for Verhulst' model. For both species the use of Verhulst' model allowed us to obtain better approximation than Gompertz' model.

Table 2 Estimations of model's parameters and respective minimal value of functional (3) without the additional condition (2)

Models	Parameters			Functional
	α	K	γ	$Q_{\min}$
Results for time series for *P. aurelia*				
1	1.174	101.05	---	966.87
2	0.532	104.49	---	1213.84
3	0.17	96.72	---	1748.43
4	1.182	101.09	0.981	966.82
Results for time series for *P. caudatum*				
1	0.849	60.41	---	929.42
2	0.449	62.3	---	976.63
3	0.093	58.23	---	1156.04
4	0.826	60.72	0.921	924.62

Table 3 Estimations of model's parameters and respective minimal value of functional (3) with the additional condition (2)

Models	Parameters			Functional
	α	K	γ	$Q_{\min}$
Results for time series for *P. aurelia*				
1	1.075	114	---	2369.47
2	0.473	114	---	1790.59
3	0.132	114	---	4454.0
4	193.0	114	$2.45\cdot10^{-3}$	1791.45
Results for time series for *P. caudatum*				
1	0.646	76	---	2633.58
2	0.316	76	---	1791.09
3	0.088	76	---	4620.0
4	151062.16	76	$2.093\cdot10^{-6}$	1791.09

Note that estimations, which are presented in Table 2, are close to estimations of Verhulst' model parameters, which are presented in G.F. Gause monograph (Gause, 1934). For *P. caudatum* it was pointed out that $\alpha = 0.794$ and $K = 64$; for *P. aurelia*: $\alpha = 1.124$ and $K = 105$.

Results of analyses of deviations between theoretical and experimental trajectories are presented in Tables 4 and 5. In spite of best results, which were obtained with Verhulst model, analyses of deviations for this model isn't so good like for all other models. Moreover, for *P. aurelia* dataset we have to conclude that Verhulst' model isn't suitable for the approximation of experimental trajectories: even with 1% level of significance we have to reject the hypothesis about Normality of the set of deviations (Shapiro–Wilk test, Table 5). The same result we have for Rosenzweig' model. At the same time there are no reasons for the rejecting of the hypothesis about Normality for the deviations between experimental points and trajectory of Gompertz' model (with 5% significance level). Very bad approximation was obtained with Svirezhev' model (Table 2). But the hypothesis about Normality for the deviations between experimental points and trajectory of Svirezhev' model cannot be rejected even with 10% significance level (Table 5). Results of approximation of *P. aurelia*' time series by some models are presented on Fig. 1.

For *P. caudatum* time series applications of Verhulst' model and Gompertz' model led to obtaining of close values for minimizing functional (3) (Table 2). For all models (Table 1) hypotheses about the Normality of deviations cannot be rejected even with 10% significance level (Table 4).

Table 4 Analysis of deviations between real datasets and theoretical trajectories for *P. caudatum*

Models	Av. ± S.E.	KS[1]	SW[2]	DW[3]
Analysis of dataset for the values from Table 2				
1	-0.183±1.967	0.145/p>0.2	0.933/p=0.276	2.318
2	0.28±2.016	0.132/p>0.2	0.97/p=0.84	2.24
3	-1.316±2.168	0.159/p>0.2	0.913/p=0.128	1.753
4	-0.027±1.963	0.15/p>0.2	0.936/p=0.306	2.338
Analysis of dataset for the values from Table 3				
1	4.496±3.103	0.13/p>0.2	0.934/p=0.28	0.875
2	2.175±2.673	0.122/p>0.2	0.949/p=0.479	1.246
3	10.758±3.396	0.177/p>0.2	0.904/p=0.094	0.551
4	2.175±2.673	0.122/p>0.2	0.949/p=0.479	1.246

[1]KS: Kolmogorov–Smirnov test; [2]SW: Shapiro–Wilk test; [3]DW: Durbin–Watson criteria

Table 5 Analysis of deviations between real datasets and theoretical trajectories for *P. aurelia*

Models	Av. ± S.E.	KS[1]	SW[2]
Analysis of dataset for the values from Table 2			
1	0.387±2.143	0.215/p>0.2	0.831/p=0.0096
2	1.017±2.389	0.19/p>0.2	0.897/p=0.0858
3	-0.533±2.882	0.208/p>0.2	0.907/p=0.122
4	0.396±2.143	0.211/p>0.2	0.831/p=0.00947
Analysis of dataset for the values from Table 3			
1	6.897±2.808	0.186/p>0.2	0.881/p=0.049
2	4.467±2.665	0.177/p>0.2	0.907/p=0.12
3	7.28±4.174	0.186/p>0.2	0.945/p=0.451
4	4.476±2.665	0.178/p>0.2	0.906/p=0.118

[1]KS: Kolmogorov–Smirnov test; [2]SW: Shapiro–Wilk test

Durbin–Watson criterion for the sample with sample size 16 and with one predictor variable has following limits: $d_U = 1.37$ and $d_L = 1.1$. If $d_U < d < 4 - d_U$, where d is the value of Durbin–Watson criterion (Table 4), the hypothesis about existing serial correlation in the sequence of residuals must be rejected with 10% significance level. If $0 < d < d_L$ or $4 - d_L < d < 4$ it means that there is the serial correlation in the sequence of residuals. Thus, we have the following result: in considering case all models can be used for the approximation of data on *P. caudatum* fluctuations.

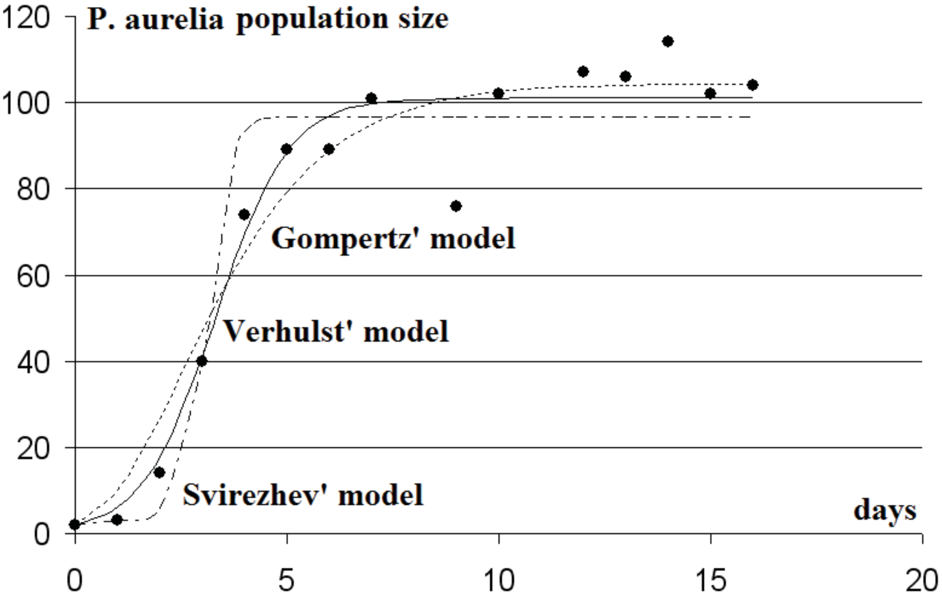

Fig. 1 Results of approximation of *P. aurelia*' time series by the trajectories of Verhulst' model, Gompertz' model, and Svirezhev' model without additional limit (2).

Thus, in two considered situations for *P. caudatum* time series (Fig. 2) we have no reasons to say that Gompertz' model allowed to obtain not so good results in approximation like Verhulst' model. Both models can be used for fitting of experimental dataset. In the case for *P. aurelia* Gompertz' model demonstrated good results for fitting. At the same time about Verhulst' model we have to conclude that it isn't applicable for the approximation of this time series.

Let's consider now variants of the approximation of the same time series (Fig. 3 and 4) when additional condition (2) are taken into account. Results of approximations are presented in Table 3. For both time series there are the similar situations: Gompertz' model gives better approximations than Verhulst' model and Svirezhev' model. Good approximation was also obtained with Rosenzweig' model. Note, that amount of parameter γ in Rosenzweig' model is sufficient small (Table 3). It corresponds to the situation when self-regulative mechanisms in population are weak.

It is interesting to note that for *P. caudatum* dataset (Table 4, Fig. 4) the property of normality for the deviations was saved for all models. It means that isn't big enough. For Verhulst' model and Svirezhev' model there are the serial correlations in the sequence of residuals. For Gompertz' model and Rosenzweig' model the respective values of Durbin–Watson criterion belong to the zone of ambiguity, $1.1 < d < 1.37$.

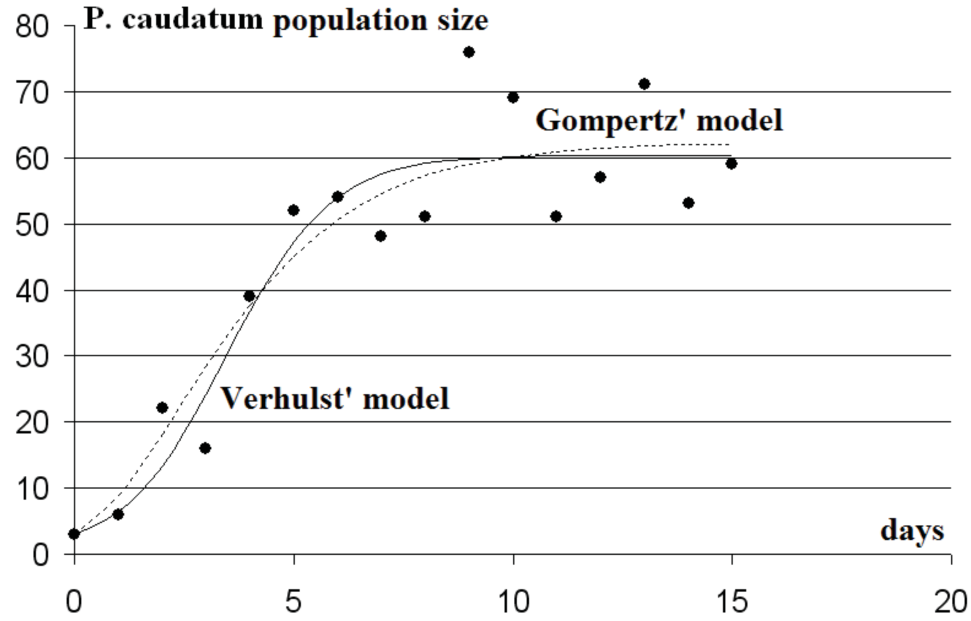

Fig. 2 Results of approximation of *P. caudatum*' time series by the trajectories of Verhulst' model and Gompertz' model without additional limit (2).

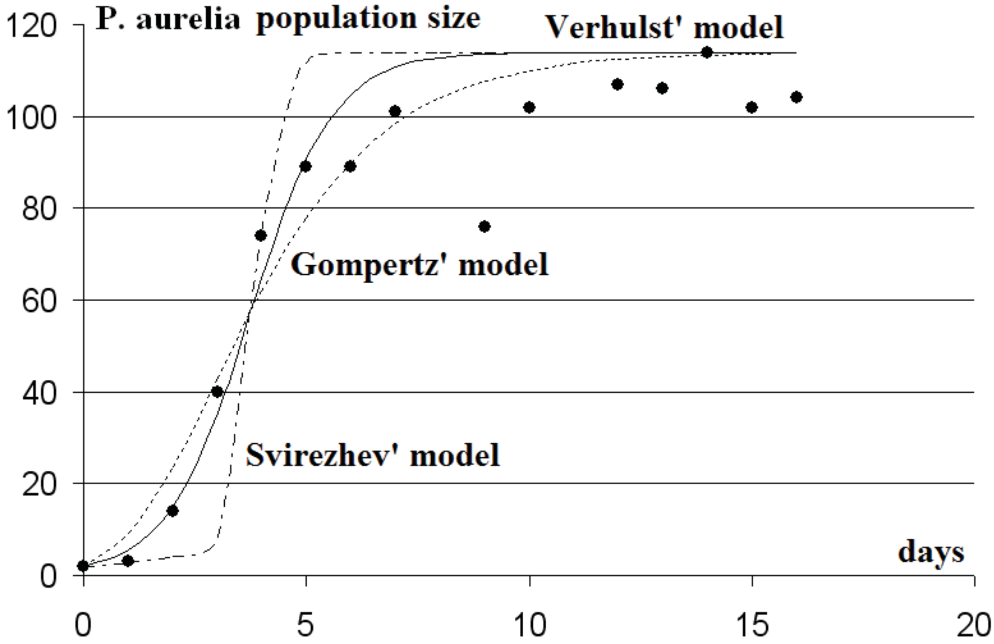

Fig. 3 Results of approximation of *P. aurelia*' time series by the trajectories of Verhulst' model, Gompertz' model, and Svirezhev' model with additional limit (2).

Shapiro–Wilk test shows that hypothesis about normality of the deviations between *P. aurelia* time series and Verhulst' model trajectory must be rejected with 5% level of significance. The respective hypothesis for

Gompertz' model cannot be rejected even with 10% level of significance. Thus, in two last situations Gompertz' model showed better results than Verhulst' model.

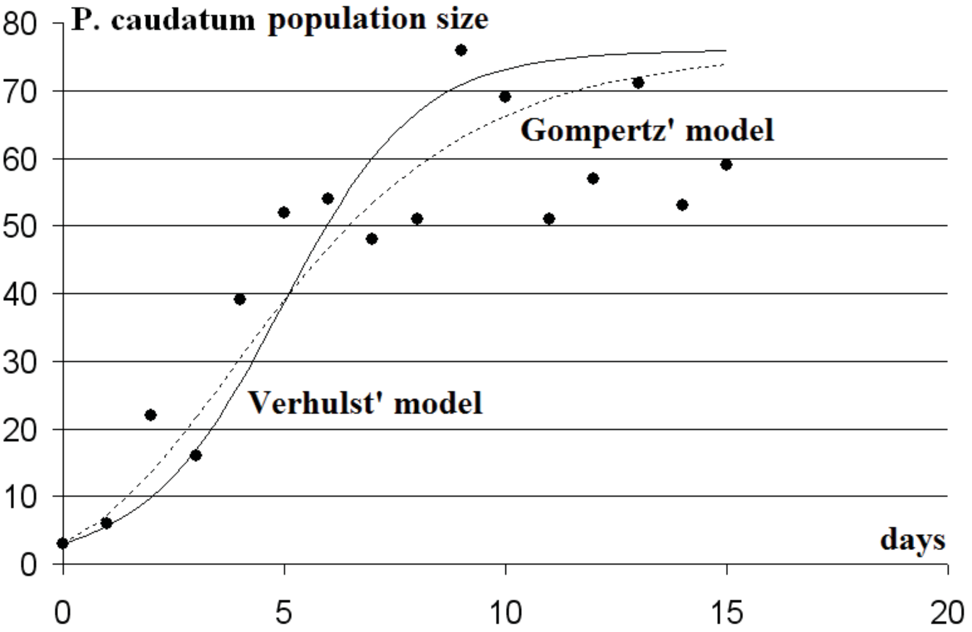

Fig. 4 Results of approximation of *P. caudatum*' time series by the trajectories of Verhulst' model and Gompertz' model with additional limit (2).

6 Conclusion

Analyses of two time series for *P. aurelia* and *P. caudatum* population fluctuations (when these species were cultivated separately; Gause, 1934, Fig. 24) allowed us to show that in some cases results obtained with Gompertz' model are close to results obtained with Verhulst' model. At least we have no reasons to say that results obtained with Verhulst' model are much better results obtained with Gompertz' model.

In other situations Gompertz' model allowed us to obtain results in approximation of time series, which are much better the results obtained with Verhulst' model. In two of four considering cases Verhulst' model was useless for fitting of experimental time series. Obtained results allow us to say about the following property of self-regulative mechanisms of considering species: its influence on population dynamics is much weaker than it is postulated in Verhulst' model. This conclusion is supported by the results obtained for Gompertz' model, where the influence of self-regulative mechanisms describes by the expression $x \ln x$, and by the results obtained for Rosenzweig' model.

When we use mathematical models for the description of population size changing in time, from time to time we have problems with biological interpretations of real sense of one or other model's parameter. And this problem is very important because it has strong influence onto the process of selection of the respective statistical criterion, and, consequently, onto the estimations of values of model parameters. Finally, it can lead to qualitatively different results.

For example, in considering situation with group of models, presented in Table 1, we have the problem with interpretation of the biological sense of parameter K. We can think about it as about simple stable stationary level, which can be observed in the system asymptotically. If so, in experiments we can observe the values of population size, which is bigger than K.

This interpretation of parameter K is possible but on the other hand it leads to some additional questions. In particular, what are the reasons, which don't allow for population to maximize its size? In considering situations we have intra-population self-regulative mechanisms only. There are no predators, parasites etc. Thus, it looks natural assumption that population tries to maximize the population size. If so, parameter K is the maximum limit level for population size. It means, that in experiments we cannot observe the values, which are greater than K.

In this last situation we have additional condition for parameter's values, and, moreover, there appear some problems with checking of the correspondence of theoretical and experimental datasets. Appearance of this additional inequality leads to the situation when traditional methods for the checking of correspondence various datasets are practically inapplicable. Checking the hypothesis about equivalence of the average of deviations to zero, checking the hypothesis about Normality of deviations, and checking the hypothesis about absence/existence of serial correlation in the sequence of residuals are less of any sense. These verifications can be provided on the initial stages of the development of population process, when population size is small enough and its value is far from the level of saturation. Starting from certain time moment all experimental points will belong to one and the same side of theoretical curve. But what kind of methods we have to use for analysis of correspondence between theoretical and experimental trajectories when population size can be close to its level of saturation – the question is open.

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