

## **Larch bud moth dynamics: can we explain periodicity of population fluctuations by the time lag dependence in birth rate?**

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### **Abstract**

Current publication is devoted to traditional and non-traditional approaches to statistical analysis of well-known time series on the dynamics of larch bud moth (*Zeiraphera diniana* Gn.) in Swiss Alps. For fitting of time series modifications with time lags of Moran – Ricker model were applied. For some particular cases it was obtained that considering models can give good quantitative and qualitative fitting of time series.

**Keywords:** larch bud moth, mathematical models, discrete time, time series, fitting

### **Introduction**

There is a lot of publications which are devoted to analysis of empirical time series and to modeling of larch bud moth (*Zeiraphera diniana* Gn.) population fluctuations (see, for example, Auer, 1977; Baltensweiler, 1964, 1978; Baltensweiler et al., 1977; Fischlin, Baltensweiler, 1979; Baltensweiler, Fischlin, 1988; Dellucchi, 1982; Isaev et al., 1984, 2001; Turchin, 2003; Turchin et al., 2003; Nedorezov, 1986, 2007 and many others). Ability of publications and models has a strong correlation with ability of various theories which are devoted to the explanation of existing periodic fluctuations of larch bud moth in Swiss Alps (Royama, 1981; Turchin, 1990; Hunter, Price, 1998; Berryman, Turchin, 2001; Kendall et al., 1999; Ginzburg and Taneyhill, 1994; Andersen, May, 1980).

In our previous publications we tried to apply simplest mathematical models with discrete time (table 1;  $x_k$  is population density at moment  $k$ ,  $k = 0, 1, 2, \dots$ ; parameters  $a$  and  $b$ , and initial population density  $x_0$  are non-negative amounts) for fitting of some time series

of larch bud moth density changing in time (Nedorezov, 2007, 2011). Using standard approach to analysis of deviations between theoretical (model) and empirical values allowed us showing that for one of time series simplest mathematical models can give sufficient approximation.

Table 1. Models used for approximation of datasets

Models	Source	Name of the model (common or used in current publication)
1 $x_{k+1} = ax_k(1 + bx_k)^{-1}$	Kostitzin, 1937	Kostitzin model
2 $x_{k+1} = ax_k(b - x_k)$	Moran, 1950; Ricker, 1954	Discrete logistic model
3 $x_{k+1} = a(1 - e^{-bx_k})$	Skellam, 1951	Skellam model
4 $x_{k+1} = ax_k^{1-b}$	Morris, 1959; Varley, Gradwell, 1960, 1970	Morris – Varley – Gradwell model
5 $x_{k+1} = ax_k e^{-bx_k}$	Moran, 1950; Ricker, 1954	Moran – Ricker model

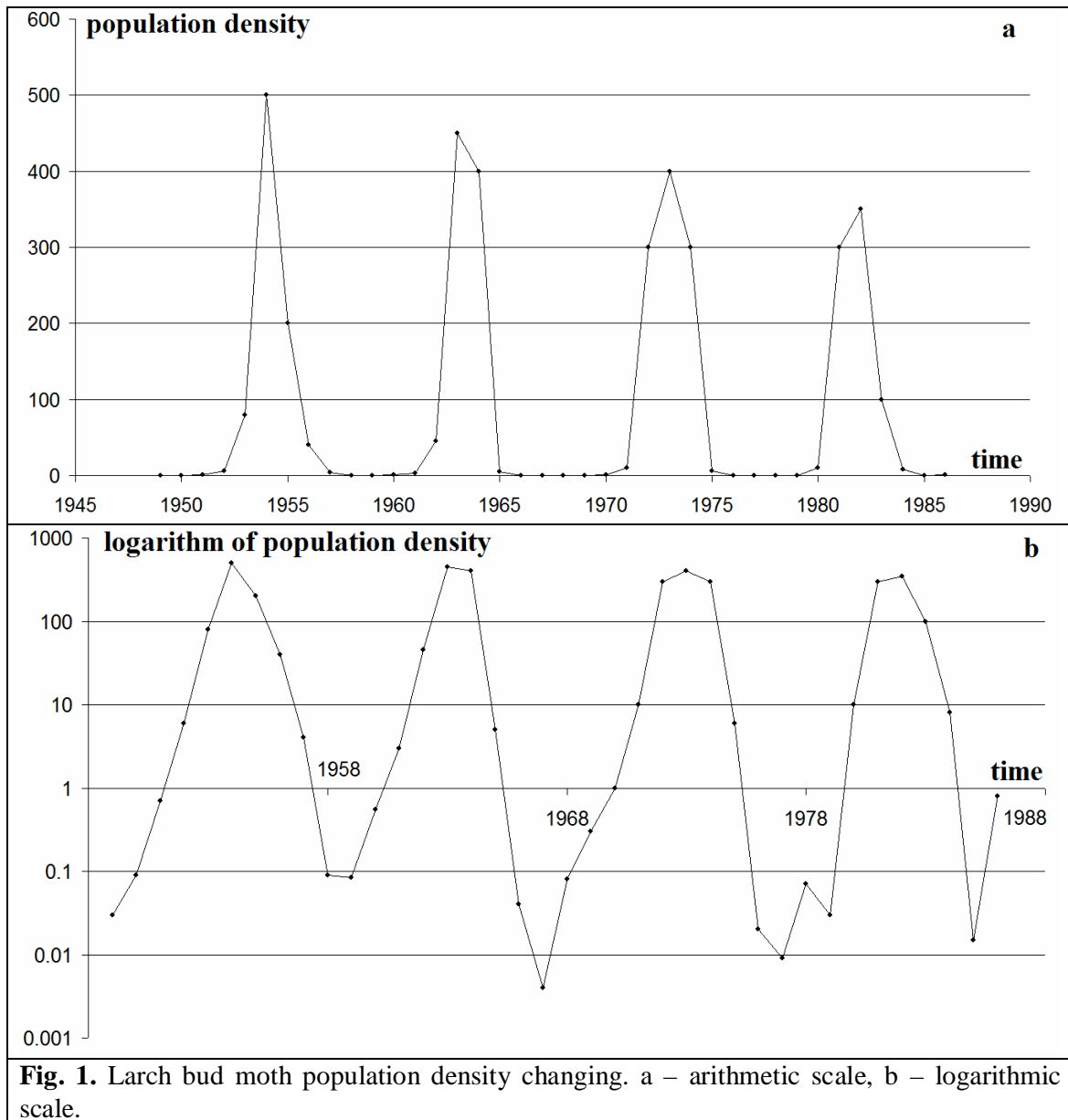
In other words, tests of sets of deviations between theoretical (model) trajectories and real time series showed that for selected 5% significance level we cannot reject hypotheses about equivalence of average to zero, about normality of sets of deviations, and about absence of serial correlation in sequences of residuals (Bolshev, Smirnov, 1983; Draper, Smith, 1986; Shapiro, Wilk, Chen, 1968; Bard, 1974). But for considering in current publication time series all models from the table 1 couldn't give sufficient approximation (Nedorezov, 2007, 2011).

In several publications it was proved that existence of time lag in reaction of main population regulators on population density changing in time can play extremely important role in realization of observed various dynamic regimes (Isaev et al., 1984, 2001; Nedorezov, 1986, 1997, 2012; Turchin P. 1990, 2003; Berryman A.A., Turchin P. 2001; Nedorezov, Utyupin, 2011). Best results were obtained for Moran – Ricker model (table 1; Moran, 1950; Ricker, 1954) which is characterized by ability of difficult dynamic regimes. It gives us a background for continuation of search of best model for fitting of larch bud moth time series.

### Datasets

Regular observations of the changing of larch bud moth population densities in time in Swiss Alps (Upper Engadine valley) had been started in 1949 (Auer, 1977; Baltensweiler, Fischlin, 1988). In current publication we use time series (fig. 1) which can be free downloaded in Internet (NERC Centre for Population Biology, Imperial College (1999) The Global Population Dynamics Database, N 1407. Unit of measurement is “number of larva per kilogram of branches”.

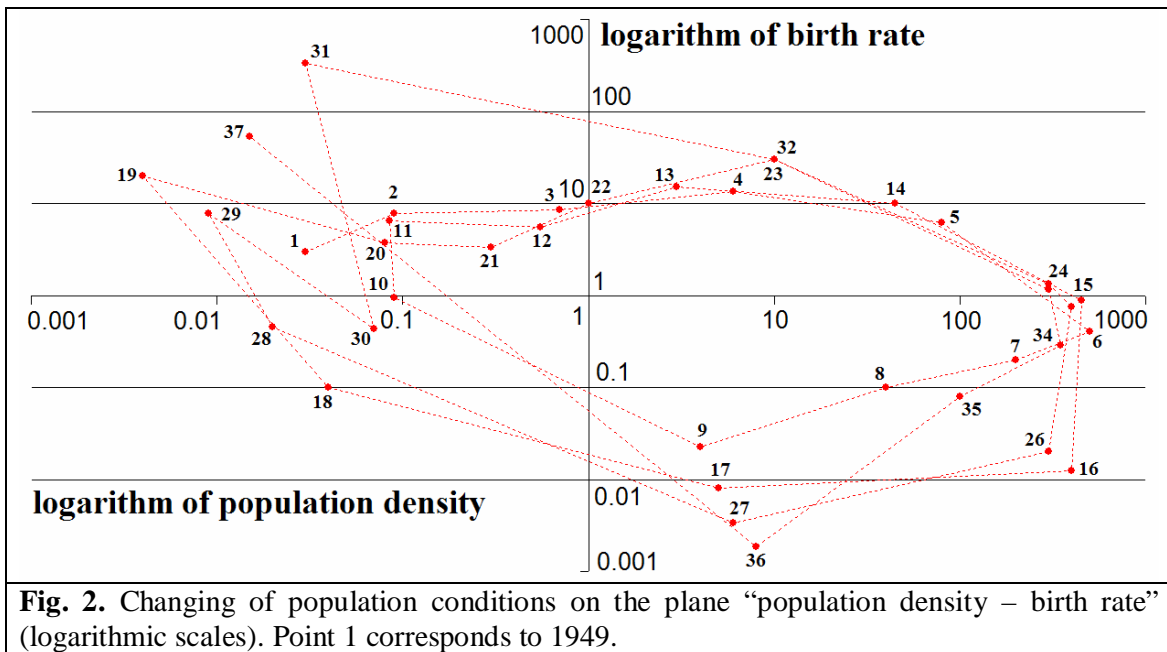
As it was pointed out in GPDD, data were collected on 1800 m above sea level that corresponds to optimal zone of species living (Isaev, Nedorezov, Khlebopros, 1980; Isaev et al., 1984, 2001). Sample contains 38 values (first point corresponds to 1949).



Population fluctuations on the plane “population density – birth rate” where birth rate is determined as relation of densities of two nearest values:

$$y_k = \frac{x_{k+1}}{x_k},$$

are presented on fig. 2. As we can see on this picture it is possible to point out some parts of empirical trajectory (11-13, 19-22) where we can observe decreasing of birth rate in upper part of plane (where birth rate is bigger than 1). Such kind of behavior of trajectory corresponds to theoretical imagination of permanent outbreak dynamics (Isaev, Nedorezov, Khlebopros, 1980; Isaev et al., 1984, 2001). Even part 29-31 of trajectory can be explained (on qualitative level) within the framework of this theory of population outbreaks (there is a special zone on phase plane where birth rate is less then one but this sub-zone belongs to outbreak zone).



**Used models**

As it was showed in our previous publications (Nedorezov, 2007, 2011, 2012), models from the table (1) cannot give a good approximation for considering time series (fig. 1 and 2). Best results were obtained for Moran – Ricker model (table 1). But application of various statistical tests to analysis of deviations between theoretical (model) trajectory and empirical time series showed that this model isn’t suitable for fitting. In current publication we apply modifications of Moran – Ricker model for fitting:

$$x_{k+1} = Ax_k \exp \left\{ - \sum_{j=0}^m a_j x_{k-j} \right\}, \quad m = 1, 2, \dots \quad (1)$$

In (1)  $a_j$  are non-negative parameters,  $x_k$  is a population density at moment  $k$ . If in (1)  $m = 0$  we have classic Moran – Ricker model (table 1).

**Statistical criterions**

In current publication we'll follow the traditional way for analysis of correspondence of real empirical time series and model trajectories. It means that for every considering model we have to estimate model parameters minimizing squared deviations between time series and model trajectories. It is rather common opinion that model gives sufficient fitting of time series if

- we cannot reject the hypothesis about equivalence of average of residuals to zero,
- we cannot reject the hypothesis about Normality of deviations (Kolmogorov – Smirnov test, Lilliefors test, Shapiro – Wilk test etc.),
- we have to reject hypotheses about existence of positive or negative serial correlation in sequence of residuals (Durbin – Watson test, analysis of behavior of auto-correlation function with testing of hypotheses about equivalence of the respective values of this function to zero).

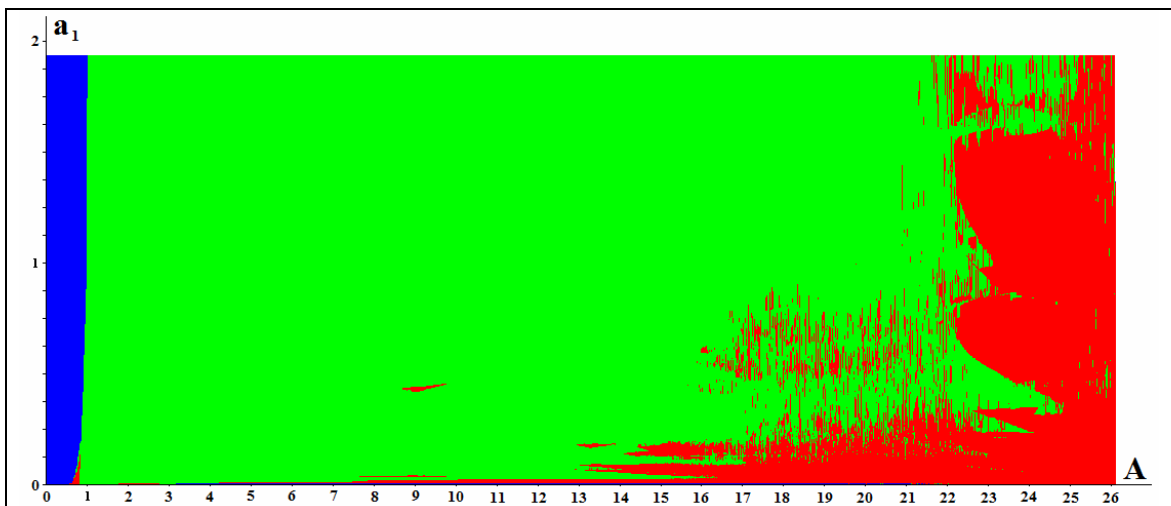
If these basic requirements are truthful for the respective set of deviations, we can talk about good correspondence between theoretical and empirical datasets. On the other hand, requirements about Normality of set of deviations are not correct, and it isn't realized for biological objects. It is obvious, if we estimate a weight of any object in grams we cannot have an error in several tons with positive probability; we cannot also obtain negative values for weight with positive probability. Thus, we have to exclude this requirement from the list. In our opinion basic requirements to set of deviations between theoretical and empirical time series must be following:

- we cannot reject the hypothesis about symmetry of distribution with respect to origin (Kolmogorov – Smirnov test, Wilcoxon test),
- density must have one maximum in origin,
- we have to be sure that theoretical trajectory has the similar features of behavior as empirical trajectory; in particular, signs of increments must be the same: if  $p$  is a frequency of situations when signs are equal, we have to reject Null hypothesis  $H_0: p = 0.5$  with alternative hypothesis  $H_1: p > 0.5$ ; the same situation must be observed for “second derivatives” etc.

As it was pointed out above, in current publication we will follow of the traditional way of analysis of correspondence of theoretical and empirical trajectories: estimation of model parameters – analysis of deviations. But in our opinion it is much better to use the inverse way: determination of set of suitable values of model parameters – choosing of values of parameters. For example, application of Wilcoxon test for checking of symmetry of deviations of empirical dataset (fig. 1) from the trajectory of Moran – Ricker model (table 1)

gave the results presenting on fig. 3. Red points on this picture correspond to situation when for determined values of model parameters we can point out at least one initial value  $x_0$  when Wilcoxon test doesn't allow rejecting Null hypothesis about symmetry with 5% significance level. Green points correspond to situation when Null hypothesis must be rejected. Blue points correspond to situation when Wilcoxon test cannot be applied to analysis of deviations (number of negative or positive deviations are equal to 5 or less than 5).

Application of Kolmogorov – Smirnov test will give us another “red points” and so on. Let's denote as  $B_j$  respective sets of “red points” we obtain in a result of application of statistical sets from the list. If intersection of all sets  $B_j$  is empty set model isn't suitable for fitting of considering time series. If intersection of all sets isn't empty we can choose any point from this set, and it gives a guarantee that all statistical tests will be satisfied.



**Fig. 3.** Results of application of Wilcoxon test to analysis of deviations between trajectories of Moran – Ricker model and larch bud moth time series.

### Results of calculations

#### *Model with time lag 1*

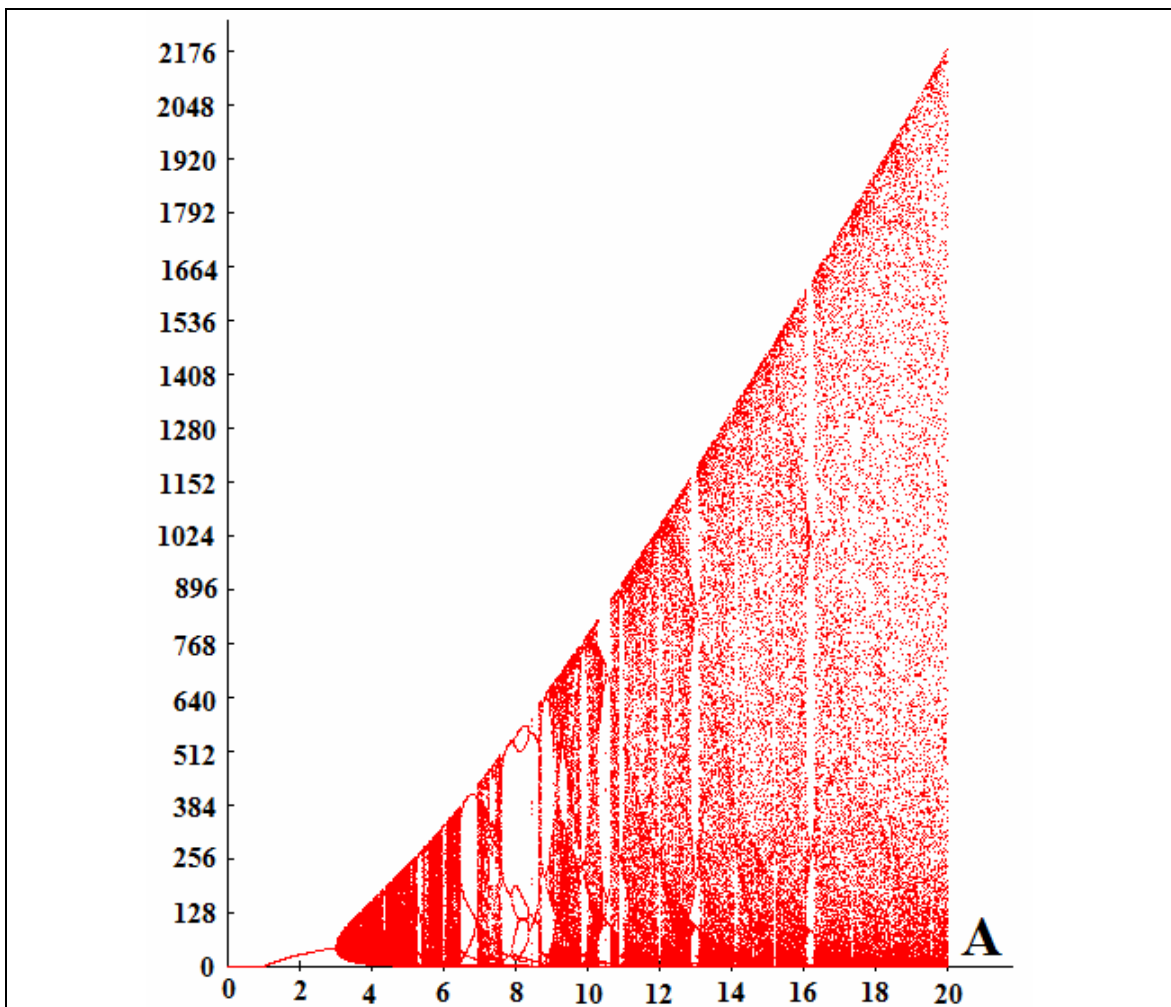
Let's consider situation when time lag is equal to 1. Modification of Moran – Ricker model will have the following form:

$$x_{k+1} = Ax_k \exp\{-a_1x_k - a_2x_{k-1}\}. \quad (2)$$

Minimum of squared deviations between real time series and model (2) trajectories  $Q_{\min} = 154148.4$  was observed for the following values of model parameters:  $x_1^0 = 9.97 \cdot 10^{-15}$ ,  $x_2^0 = 0.1274$ ,  $A = 8.2996$ ,  $a_1 = 2.205 \cdot 10^{-3}$ ,  $a_2 = 0.02214$ . It is interesting

to note that  $a_2 > a_1$ . It means that influence of the respective generation is much more strong than influence of previous generation on population density changing.

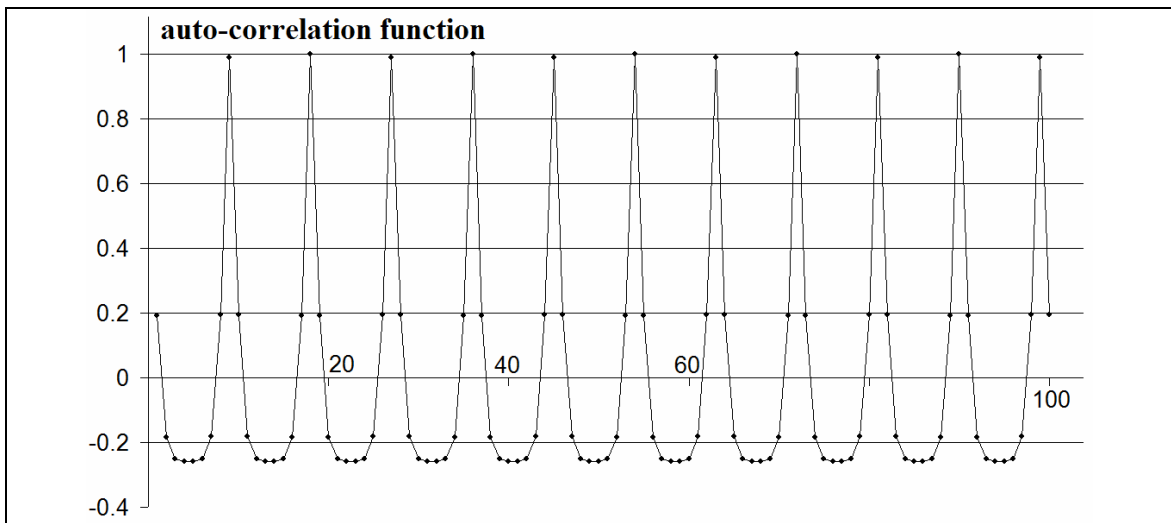
For these parameters model (2) has bifurcation diagram presented on fig. 4. Number of “empty steps” is equal to 20000. After empty steps 200 obtained values of population densities were printed on straight line  $A = const$  (for every fixed value of this parameter). Initial values of population densities were found randomly in intervals  $[0, (A + 1)^2]$ .



**Fig. 4.** Bifurcation diagram of model (2) for estimated values of parameters  $a_1$  and  $a_2$ .

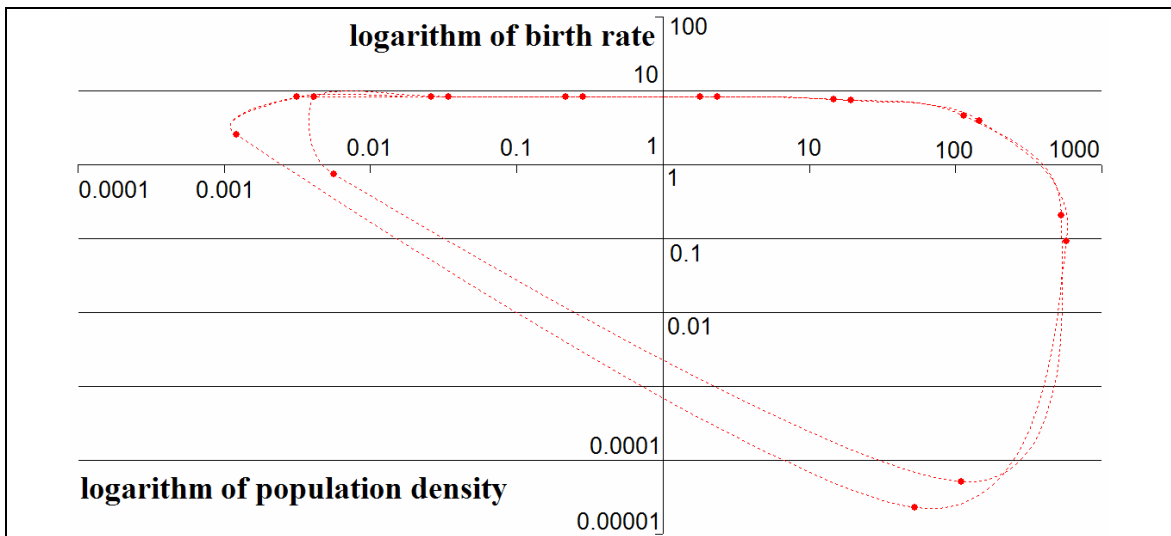
As we can see on fig. 4 process of changing of population density at  $A \approx 8.3$  is periodic. But it isn't easy to find a length of this cycle using bifurcation diagram. For determination of the length of cycle we can use auto-correlation function for model trajectory obtained for asymptotic stabilized regime. In this occasion model had 200000 “empty steps”. After these “empty steps” auto-correlation function for 20000 obtained values of population density with model (2) was calculated (fig. 5).

As we can see on this figure 100 values of this function are very close to 1 periodically (values are equal to 0.988546 and 0.99995). It allows us concluding that observed asymptotic dynamic regime is close to 9-cycle. It corresponds to observed time series (Auer, 1977; Baltensweiler, 1964, 1978; Baltensweiler et al., 1977; Fischlin, Baltensweiler, 1979; Baltensweiler, Fischlin, 1988).



**Fig. 5.** Auto-correlation function for stable asymptotic dynamic regime obtained for estimated values of model parameters (first 100 values).

On fig. 6 there are the points of asymptotically stable dynamic regime on the plane “population density – birth rate” (both coordinate lines are in logarithmic scale).



**Fig. 6.** Model trajectory for asymptotic dynamic regime on the plane “population density – birth rate” (logarithmic scales).



As we can see on this picture, trajectory of population density changing is rather difficult: we can see double 9-cycle with rather close coordinates. We cannot exclude hypothesis that in nature fluctuations of larch bud moth correspond to double cycle. But monotonic behavior of birth rate (fig. 6) doesn't correspond to non-monotonic behavior of birth rate for real datasets (fig. 2). Thus, we cannot conclude that we have qualitative correspondence between model trajectory and real datasets. It doesn't also correspond to theoretical imaginations about permanent outbreak trajectory (Isaev, Nedorezov, Khlebopros, 1980; Isaev et al., 1984, 2001).

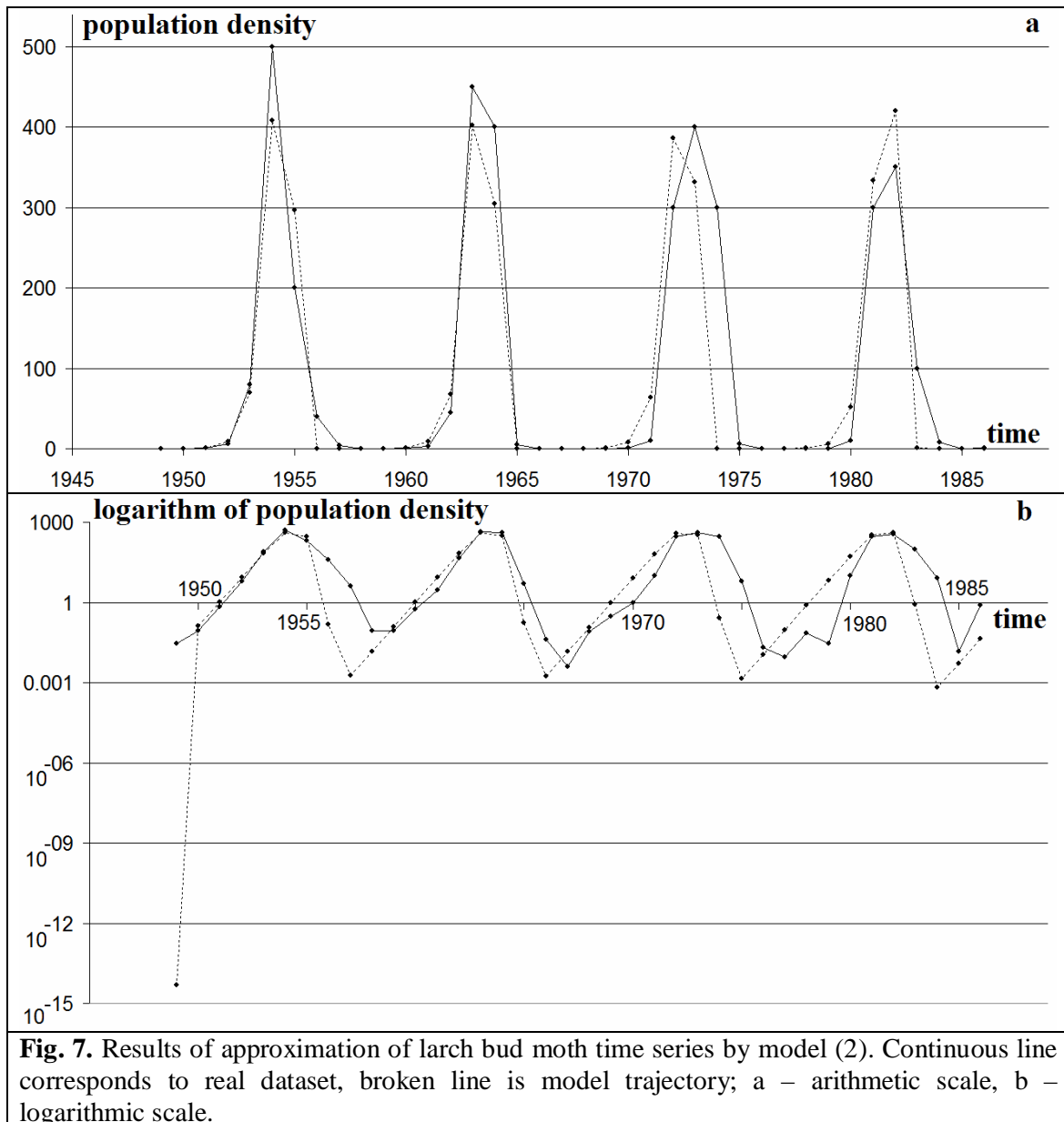
Analysis of deviations showed that average plus/minus standard error is equal to  $-9.172 \pm 10.36$  (thus, we can't reject hypothesis about equivalence of average to zero with 5% significance level), for Kolmogorov – Smirnov test  $d = 0.307$  with  $p < 0.01$ , for Lilliefors test  $p < 0.01$ , for Shapiro – Wilk test  $W = 0.71379$  with  $p < 10^{-5}$ , for Durbin – Watson criteria  $d = 1.8476$  (critical level for this test is  $d_u = 1.535 < d$  - there are no serial correlations). Thus, traditional approach to analysis of deviations allows concluding that model (2) isn't suitable for fitting of considering empirical time series.

Analysis of symmetry of deviations with respect to origin by the Kolmogorov – Smirnov test shows that  $d = 0.1722$  with the respective probability  $p = 0.916$ . Thus, we have to accept the hypothesis about symmetry (probability is very big). Comparison of increments of real trajectory and model trajectory shows that signs of increments are the same in 78.38% of all cases. For 37 degrees of freedom and 5% significance level theoretical value of Student test is equal to 2.0262. Checking of the hypothesis that frequency is equal to 0.5 we obtain that real value of t-test is equal to 3.5689 (we have to reject Null hypothesis  $p = 0.5$ ). Thus, we have a background for conclusion that there is rather good correspondence between changing of increments of real and model trajectories.

For “second derivatives” we have better correspondence (estimation of probability is close to one):  $p = 0.916667$ . Thus, in considering situation we have also to reject Null hypothesis  $H_0: p = 0.5$ . Taking into account that there are no serial correlations (Durbin – Watson test showed that  $d = 1.8476$  - this value belongs to zone of absence of serial correlation in the sequence of residuals) we obtain a good background for conclusion that model (2) gives good fitting for larch bud moth time series (fig. 1 and 2). Note, this conclusion is in contradiction with conclusion we obtained with traditional approach to analysis of deviations. Finally, we can say that in considering situation we have quantitative

correspondence between theoretical and empirical trajectories but it is without of the qualitative correspondence.

Results of approximation of larch bud moth time series by model (2) are presented on figure 7 (in arithmetic and logarithmic scales). Continuous line corresponds to real dataset, broken line is model trajectory.

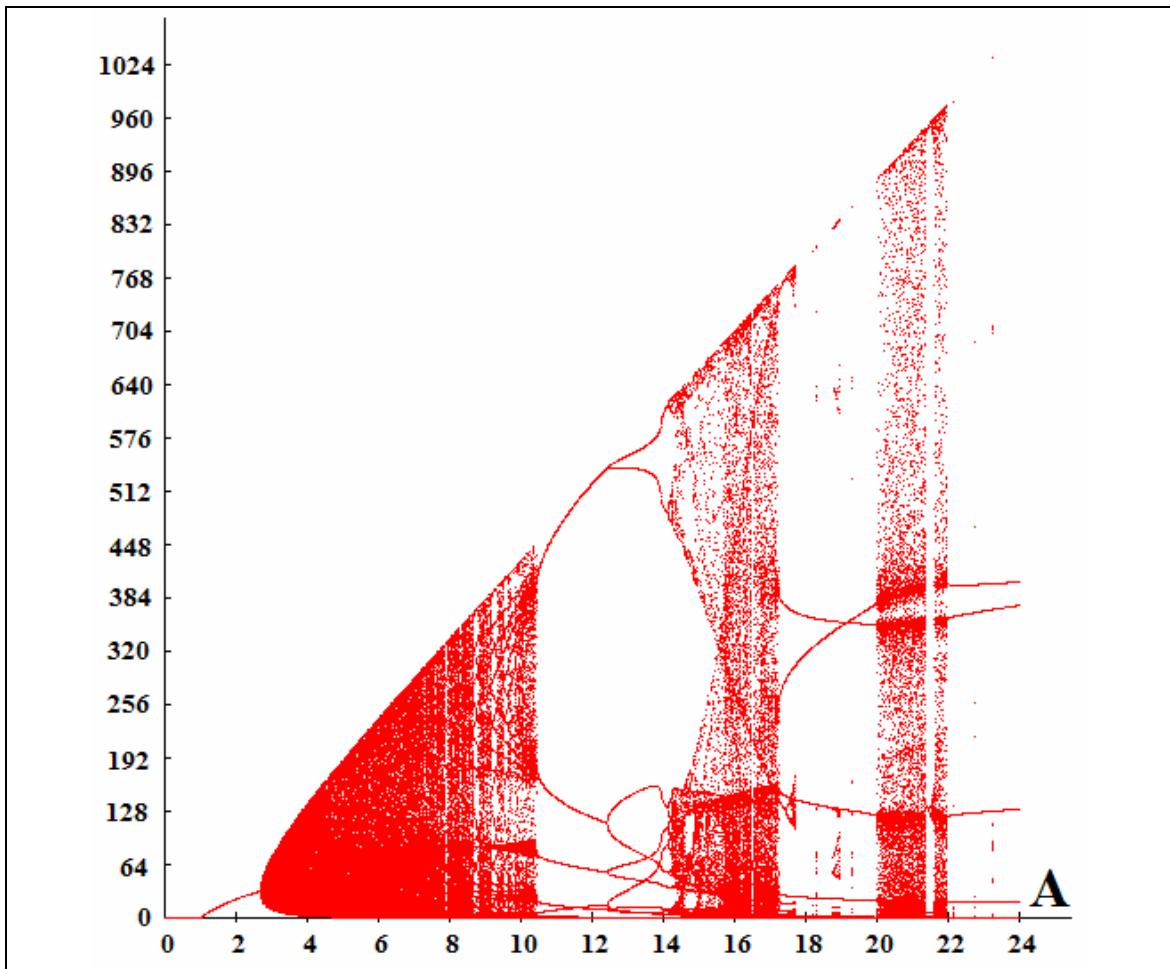


**Model with time lag 2**

Let's consider situation when time lag is equal to 2. Modification of Moran – Ricker model will have the following form:

$$x_{k+1} = Ax_k \exp\{-a_1x_k - a_2x_{k-1} - a_3x_{k-2}\}. \quad (3)$$

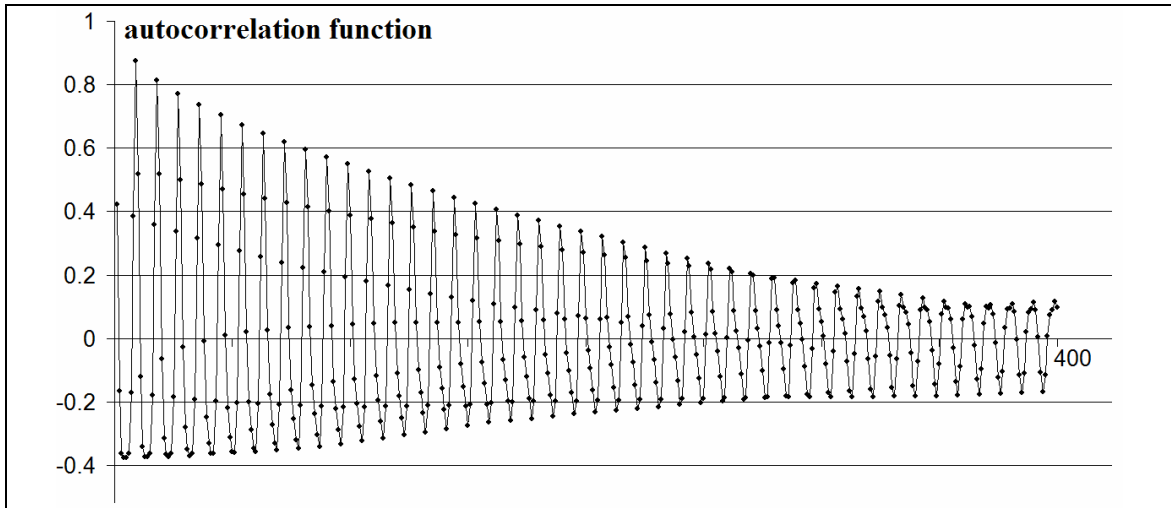
Minimum of squared deviations between real time series and model trajectories  $Q_{\min} = 92099.1$  was observed for the following values of model parameters:  $x_1^0 = 5.638 \cdot 10^{-15}$ ,  $x_2^0 = 2.653 \cdot 10^{-16}$ ,  $x_3^0 = 0.07208$ ,  $A = 20.076$ ,  $a_1 = 8.155 \cdot 10^{-3}$ ,  $a_2 = 1.6994 \cdot 10^{-3}$ ,  $a_3 = 0.02097$ . For these parameters model (3) has bifurcation diagram presented on figure 8. Number of “empty steps” is equal to 20000. After empty steps 200 obtained values of population densities were printed on straight line  $A = const$ . Bifurcation diagram doesn't allow determination of asymptotic stable dynamic regime for  $A = 20.076$  - it is obvious that observed regime isn't cyclic with rather small number of points (in 8 or 9 points like it is observed for larch bud moth fluctuations).



**Fig. 8.** Bifurcation diagram of model (3) for estimated values of parameters  $a_1, \dots, a_3$ .

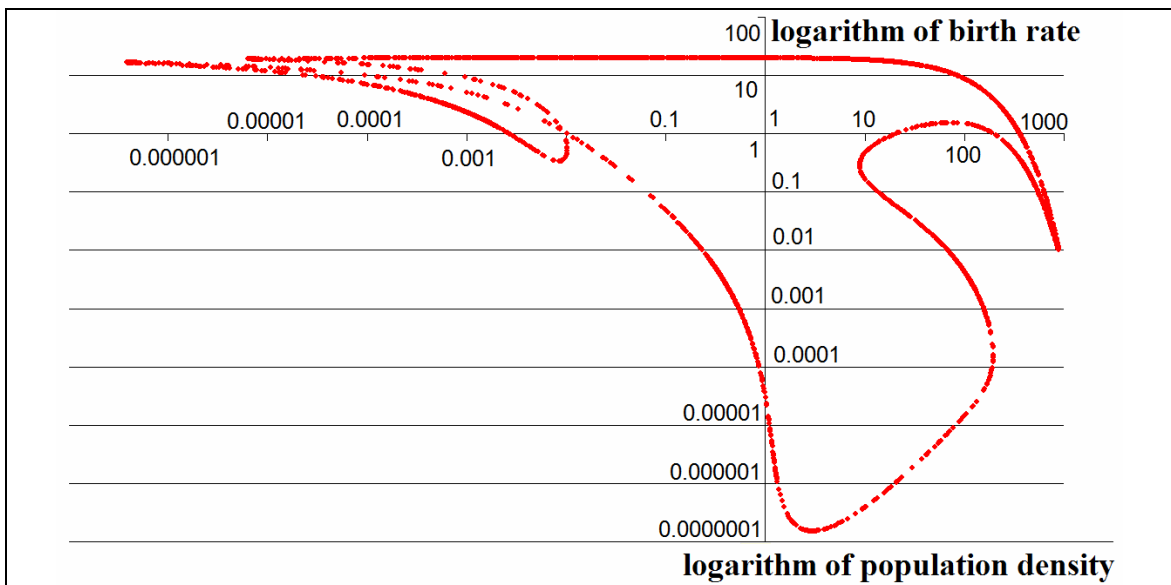
After 200000 “empty steps” auto-correlation function for 20000 obtained values of population density with model (3) was calculated (fig. 9). As we can see on this figure 400

values of this function are less than 1. It means that for estimated values of model parameters asymptotic stable dynamic regime isn't periodic with length of cycle in 400 steps or less. Moreover, maximum value of autocorrelation function is equal to 0.8754 for 1000 values. Thus, if observed regime is cyclic the length of cycle is bigger than 1000.



**Fig. 9.** Auto-correlation function for stable asymptotic dynamic regime obtained for estimated values of model parameters (first 400 values).

On figure 10 there are 19999 points which belong to asymptotic stable dynamic regime on the plane “population density – birth rate” (both coordinate lines are presented in logarithmic scale).



**Fig. 10.** Model trajectory for asymptotic dynamic regime on the plane “population density – birth rate” (logarithmic scales).

As we can see on this picture dynamic regime is rather difficult. But we haven't a background for conclusion that we have correspondence between this regime (fig. 10), and empirical regime (fig. 2).

Analysis of deviations showed that average plus/minus standard error is equal to  $-0.1948 \pm 8.093$  (thus, we can't reject hypothesis about equivalence of average to zero with 5% significance level), for Kolmogorov – Smirnov test  $d = 0.2559$  with  $p < 0.05$ , for Lilliefors test  $p < 0.01$ , for Shapiro – Wilk test  $W = 0.7579$  with  $p < 10^{-5}$ , for Durbin – Watson criteria  $d = 1.8476$  ( $d_u = 1.535 < d$  - there are no serial correlations). Thus, traditional approach to analysis of deviations allows concluding that model (3) isn't suitable for fitting of considering empirical time series.

Analysis of symmetry of deviations with respect to origin by the Kolmogorov – Smirnov test shows that  $d = 0.4423$  with the respective probability  $p = 0.056$ . Thus, we can't reject the hypothesis about symmetry with 5% significance level. But probability is very close to critical level 0.05.

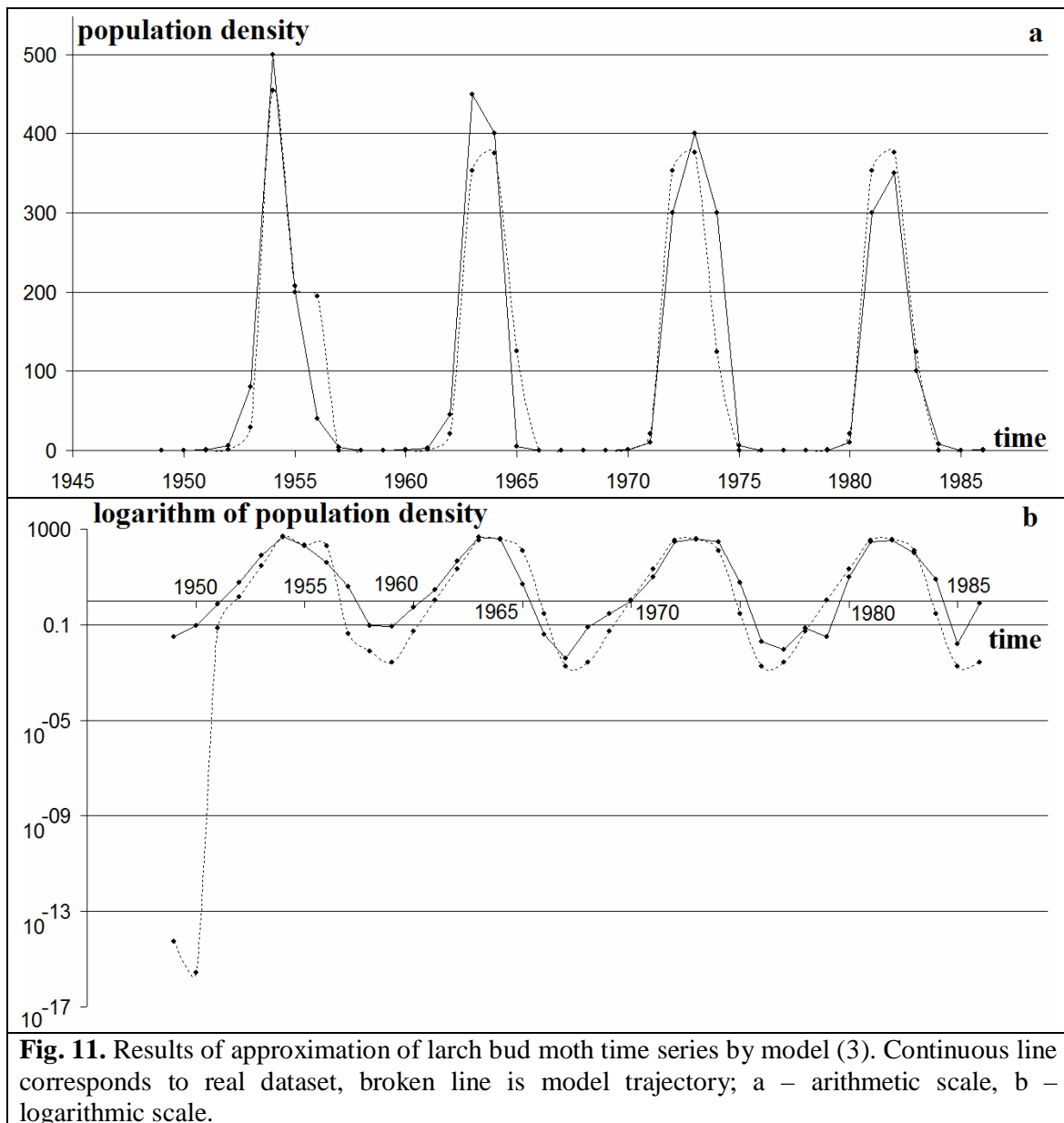
Comparison of increments of real trajectory and model trajectory shows that signs of increments are the same in 89.19% of all cases. Checking of the hypothesis that frequency is equal to 0.5 we obtain that real value of t-test is equal to 4.7676 (it is bigger than critical value 2.0262; we have to reject Null hypothesis  $p = 0.5$ ).

For “second derivatives” we have better correspondence:  $p = 0.916667$ . Thus, in considering situation we have also to reject Null hypothesis  $H_0 : p = 0.5$ . Taking into account that there are no serial correlations (Durbin – Watson test  $d = 1.8476$ ) we obtain a good background for conclusion that model (3) gives good fitting for larch bud moth time series (fig. 1). Note this conclusion is also in contradiction with conclusion we obtained with traditional approach to analysis of deviations. Finally, like in previous case we can say that in considering situation we have quantitative correspondence between theoretical and empirical trajectories but it is without of the qualitative correspondence. Results of approximation of considering datasets by trajectories of model (3) are presented on figure 11.

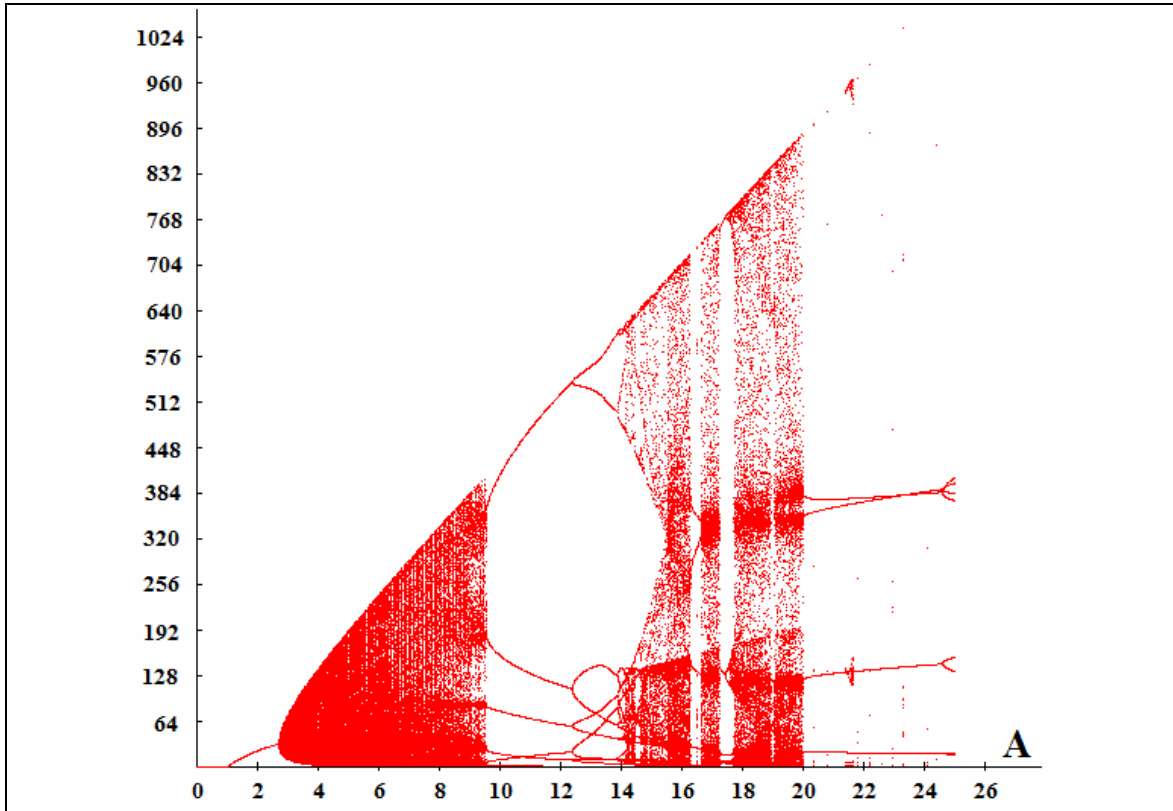
### ***Model with time lag 3***

Let's consider situation when time lag is equal to 3. Modification of Moran – Ricker model will have the following form:

$$x_{k+1} = Ax_k \exp\{-a_1x_k - a_2x_{k-1} - a_3x_{k-2} - a_4x_{k-3}\}. \quad (4)$$

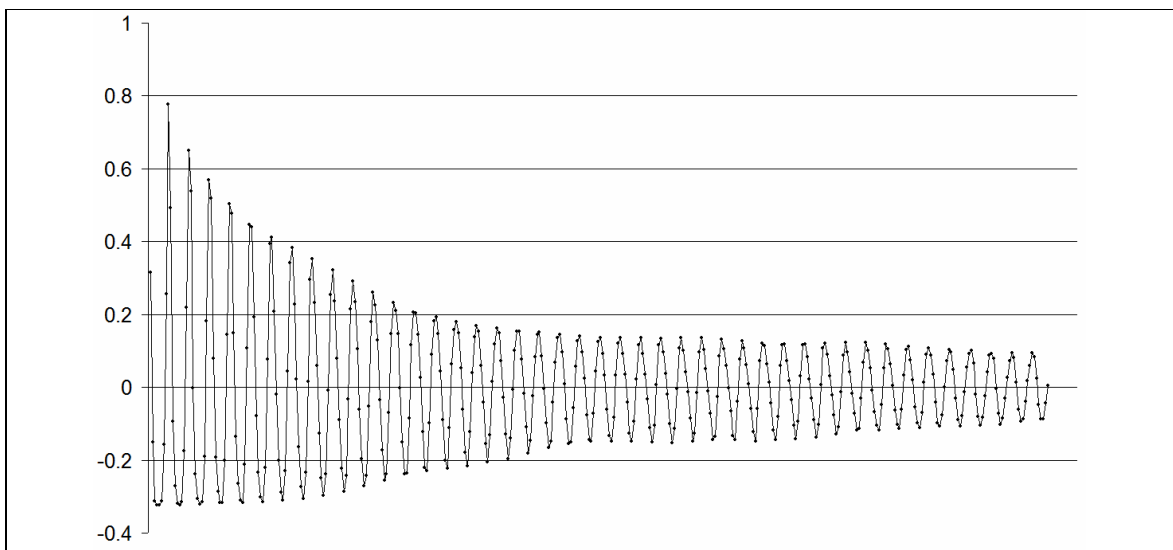


Minimum of squared deviations between real time series and model trajectories  $Q_{\min} = 92018.9$  was observed for the following values of model parameters:  $x_1^0 = 4.97 \cdot 10^{-14}$ ,  $x_2^0 = 1.61 \cdot 10^{-16}$ ,  $x_3^0 = 4.2 \cdot 10^{-16}$ ,  $x_4^0 = 1.4837$ ,  $A = 19.8439$ ,  $a_1 = 0.0081$ ,  $a_2 = 0.0018$ ,  $a_3 = 0.0186$ ,  $a_4 = 0.0021$ . For these parameters model (4) has bifurcation diagram presented on fig. 12. Number of “empty steps” is equal to 10000. After empty steps 200 obtained values of population densities were printed on straight line  $A = const$  (for every fixed value of this parameter). Initial values of population densities were found randomly in intervals  $[0, (A + 1)^2]$ .



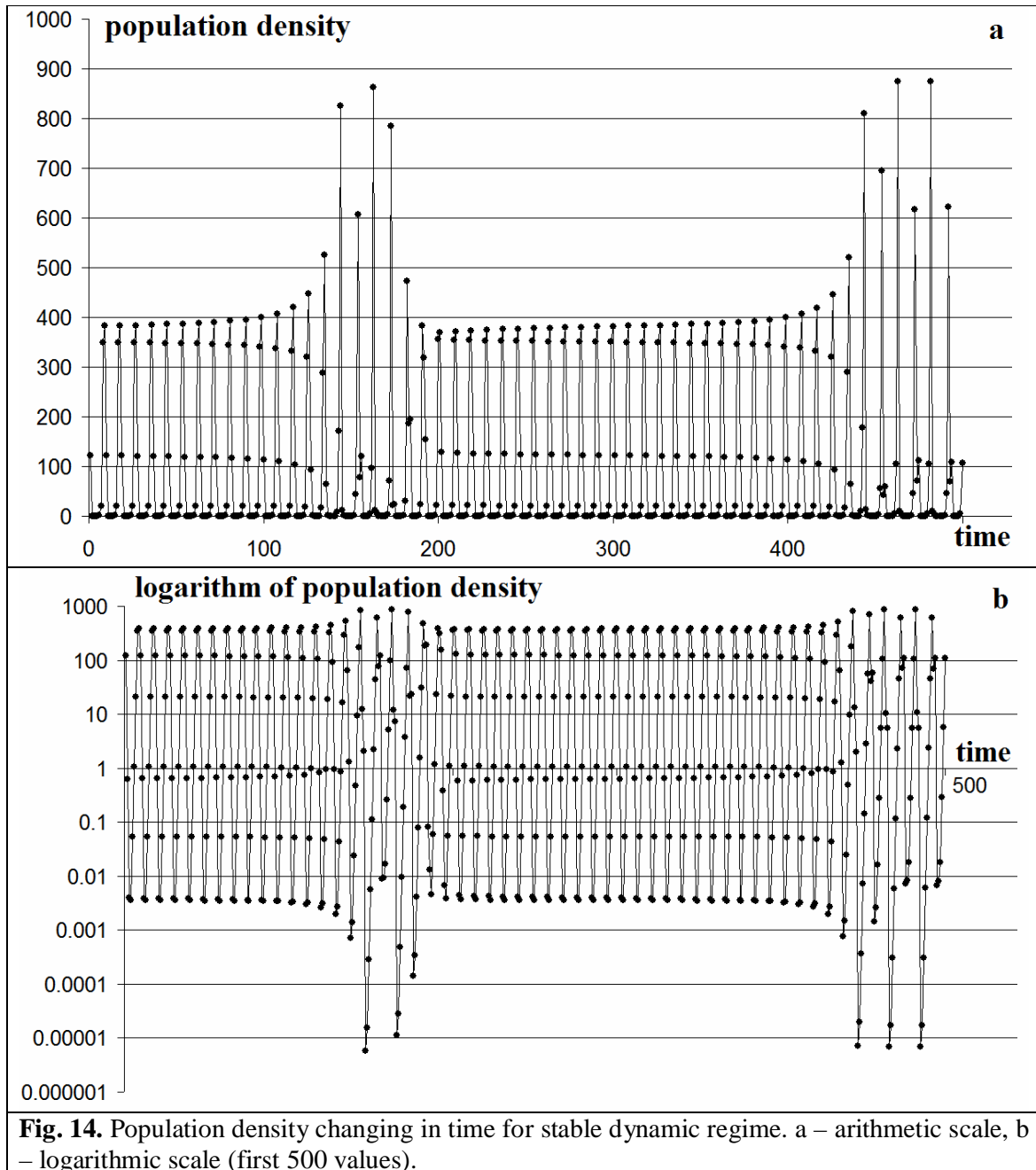
**Fig. 12.** Bifurcation diagram of model (4) for estimated values of parameters  $a_1, \dots, a_4$ .

After 200000 “empty steps” auto-correlation function for 20000 obtained values of population density with model (4) was calculated (fig. 13). As we can see on this fig. 13 400 values of this function are less than 1. It means that for estimated values of model parameters asymptotic stable dynamic regime isn’t periodic with length of cycle in 400 steps or less.



**Fig. 13.** Auto-correlation function for stable asymptotic dynamic regime obtained for estimated values of model (4) parameters (first 400 values).

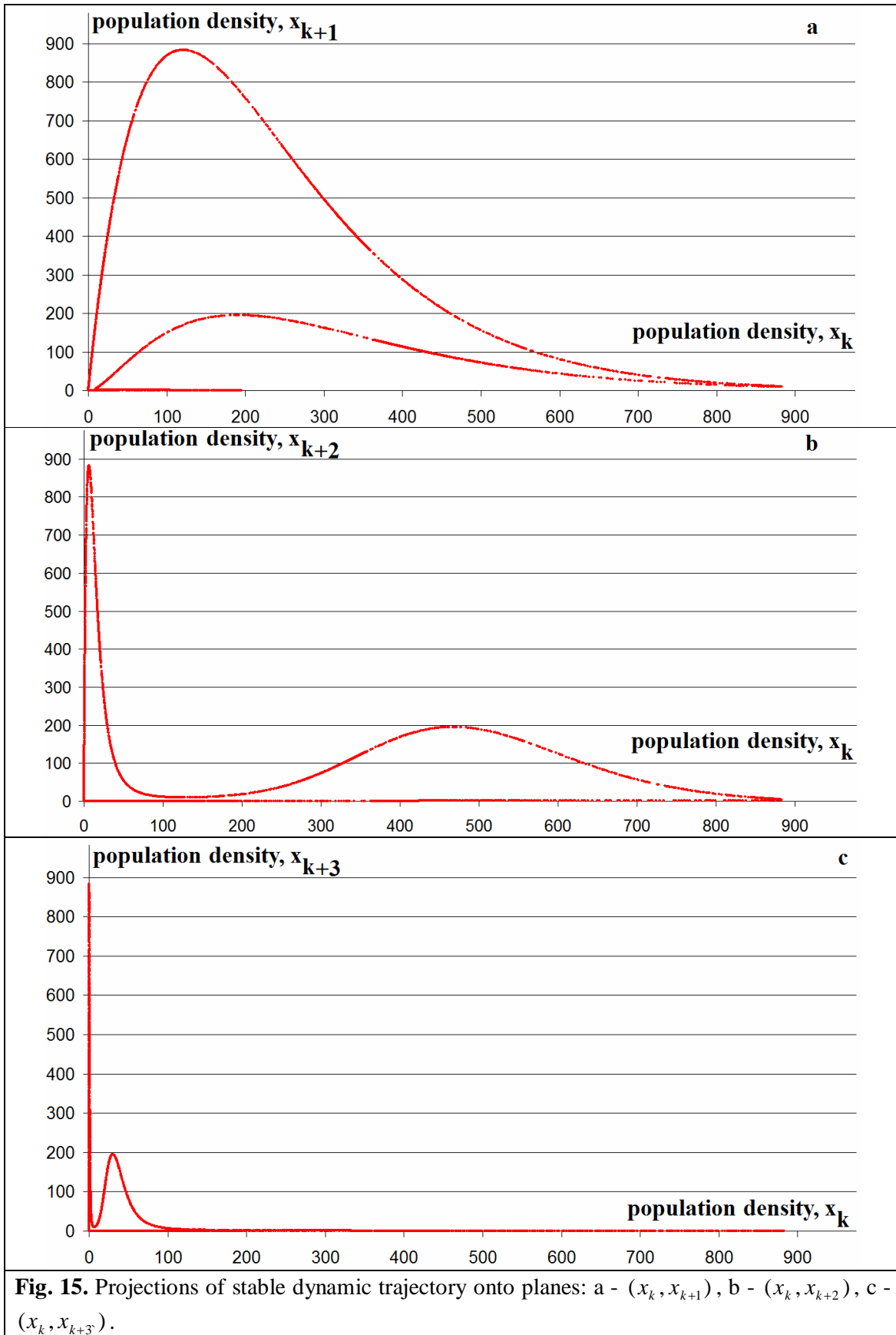
Maximum value for auto-correlation function for 1000 values is equal to 0.776365. It means that observed dynamic regime isn't periodic with period in 1000 steps or less. On fig. 14 there are the values of population density obtained for stable regime.



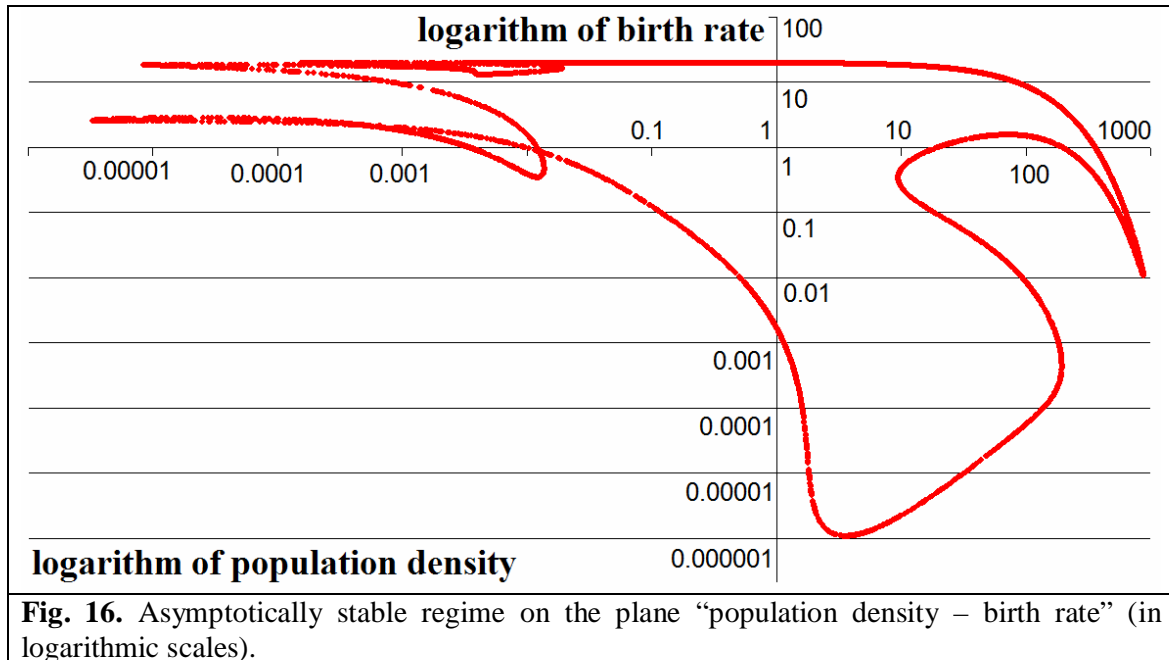
**Fig. 14.** Population density changing in time for stable dynamic regime. a – arithmetic scale, b – logarithmic scale (first 500 values).

Projections of stable dynamic trajectory onto various planes  $(x_k, x_{k+1})$ ,  $(x_k, x_{k+2})$ , and  $(x_k, x_{k+3})$  are presented on fig. 15.





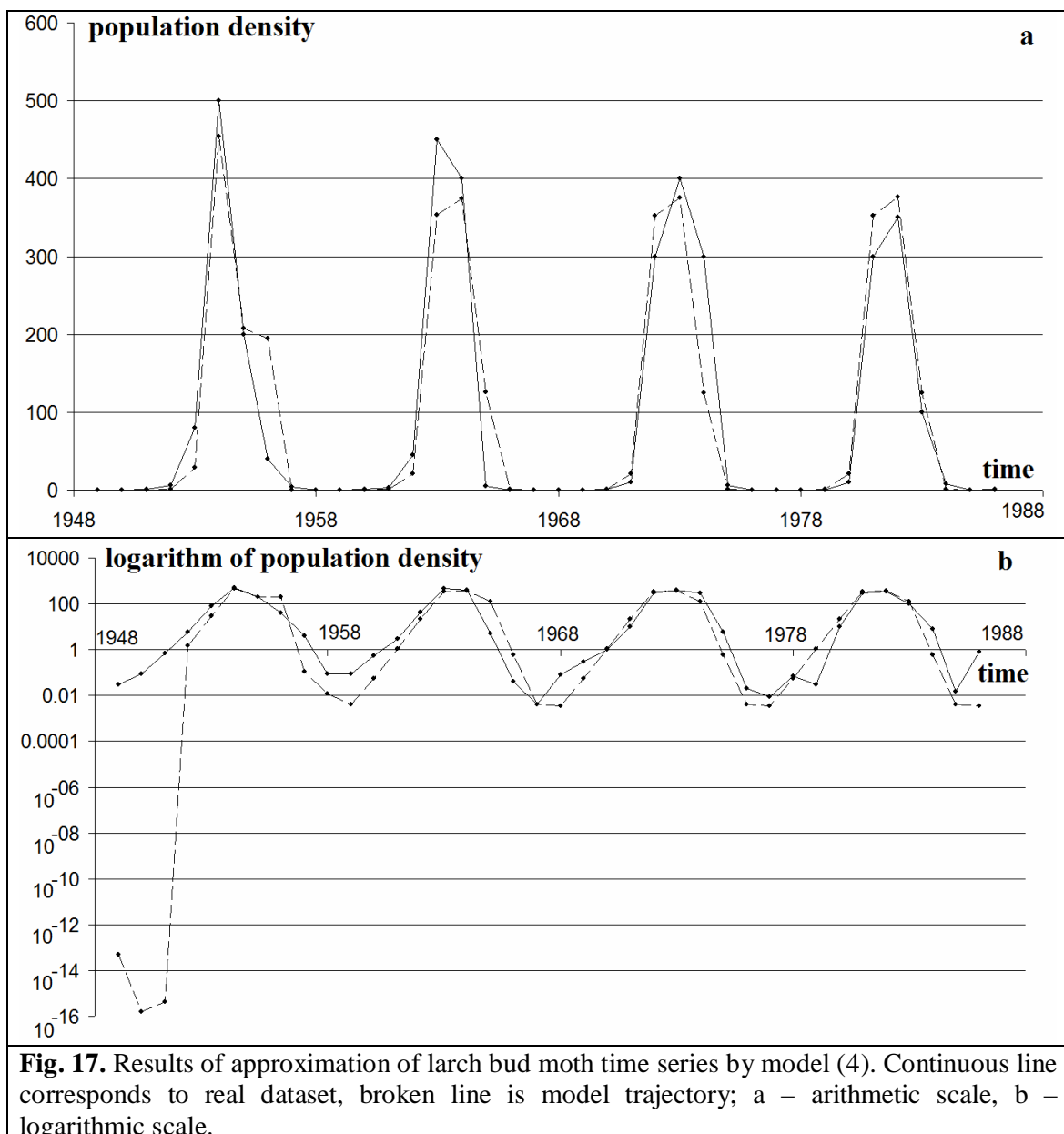
On fig. 16 there are the points of asymptotically stable regime on the plane “population density – birth rate”. As we can see on these pictures (fig. 15 and 16), trajectory of population density changing is rather difficult but it doesn’t correspond to theoretical imaginations about permanent outbreak trajectory (Isaev et al., 1984, 2001).



Analysis of deviations showed that average plus/minus standard error is equal to  $-0.1239 \pm 8.09$  (thus, we can’t reject hypothesis about equivalence of average to zero with 5% significance level), for Kolmogorov – Smirnov test  $d = 0.25791$  with  $p < 0.05$ , for Lilliefors test  $p < 0.01$ , for Shapiro – Wilk test  $W = 0.7576$  with  $p < 10^{-5}$ , for Durbin – Watson criteria  $d = 1.7497$ . Thus, traditional approach to analysis of deviations allows concluding that model (4) isn’t suitable for fitting of considering empirical time series.

Analysis of symmetry of deviations with respect to origin by the Kolmogorov – Smirnov test shows that  $d = 0.3723$  with the respective probability  $p = 0.144$ . Thus, we can’t reject the hypothesis about symmetry even with 10% significance level. Comparison of increments of real trajectory and model trajectory shows that signs of increments are the same in 86.84% of all cases. For 37 degrees of freedom and 5% significance level theoretical value of Student test is equal to 2.0262. Checking of the hypothesis that frequency is equal to 0.5 we obtain that real value of t-test is equal to 4.5422 (we have to reject Null hypothesis  $p = 0.5$ ). Thus, we have a background for conclusion that there is a good correspondence between changing of increments of real and model trajectories.

For “second derivatives” we have better correspondence:  $p = 0.916667$ . Thus, in considering situation we have also to reject Null hypothesis  $H_0: p = 0.5$ . Taking into account that there are no serial correlations (Durbin – Watson test) we obtain a good background for conclusion that model (4) gives good fitting for larch bud moth time series (fig. 1 and 2). Note, this conclusion is also in contradiction with conclusion we obtained with traditional approach to analysis of deviations. Finally, we can say that in considering situation we have the same result – we have quantitative correspondence between theoretical and empirical trajectories but it is without of the qualitative correspondence. Results of approximation of larch bud moth time series by model (4) are presented on figure 17.

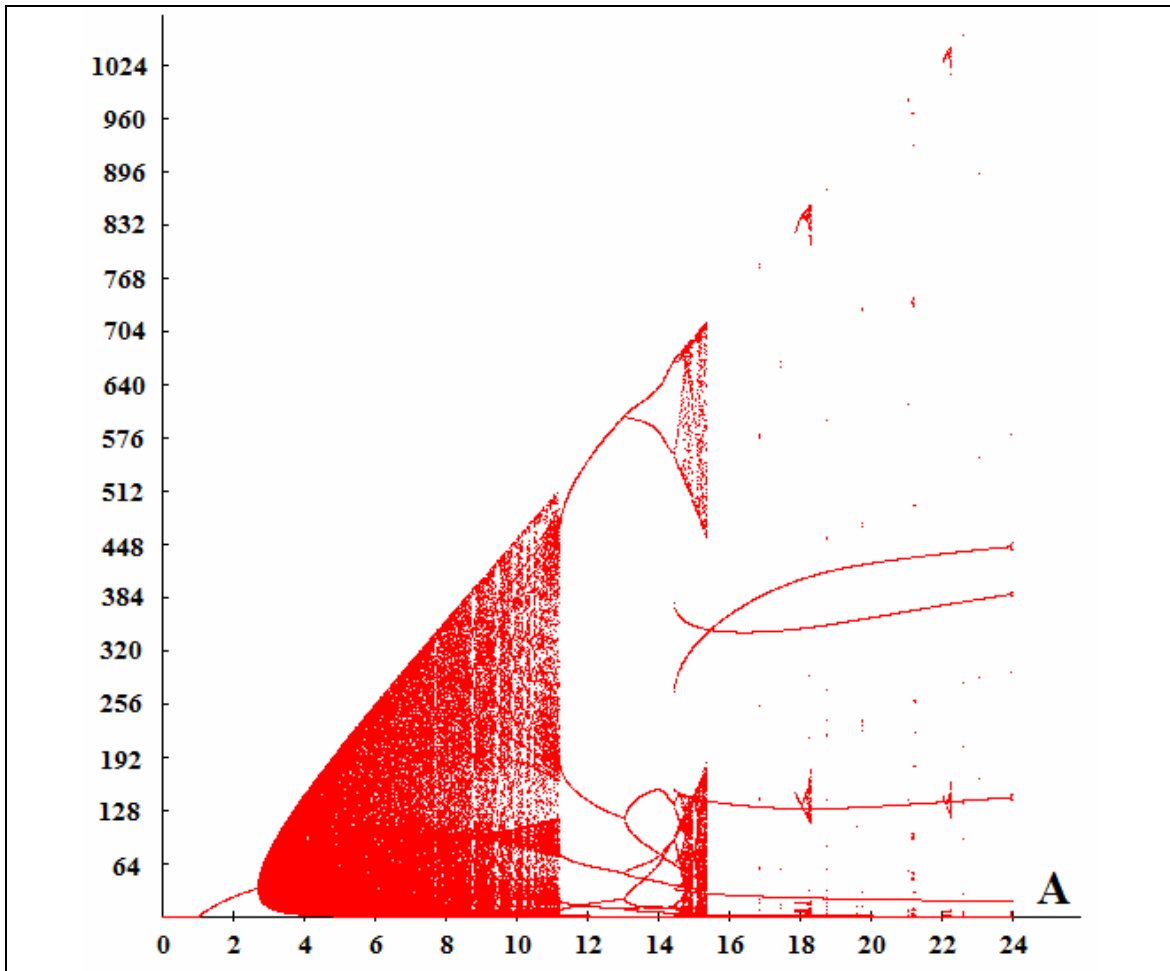


**Model with time lag 4**

Let's consider situation when time lag is equal to 4. Modification of Moran – Ricker model will have the following form:

$$x_{k+1} = Ax_k \exp\{-a_1x_k - a_2x_{k-1} - a_3x_{k-2} - a_4x_{k-3} - a_5x_{k-4}\}. \quad (5)$$

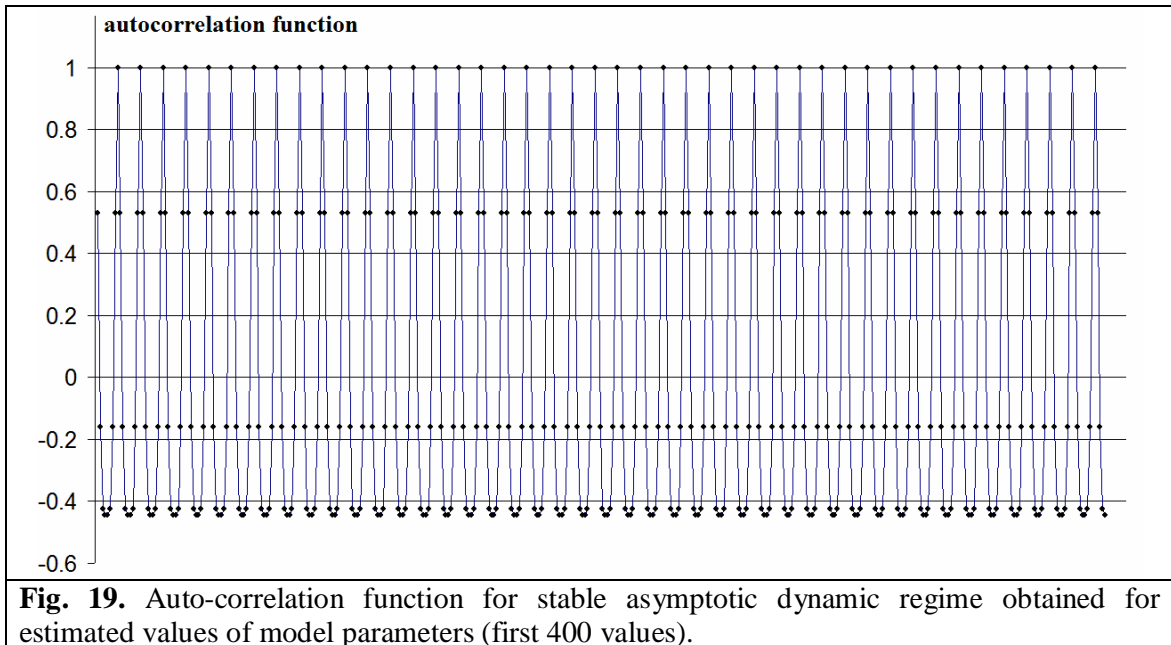
Minimum of squared deviations between real time series and model trajectories  $Q_{\min} = 92018.9$  was observed for the following values of model parameters:  $x_1^0 = 0.03$ ,  $x_2^0 = 7.828 \cdot 10^{-14}$ ,  $x_3^0 = 3.952 \cdot 10^{-15}$ ,  $x_4^0 = 4.544 \cdot 10^{-16}$ ,  $x_5^0 = 36.349$ ,  $A = 16.755$ ,  $a_1 = 7.723 \cdot 10^{-3}$ ,  $a_2 = 1.314 \cdot 10^{-3}$ ,  $a_3 = 0.0189$ ,  $a_4 = 7.0889 \cdot 10^{-4}$ ,  $a_5 = 5.3848 \cdot 10^{-22}$ . For these parameters model (5) has bifurcation diagram presented on fig. 18. Number of “empty steps” is equal to 10000.



**Fig. 18.** Bifurcation diagram of model (5) for estimated values of parameters  $a_1, \dots, a_5$ .

After 200000 “empty steps” auto-correlation function for 20000 obtained values of population density with model (5) was calculated (fig. 19). As we can see on fig. 19 values of this

function are very close to 1 periodically (maximum of function is equal to 0.99995). It means that for estimated values of model parameters asymptotic stable dynamic regime is close to 9-cycle. It is interesting to note that taking into account of rather small amount (coefficient  $a_5$  is much smaller than all other coefficients) describing the dependence of birth rate on values of population density of 5 years ago led to qualitative changing of dynamic regime: on previous step non-periodic regime was observed, and it was transformed in 9-cycle.

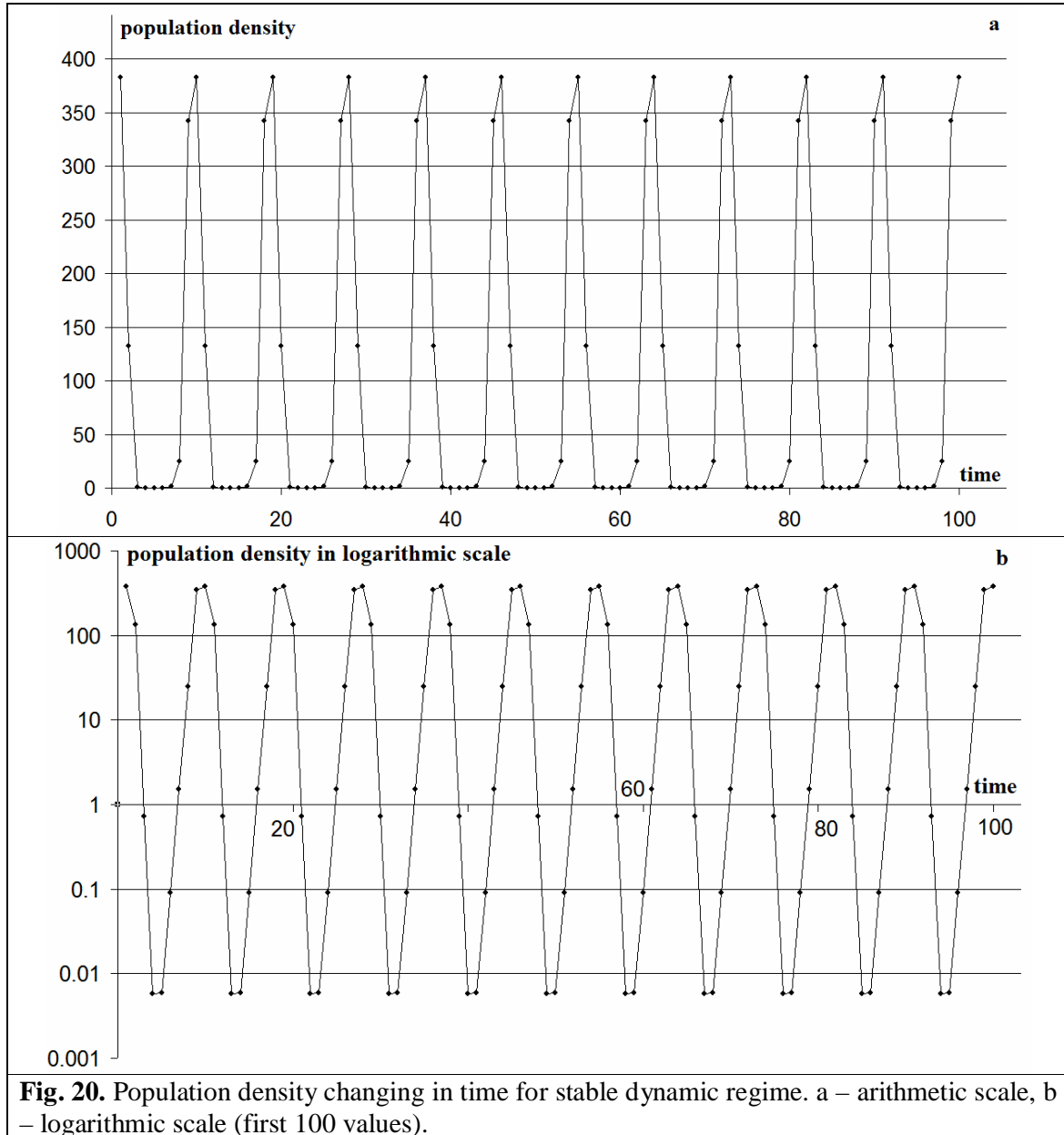


On fig. 20 there are the values of population density obtained for stable regime (in arithmetic and logarithmic scales).

On fig. 21 there are the points of asymptotically stable regime on the plane “population density – birth rate”. As we can see on this picture, trajectory of population density changing is rather difficult but it doesn’t correspond to theoretical imaginations about permanent outbreak trajectory (Isaev et al., 1984, 2001).

Analysis of deviations showed that average plus/minus standard error is equal to  $-0.8388 \pm 7.9869$  (thus, we can’t reject hypothesis about equivalence of average to zero with 5% significance level), for Kolmogorov – Smirnov test  $d = 0.258$  with  $p < 0.05$ , for Lilliefors test  $p < 0.01$ , for Shapiro – Wilk test  $W = 0.754$  with  $p < 10^{-5}$ , for Durbin – Watson criteria  $d = 1.7574$  ( $d_u = 1.535 < d$  - there are no serial correlations). Thus, traditional approach to analysis of deviations allows concluding that model (5) isn’t suitable for fitting of considering empirical time series.

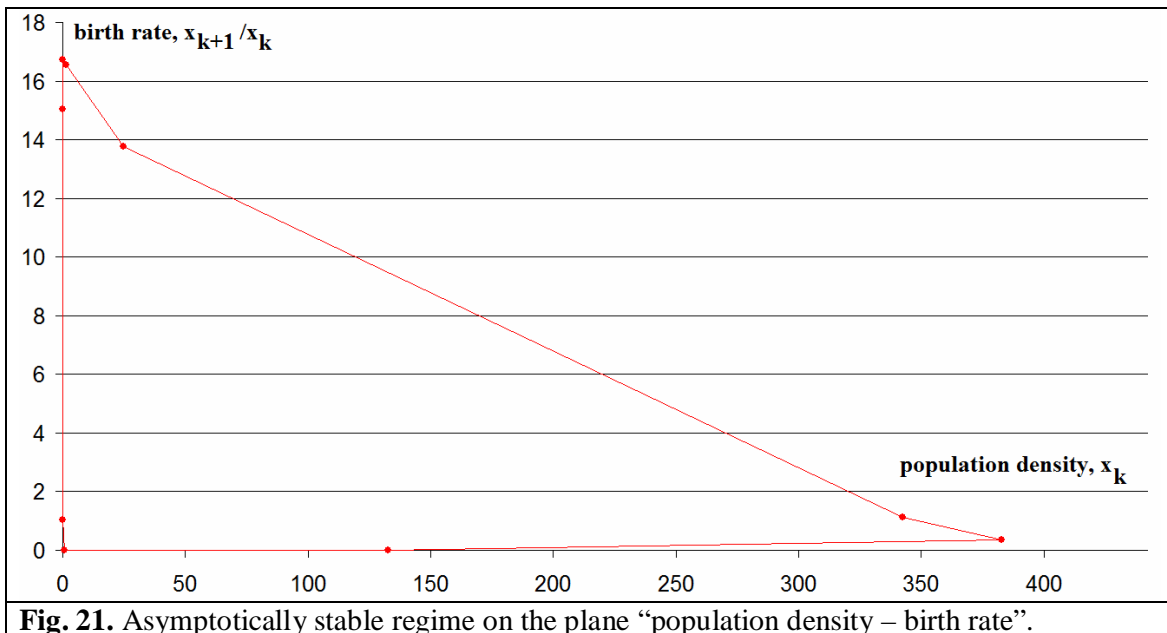
Analysis of symmetry of deviations with respect to origin by the Kolmogorov – Smirnov test shows that  $d = 0.2957$  with the respective probability  $p = 0.344$ . Thus, we can't reject the hypothesis about symmetry of distribution.



**Fig. 20.** Population density changing in time for stable dynamic regime. a – arithmetic scale, b – logarithmic scale (first 100 values).

Comparison of increments of real trajectory and model trajectory shows that signs of increments are the same in 83.87% of all cases. For 37 degrees of freedom and 5% significance level theoretical value of Student test is equal to 2.0262. Checking of the hypothesis that frequency is equal to 0.5 we obtain that real value of t-test is equal to 4.11 (we

have to reject Null hypothesis  $p = 0.5$ ). Thus, we have a background for conclusion that there is a good correspondence between changing of increments of real and model trajectories.



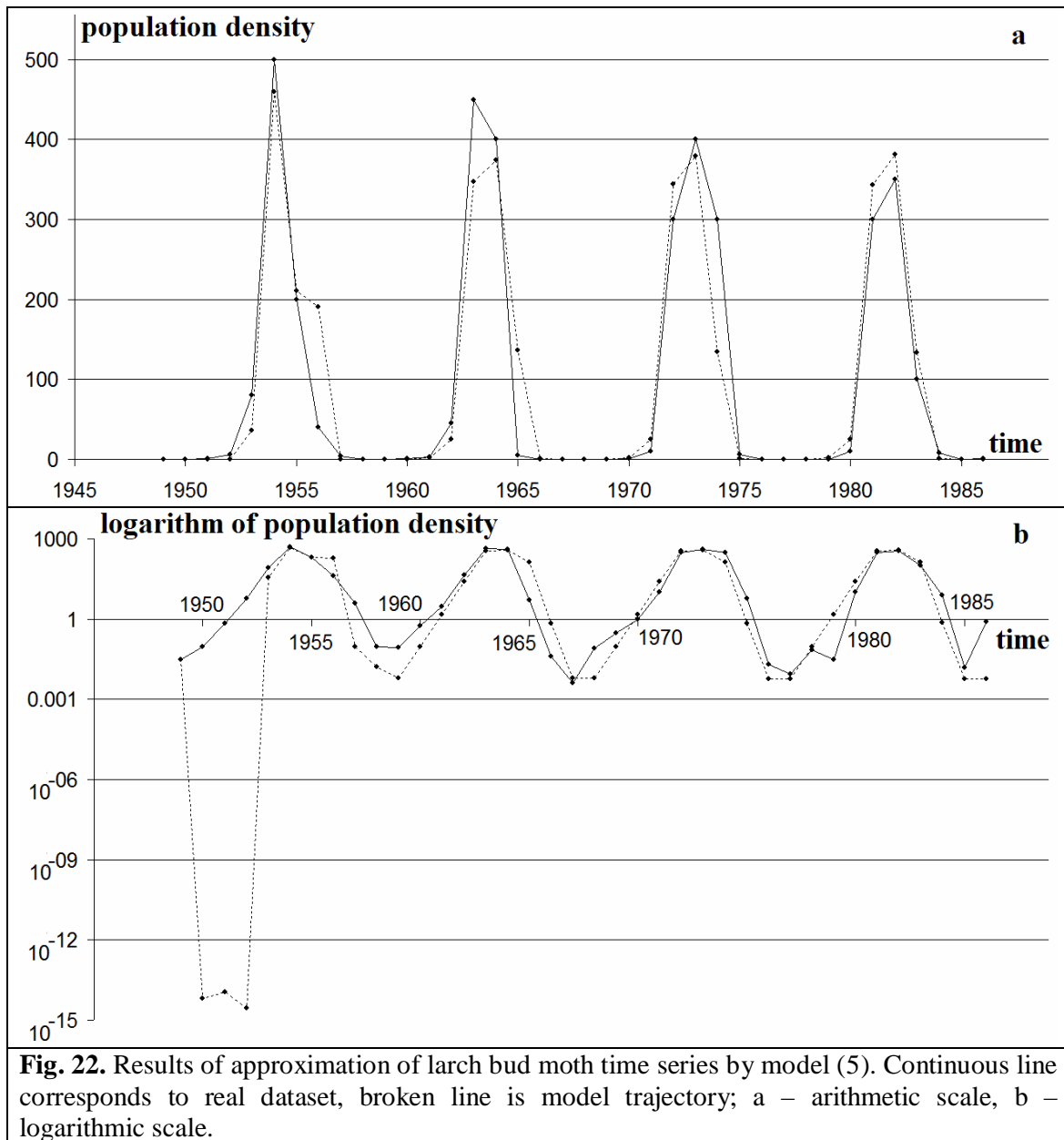
**Fig. 21.** Asymptotically stable regime on the plane “population density – birth rate”.

For “second derivatives” we have better correspondence:  $p = 0.7778$ . Thus, in considering situation we have also to reject Null hypothesis  $H_0: p = 0.5$  (real value of t-test is equal to 3.3333, and critical level is 2.03011). Taking into account that there are no serial correlations (Durbin – Watson test) we obtain a good background for conclusion that model (5) gives good fitting for larch bud moth time series (fig. 1). Note this conclusion is also in contradiction (like in previous cases) with conclusion we obtained with traditional approach to analysis of deviations. Finally, we can say that in considering situation we have quantitative correspondence between theoretical and empirical trajectories but it is without of the qualitative correspondence (fig. 22).

### Conclusion

Fitting of time series of larch bud moth fluctuations by the modifications of Moran – Ricker model when we take into account an existence of time lag dependence of birth rate on population density in previous years (lag is equal or less than 4), allows us concluding that we can obtain good approximation. Behavior of trajectories of models with time lags (with estimated values of model parameters) corresponds to behavior of real datasets on quantitative level. But this results were obtained when we used non-traditional approach to analysis of deviations between theoretical (model) and empirical trajectories. When we used traditional

approach and tested sets of deviations on corresponding of distributions to Normal, we obtained that all models are not suitable for fitting of empirical datasets. Hypotheses about Normality must be rejected with very small significance level (Shapiro – Wilk test).



It is very important to note that requirement to deviations to have a Normal distribution is very strong, and it is not applicable to biological objects. In our opinion for testing of deviations we have to use softer criterions. For example, we have to test deviations on symmetry of their distribution with respect to origin. May be, we have to test on monotonic changing of negative and positive branches of density function.



But main problem of testing of correspondence of models to real datasets is in order of providing of statistical calculations. Within the limits of traditional approach for the first time we have to estimate model parameters, and after that we have to analyze sets of deviations with group of statistical tests. If all tests show good results we obtain a background for conclusion that considering model is suitable for fitting. If not, we say that model isn't suitable for fitting. It means that final conclusion about model and its applicability for fitting we make using one point from the space of model parameters.

In our opinion it is much better to use other way for statistical calculations. First of all, we have to determine a list of statistical criteria we assume to use for analysis of deviation. For every criterion we have a set in space of model parameters where criterion shows good results. Intersection of all these sets gives us a set where every point can be used as estimation of model parameters. We cannot exclude the situation that this set is empty, and it corresponds to the situation when model isn't suitable for fitting. But for this conclusion we have to test all points of a space of model parameters.

And the last remark is following. When we have several one-dimensional time series for one and the same mathematical model, we have a serious problem in finding of minimizing functional form (see, for example, Tonnang et al., 2009, 2010). Sometimes we have to summarize numbers of rabbits and foxes, predators and preys with some weights. But it looks rather strange. If for the first time we determine a suitable set of points in space of model parameters we haven't this problem.

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