Dynamics of *Bupalus piniarius* in Germany: search for stationary dynamical regimes

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Abstract

In current publication possible population dynamics regimes are analyzed using pre-model statistical method. Method was applied to well-known *Bupalus piniarius* L. time series (Schwerdtfeger, 1944, 1968) and showed that that observed fluctuations don't correspond to strong 2-, 3-,…, or 9-year cycles which can be generated by one-dimensional discrete models. At the same time provided analysis shows that dynamics of pine looper can be very close to cyclic fluctuations with the length 8.

Keywords: pine looper population fluctuations, time series, pre-model statistical analysis, approximation, stationary dynamical regime

Introduction

Search for suitable mathematical model, estimation of model parameters using empirical datasets, and determination of basic features of population phase portraits are the main elements of population dynamics analysis (Isaev et al., 1984, 2001; McCallum, 2000; Nedorezov, 1986; Tonnang et al., 2009, 2010; Turchin, 2003; Wood, 2001 and many others). Without finding of suitable model (or without constructing of new suitable model) it is impossible to prepare strong scientifically-based forecasts of pest population changing and optimal methods of its management. But up to current moment there are no criterions, which can help in finding of a suitable model before comparison of theoretical and empirical datasets (Isaev et al., 1984, 2001; Nedorezov, Utyupin, 2011). In such a situation preliminary and pre-model statistical analysis of existing time series can be very useful in the process of searching of suitable model or group of suitable models.

It is possible to point out different variants of preliminary statistical analysis which can be very useful in choosing of a mathematical model. In particular, without using of any model it is possible to check hypotheses about correspondence of observed fluctuations to cyclic dynamics with fixed size n ($n = 1,2,3...$). Respectively, all deviations from coordinates of n-cycle can be explained as results of influence of external stochastic factors, by used methods of data collection etc. In other words, before choosing of model we can try to determine a dynamical regime which is observed in natural conditions. More precisely, we can try to find a dynamical regime with the following property: modern statistical methods don't allow us concluding that considering regime doesn't correspond to observed fluctuations (Nedorezov, 2011a, 2012a).

It is known, that for estimation of model parameters under the use of *global fitting* for empirical time series, researches use *initial parts* of model trajectories, and don't use parts of trajectories which correspond to *stabilized regime* of population fluctuations (McCallum, 2000; Nedorezov, 2010, 2012 a; Turchin, 2003; Wood, 2001 and others). Approximation of empirical time series by initial parts of model trajectories is correct if we analyze a process of population size changing in time which corresponds to *non-stabilized dynamic regime* (Nedorezov, 2011 b, 2012 a, b). But if we analyze dynamics of species which exist in local habitat (and where datasets were collected) during long time period the use of initial parts of model trajectories for fitting of empirical time series needs in additional explanation.

Algorithm

Let $x_1, x_2, \ldots, x_N$ be a time series of considering hypothetical population. Time step is equal to one year, thus x_k is a population size (or density) at k th year. First of all, we have to solve the following question: what kind of datasets we have now? If, for example, we analyze time series presented in book by G.F. Gause (1934), it is obvious, that for every trajectory we can point out initial part (it can be exponential phase of population growth), mid part of trajectory (where we can observe growth of influence of intra-population self-regulative mechanisms on process of population size changing), and stabilized behavior (fluctuations near asymptotical stable level). In such a situation we have a good background for application of initial parts of trajectories for fitting of experimental datasets (Nedorezov, 2011 b, 2012 b).

But in the case when we analyze insect population dynamics in locations where insects live thousands and thousands years, we haven't a background with the same properties. In these situations we observe *stabilized dynamical regime*. Thus, for the estimation of model parameters we have to minimize, for example, the sum of squared deviations of real datasets from coordinates of *asymptotically stable attractors*.

First of all, we must determine a dynamical regime which is realized for population: it is hypothesis we have to check. For example, we can start with assumption that observed fluctuations of population size correspond to cycle of the length two: *ababab...* Let's assume that minimizing functional form is equal to sum of deviations squared. In this case we have:

$$Q(a,b) = \sum_k (x_k - a)^2 + \sum_k (x_k - b)^2 \to \min_{a,b} . \tag{1}$$

From (1) we get the following estimations for coordinates of 2-cycle:

$$a = \frac{1}{N^*} \sum_k x_k \ , \ b = \frac{1}{N^{**}} \sum_k x_k \ , \tag{2}$$

where $N^* + N^{**} = N$, and $N^* = N^{**}$ or $N^* = N^{**} + 1$. After estimations (2) of coordinates of 2-cycle we have to check hypothesis that observed regime is 2-cycle: more precisely, we have to analyze two sequences $x_1 - a$, $x_3 - a$,... and $x_2 - b$, $x_4 - b$,… and to show that arithmetic averages are equal to zeros, distribution functions for both sets are symmetric functions, and there are no serial correlation in both sequences ((Draper, Smith, 1986, 1987)). Moreover, we have to reject Null hypothesis about equivalence of coordinates of cycle: Null hypothesis is $a = b$.

If all used tests show that there are no reasons for rejecting of the respective Null hypotheses and Null hypothesis $a = b$ must be rejected for selected significance level, we have to start the process of selection of mathematical model. It is obvious, if observed changing of population size corresponds to 2-cycle there are no reasons for consideration of the Skellam model or Kostitzin model – in both models there are the regimes of asymptotic stabilizations of population size at any levels only for all values of model parameters (Skellam, 1951; Kostitzin, 1937; Beverton, Holt, 1957). In this situation it is better to use Moran – Ricker model or discrete logistic model which contain a lot of various dynamical regimes (Moran, 1950; Ricker, 1954; Isaev et al., 1984, 2001; Bazykin, 1985; Nedorezov, 1986, 1997; Svirezhev, 1987). Let's assume that we decided to choose Moran – Ricker model for the description of population size dynamics:

$$y_{k+1} = Ay_k e^{-\alpha y_k} , \tag{3}$$

where $A, \alpha = const > 0$, y_k is population size at time moment k. If we observe 2-cycle for model (3) it means that following relations must be truthful for coefficients:

$$a = Abe^{-\alpha b} , \ b = Aae^{-\alpha a} .$$

Values of model (3) parameters must be obtained as solutions of this system of non-linear algebraic equations. After logarithmic transformation of this system of algebraic equations we get new linear system for variables α and $w = \ln A$:

$$\ln a - \ln b = w - \alpha b, \ \ln b - \ln a = w - \alpha a.$$

For $b \neq a$ basic determinant of this linear system doesn't equal to zero, and, respectively, solutions of this system exist and unique:

$$\alpha = \frac{2(\ln a - \ln b)}{a-b}, \ w = \ln a - \ln b + b\frac{2(\ln a - \ln b)}{a-b}.$$

After obtaining of model parameter estimations we have to check a stability of 2-cycle: if it isn't asymptotically stable model cannot give us a sufficient approximation of datasets. The similar relations can be obtained for all other cyclic regimes (Nedorezov, 2012 a, 2013).

Datasets

In current publication algorithm described above was applied to time series on *Bupalus piniarius* L. (Schwerdtfeger, 1944, 1968; Varley, 1949; NERC Centre for Population Biology, Imperial College (1999) The Global Population Dynamics Database, N 3759). Population densities are presented in units "logarithm of individuals (larvae) per squared meter" from 1881 to 1940. Total sample size is 58 values (data for 1911 and 1912 are absent).

On figure 1 there are graphics of changing of density of larvae of pine looper (curve 2) and logarithm of density (curve 1) in time. These fluctuations look like as periodic process under strong influence of external stochastic factors. This influence leads to changing of amplitude of observed fluctuations; thus, hypothesis about periodicity of observed fluctuations cannot be rejected a'priori.

Results

In table 1 there are the estimations of cycle's coordinates (under the assumptions that one or other attractor is realized for pine looper fluctuations), and respective values of minimizing functional form Q (it is a sum of squared deviations of real values from the estimated coordinates of cycle; in particular case (1) Q is presented for 2-cycle). It was assumed that maximum length of cycle is 9.

It is obvious, that increasing of the length of cycle must lead to decreasing of the value of minimizing functional form Q (as we can see from the table 1, process of decreasing can be nonmonotonic). If length of cycle is equal to 58 (in considering situation it is equal to sample size) $Q = 0$. But in table 1 there is no strong decreasing of Q. Differences between values are rather small.

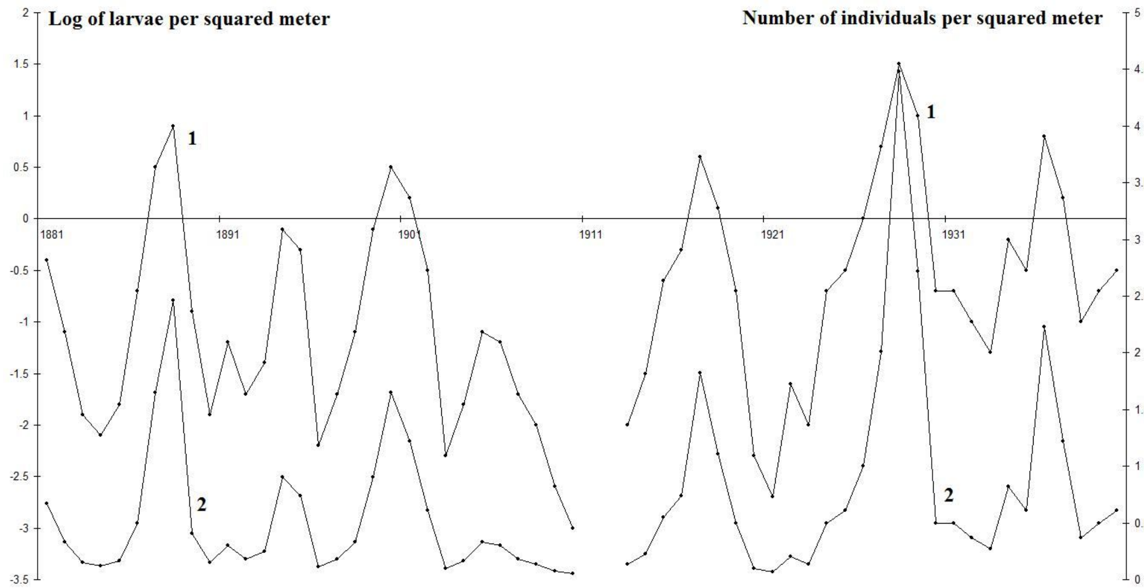

Fig. 1 Changing in time of logarithm of individuals per squared meter (curve 1, left ordinate line) and density of individuals per squared meter (curve 2, right ordinate line).

Table 1
Estimations of coordinates of cycles and respective values of sums of squared deviations between theoretical and empirical trajectories

	1*	2	3	4	5	6	7	8	9
1	0.693	0.654	0.646	0.676	0.694	1.01	0.794	0.717	0.756
2		0.732	0.747	0.493	0.797	1.108	0.465	0.301	1.1
3			0.687	0.63	0.827	0.566	0.403	0.402	1.115
4				0.989	0.652	0.318	0.433	0.538	0.694
5					0.504	0.422	0.578	0.63	0.372
6						0.808	0.994	0.712	0.406
7							1.2	0.934	0.47
8								1.591	0.71
9									0.515
Q	37.232	37.143	37.133	35.344	36.452	32.351	32.565	29.912	33.112

*1-cycle is stationary level

If we assume that considering time series correspondents to stochastic fluctuations near one stable level, we have to check Normality of deviations and existing/absence of serial correlation. Kolmogorov – Smirnov test gives $d = 0.2323$, and probability $p < 0.01$ (this is the probability of event that distribution of deviations is Normal); Lilliefors test shows $p < 0.01$; Shapiro – Wilk test: $W = 0.7128$ and $p < 10^{-5}$ (Lilliefors, 1967; Shapiro, Wilk, Chen, 1968; Bolshev, Smirnov, 1983). Durbin – Watson criteria (Draper, Smith, 1986, 1987) is equal to 0.8544, and it means that in sequence of residuals the negative serial correlation is observed (for sample size 58 and one predictor critical values of this criterion for 5% significance level are following: $d_L = 1.54$ and $d_U = 1.61$; and $d_L = 1.37$ and $d_U = 1.44$ for 1% significance level). Thus, with 1% significance level our hypothesis that considering sample is stochastic fluctuations near stationary level must be rejected.

If we assume that observed fluctuations correspond to 2-cycle *abab...*, we have to divide initial sample on two sub-samples x_1, x_3,… and x_2, x_4,…, and check the hypothesis H_0 : $a = b$ against alternative hypothesis H_1 : $a \neq b$. If with rather big significance level H_0 cannot be rejected we have not a background for conclusion that 2-cycle is realized for population. For considering situation (for first sub-sample $x_1 - a$, $x_3 - a$,…) the following results were obtained: Kolmogorov – Smirnov test – $d = 0.2182$, $p < 0.15$; Lilliefors test – $p < 0.01$; Shapiro – Wilk test – $W = 0.796$, $p = 0.00007$. Durbin – Watson criteria is equal to 1.54. For the second sub-sample $x_2 - a$, $x_4 - a$,… obtained results are following: Kolmogorov – Smirnov test – $d = 0.2427$, $p < 0.05$; Lilliefors test – $p < 0.01$; Shapiro – Wilk test – $W = 0.666$, $p < 10^{-5}$. Thus, with 1% significance level hypotheses about Normality of two sub-samples must be rejected, and we haven't a background for application of parametric statistical criterions for checking of the hypothesis H_0. Durbin – Watson criteria is equal to 1.981. For sample size 29 and one predictor critical values of this criterion for 5% significance level are following: $d_L = 1.34$ and $d_U = 1.48$; and $d_L = 1.12$ and $d_U = 1.25$ for 1% significance level).

In tables 2-8 there are the results of analyses of sets of deviations between coordinates of cycles and time series. As we can see in all analyzed situations we have to reject hypotheses about Normality of deviations. For 3-cycle Shapiro – Wilk test allows rejecting Null hypothesis with 1% significance level (table 2). In two of three cases Lilliefors test allows rejecting Null hypothesis with 1% significance level too (table 2).

Table 2

Results of analyses of deviations between time series and 3-cycle

Estimations of coordinates of cycle	KS[1]	Lilliefors	SW[2]	DW[3]
0.646±0.163	0.231/p>0.2	p<0.05	0.761/p=0.00033	2.265
0.747±0.177	0.286/p<0.1	p<0.01	0.793/p=0.00089	2.685
0.687±0.214	0.295/p<0.05	p<0.01	0.551/$p<10^{-5}$	2.008

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

Table 3

Results of analyses of deviations between time series and 4-cycle

Estimations of coordinates of cycle	KS[1]	Lilliefors	SW[2]	DW[3]
0.676±0.197	0.238/p>0.2	p<0.05	0.777/p=0.0019	2.434
0.493±0.084	0.182/p>0.2	p<0.2	0.922/p=0.21	2.739
0.63±0.151	0.231/p>0.2	p<0.05	0.808/p=0.0063	2.655
0.989±0.344	0.291/p<0.2	p<0.01	0.734/p=0.0009	2.556

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

Table 4

Results of analyses of deviations between time series and 5-cycle

Estimations of coordinates of cycle	KS[1]	Lilliefors	SW[2]	DW[3]
0.694±0.187	0.197/p>0.2	p>0.2	0.853/p=0.0469	1.809
0.797±0.221	0.266/p>0.2	p<0.05	0.796/p=0.0083	3.037
0.827±0.386	0.384/p<0.05	p<0.01	0.608/p=0.0001	2.487
0.652±0.206	0.278/p>0.2	p<0.01	0.704/p=0.0009	1.722
0.504±0.124	0.24/p>0.2	p<0.1	0.819/p=0.0157	1.823

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

Table 5

Results of analyses of deviations between time series and 6-cycle

Estimations of coordinates of cycle	KS[1]	Lilliefors	SW[2]	DW[3]
1.01±0.291	0.214/p>0.2	p>0.2	0.885/p=0.179	3.269
1.108±0.274	0.216/p>0.2	p>0.2	0.871/p=0.126	2.462
0.566±0.126	0.169/p>0.2	p>0.2	0.876/p=0.116	1.515
0.318±0.091	0.232/p>0.2	p<0.15	0.774/p=0.007	2.261
0.422±0.185	0.314/p>0.2	p<0.01	0.619/p=0.00009	2.403
0.808±0.416	0.397/p<0.1	p<0.01	0.551/p=0.00001	2.095

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

Table 6

Results of analyses of deviations between time series and 7-cycle

Estimations of coordinates of cycle	KS[1]	Lilliefors	SW[2]	DW[3]
0.794±0.237	0.308/p>0.2	p<0.05	0.815/p=0.03	1.955
0.465±0.179	0.365/p<0.15	p<0.01	0.684/p=0.0009	2.174
0.403±0.118	0.246/p>0.2	p<0.15	0.805/p=0.032	1.551
0.433±0.096	0.269/p>0.2	p<0.1	0.873/p=0.163	1.851
0.578±0.234	0.287/p>0.2	p<0.05	0.759/p=0.01	1.966
0.994±0.529	0.352/p>0.2	p<0.01	0.66/p=0.0008	2.472
1.2±0.333	0.131/p>0.2	p>0.2	0.94/p=0.606	1.403

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

Table 7

Results of analyses of deviations between time series and 8-cycle

Estimations of coordinates of cycle	KS[1]	Lilliefors	SW[2]	DW[3]
0.717±0.315	0.271/p>0.2	p<0.1	0.748/p=0.0077	1.703
0.301±0.039	0.144/p>0.2	p>0.2	0.962/p=0.824	2.132
0.402±0.093	0.172/p>0.2	p>0.2	0.892/p=0.243	2.77
0.538±0.178	0.218/p>0.2	p>0.2	0.808/p=0.035	2.791
0.63±0.247	0.278/p>0.2	p<0.1	0.829/p=0.0783	2.69
0.712±0.136	0.188/p>0.2	p>0.2	0.929/p=0.539	2.203
0.934±0.3	0.27/p>0.2	p<0.2	0.905/p=0.406	2.095
1.591±0.729	0.287/p>0.2	p<0.15	0.839/p=0.127	1.868

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

Table 8

Results of analyses of deviations between time series and 9-cycle

Estimations of coordinates of cycle	KS[1]	Lilliefors	SW[2]	DW[3]
0.756±0.218	0.193/p>0.2	p>0.2	0.912/p=0.4095	2.554
1.1±0.334	0.236/p>0.2	p>0.2	0.893/p=0.2928	1.33
1.115±0.591	0.33/p>0.2	p<0.05	0.712/p=0.005	1.987
0.694±0.412	0.368/p>0.2	p<0.01	0.658/p=0.0022	2.51
0.372±0.132	0.238/p>0.2	p>0.2	0.879/p=0.266	2.631
0.406±0.09	0.233/p>0.2	p>0.2	0.894/p=0.2956	1.45
0.47±0.239	0.402/p>0.2	p<0.01	0.658/p=0.0022	1.446
0.71±0.354	0.407/p>0.2	p<0.01	0.645/p=0.0015	1.409
0.515±0.101	0.169/p>0.2	p>0.2	0.954/p=0.771	1.311

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

For 4-cycle Shapiro – Wilk test allows rejecting Null hypothesis with 1% significance level (table 3) in three of four cases. In one of four cases Lilliefors test allows rejecting Null hypothesis with 1% significance level too (table 3). For 5-cycle Shapiro – Wilk test allows rejecting Null hypothesis with 1% significance level (table 4) in three of five cases, and Null hypothesis must be rejected in five cases with 5% significance level (table 3). In two of five cases Lilliefors test allows rejecting Null hypothesis with 1% significance level too (table 4).

For 6-cycle Shapiro – Wilk test allows rejecting Null hypothesis with 1% significance level (table 5) in three of six cases. In two of six cases Lilliefors test allows rejecting Null hypothesis with 1% significance level too (table 5). For 7-cycle Shapiro – Wilk test allows rejecting Null hypothesis with 1% significance level (table 6) in three of seven cases, and Null hypothesis must be rejected in five of seven cases with 5% significance level (table 6). In two of seven cases Lilliefors test allows rejecting Null hypothesis with 1% significance level, and four of seven cases Lilliefors test allows rejecting Null hypothesis with 5% significance level (table 6).

The best result was obtained for 8-cycle (table 7). In one of eight cases only Shapiro – Wilk test allows rejecting Null hypothesis with 1% significance level (and in two of eight cases with 5% significance level). Lilliefors test doesn't allow rejecting Null hypothesis even with 5% significance level (table 7). Additionally, minimum of squared deviations is also observed for 8-cycle (table 1). It gives us a background for the following conclusion (hypothesis): dynamics of pine looper corresponds to 8-cycle.

For 9-cycle Shapiro – Wilk test allows rejecting Null hypothesis with 1% significance level (table 8) in four of nine cases. In three of nine cases Lilliefors test allows rejecting Null hypothesis with 1% significance level (table 8).

On fig. 2 there are 8-cycle (red line) and respective empirical values. Positions of coordinates of 8-cycle allows us concluding that this cycle cannot be generated by models of Moran – Ricker type (3) which have one non-trivial stationary state: for one and the same interval of population density changing we have to have birth rate which is less than one (it describes population density decreasing) and bigger than one. Such behaviour can be generated by birth rates with several non-trivial stationary states in positive part of phase space, but it needs in further analysis.

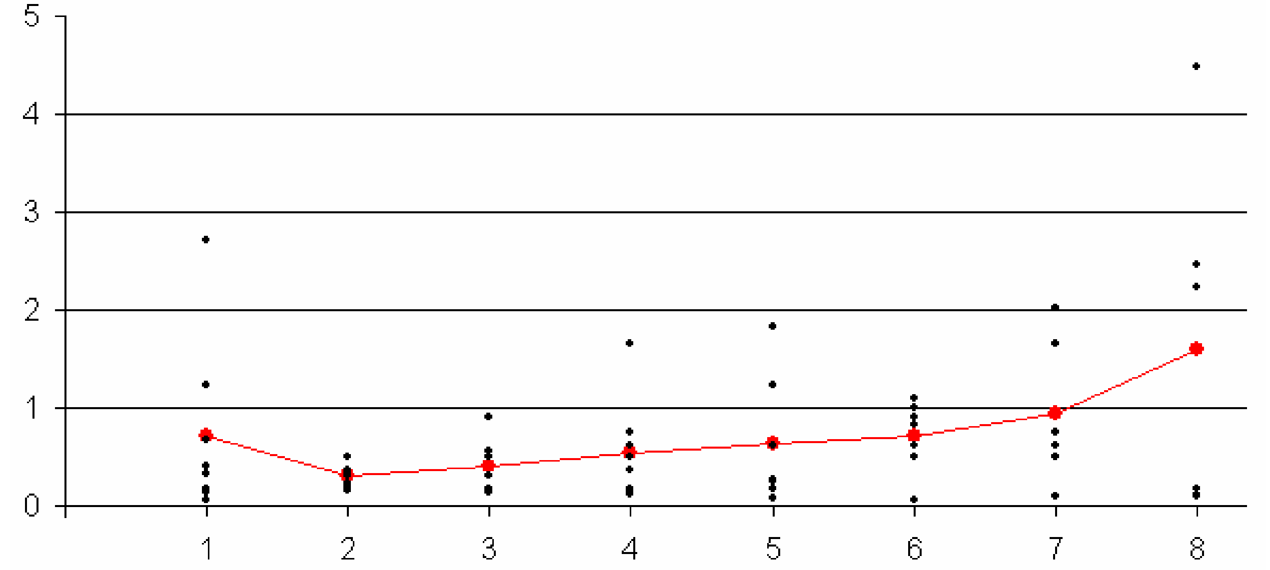

Fig. 2 8-cycle of pine looper dynamics (red line) and corresponding empirical points (black points).

Discussion

Provided analysis of dynamics of pine looper showed that best results are observed for 8-cycle. Results of analysis for this case are presented in table 7. In one of eight cases only Shapiro – Wilk test allows rejecting Null hypothesis with 1% significance level. Lilliefors test doesn't allow rejecting Null hypothesis even with 5% significance level for all estimated values of 8-cycle coordinates. Additionally, minimum of squared deviations between estimated coordinates of cycle and other empirical values is also observed for 8-cycle (results are presented in table 1). It gives us a background for the following conclusion (hypothesis): dynamics of pine looper corresponds to 8-cycle (fig. 2).

Preliminary analysis of 8-cycle shows that it cannot be generated by simplest discrete models (like Kostitzin model, Moran – Ricker model, discrete logistic model etc.). For finding of suitable approximation of empirical datasets we have to use more complicated mathematical models which have, for example, several stationary states in phase space.

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