

INVESTIGATION OF PREDATOR-PREY INTERACTIONS BETWEEN FISH POPULATIONS IN LAKE RAZNA (LATVIA) WITH GENERAL DISCRETE TIME-DEPENDENT LOTKA-VOLTERRA MODEL

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ABSTRACT

Investigation of predator-prey interaction between fish species within lakes represents difficulties not only in data collection (David et al., 2006; Jost & Arditi, 2000), but further also at the stage of computations as well as in interpretation of results. Through identification of non-stationary coefficients of the discrete Lotka-Volterra model the present paper puts forward an interpretation of modeling results based on the aggregate catch biomass of the considered predator-prey species in Lake Razna (Latvia). The respective data were collected over a period of time of several decades. Modeling of the observed predator-prey biomass involved a general discrete non-stationary Lotka-Volterra-type model, for which the population of predators was determined not only by the number of prey consumed but also by other factors, which were not directly measured in the data collected. The paper presents identification of non-stationary coefficients of the Lotka-Volterra simulation model which resulted in obtaining quantitative characteristics of species dynamics. Basing on the modeling results, the paper discusses the obtained dependencies for the two interacting predator and prey species in Lake Razna.

Key words: Lotka-Volterra, model, fish, lake, predator, prey, population, species, interaction, simulation

INTRODUCTION

The paper presents results of analysis of predator-prey interaction in Lake Razna, Latvia based on catch values of predators and prey biomass for the period of time 1950-1968. The analysis based on identification of non-stationary coefficients of the Lotka-Volterra simulation model allowed evaluating quantitative characteristics dynamics of the species.

The validation of the model used in the research and, consequently, proof of its adequacy was performed through numerous experiments. A further proof of models adequacy is the

consistency of its results with those obtained from independent research, whereas the higher the number of independent research available for the reference, the higher level of validation has the model. Since research of discrete non-stationary equations of Lotka-Volterra-type models is a relatively new research field (Vano et al., 2006; Liu & Xiao, 2007; Peitgen & Richter, 1986), at the present time other non-stationary models adequately describing predator-prey relationships in a lake environment with identified coefficients are unknown to the authors. Thus it is impossible to obtain comparative characteristics of the results vis-à-vis other models.

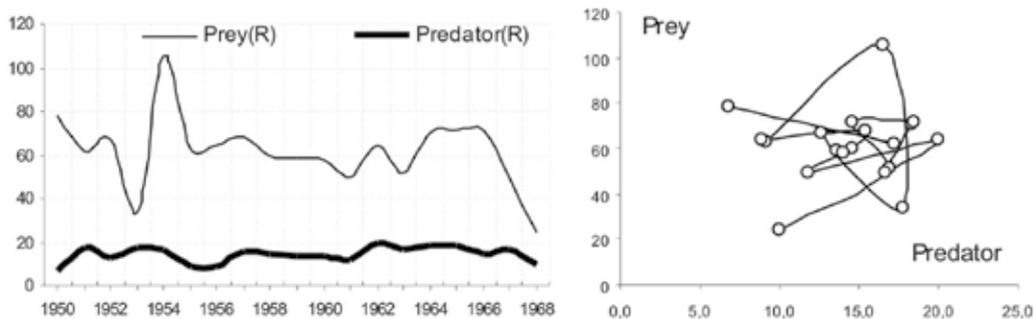


Figure 1. Left-hand side pane presents time series of observations of annual biomass catch values (in tons) of predator and prey species (predator time series depicted thick) in Lake Razna (Latvia). The right-hand-side pane features the same data as scatterplot in the predator/prey coordinates.

INPUT DATA

The analysis is based on the data collected over the period of time 1950-1968 concerning biomass in Lake Razna. The input data for the period of nineteen years represent two sets of data, namely Predator $H_{TS}(t_i)$ and biomass of prey $P_{TS}(t_i)$ at discrete points of time t_i :

$$\begin{aligned} P_{TS}(t) &= \{ \dots, P_{TS}(t_7), P_{TS}(t_6), \dots, P_{TS}(t_2), P_{TS}(t_1) \}, \\ H_{TS}(t) &= \{ \dots, H_{TS}(t_7), H_{TS}(t_6), \dots, H_{TS}(t_2), H_{TS}(t_1) \}. \end{aligned} \quad (1)$$

The respective time series of the predator and prey biomass catch observations (in tons) at discrete points of time t_i are depicted in Figure 1 left-hand-side pane, whereas the right-hand-side graph features the same data in scatter plot form in predator/prey axes.

In previous works it was attempted to fit the constant parameters of the stationary Lotka-Volterra equation for the input time series (David et al., 2006; Jost & Arditi, 2000; Gómez & Vélez, 2010; Cao, 2008). However, these parameters for fish populations in a lake environment may vary significantly over time, therefore the present work concentrates on evaluation of dynamically varying parameters and brings forward a discussion on the reasons of these variations.

APPLICATION OF LOTKA-VOLTERRA MODEL

A general discrete non-stationary Lotka-Volterra model (Liu & Xiao, 2007; Peitgen & Richter, 1986; Freedman, 1980; Brauer & Castillo-Chavez, 2012; Murray, 2003) with unknown stationary parameters $R_p(t_i)$, $R_h(t_i)$, $C_p(t_i)$, $C_h(t_i)$, $a(t_i)$, $b(t_i)$ is formalized as follows:

$$\begin{aligned} P(t_{i+1}) &= R_p(t_i) P(t_i) (1 - P(t_i)/C_p(t_i)) + a(t_i) P(t_i) H(t_i) \\ H(t_{i+1}) &= R_h(t_i) H(t_i) (1 - H(t_i)/C_h(t_i)) + b(t_i) a(t_i) P(t_i) H(t_i) \end{aligned} \quad (2)$$

The equations describe prey and predator species population growth under the conditions of usual interaction between the populations through biomass reproduction in the next period with coefficient $a(t_i)$. From the first equation it follows that at time t_{i+1} which is the next point of time following t_i biomass of the prey $P(t_{i+1})$ is determined by a logarithmic increase in population of prey species, less prey biomass consumed by the predators $a(t_i) P(t_i) H(t_i)$. The first term of the equation (2) defines the increase of the prey population with the parameters of growth rate $R_p(t_i)$ and carrying capacity $C_p(t_i)$.

An analogical equation defines the population of the predators $H(t_{i+1})$. Natural biological conditions limit the coefficients to the following ranges: $a(t_i) < 0$, $b(t_i) < 0$, $C_p(t_i) > 0$, $C_h(t_i) > 0$, $0 < b(t_i) < 1$.

In a general case, the population growth factors cannot be limited to the consumed prey only; therefore, logarithmic growth was also assumed for the population of predators.

The first step of the research is finding such parameters of the model $R_p(t_i)$, $R_h(t_i)$, $C_p(t_i)$, $C_h(t_i)$, $a(t_i)$, $b(t_i)$ that the error of the model E_{model} does not exceed the initially defined maximum error level E_{max} at each discrete point of time t_i ($i=1,2,\dots,19$):

$$E(i)_{model} = \max\{Abs[(P_{TS}(t_i) - P(t_i))] , Abs[(H_{TS}(t_i) - H(t_i))]\} < E_{max} \quad (3)$$

In case the inequality (3) holds at all points of discrete time t_i ($i=1,2,\dots,19$), the error of the model will not exceed the value of the absolute deviation $Abs[(P_{TS}(t_i)-P(t_i))]$ for the prey or the value of the absolute deviation $Abs[(H_{TS}(t_i)-H(t_i))]$ for the predators. The value of E_{max} is initially set and this value depends on the chosen level of model fitting to the observations. Thus, for identification of the parameters of the model the criterion $E(i)_{model}$ should be minimized using not less than four observations $P_{TS}(t_{i-1})$, $H_{TS}(t_{i-1})$, $P_{TS}(t_i)$, $H_{TS}(t_i)$ for each pair of times $[t_{i-1}, t_i]$.

ANALYSIS AND INTERPRETATION OF RESULTS

There have been calculated coefficients of

equations (2) which were later used for calculation of biomasses of prey and predators, which are $P_m(R)$ and $H_m(R)$ respectively. Figure 2a presents a comparison of the modeled and observed data. It can be seen that the modeled data using equation (2) with coefficients obtained earlier show a high degree of modeling precision.

Let us consider peculiarities in the dynamics of the identified coefficients of the equations (2). Figure 3 presents the graphs of carrying capacity and growth rate of the prey population. Since equations (2) belong to the so-called determined chaos type of equations (Vano et al., 2006), sensitivity of the solutions to minor variations of the initial data can be very high. Both high precision level of the observations of the biomass catch records as well as the transfer of its values on the value of the whole respective population cannot be assumed, so this causes a certain level of error. Since the time frame of the observations is rather short and there can be observed significant deviations from the average, application of ‘moving average’ type of statistical methods to the problem in focus proved to be inefficient. Therefore, there was applied a non-linear filter 4253H implemented in the Statsoft Statistica software (Hill & Lewicki, 2007).

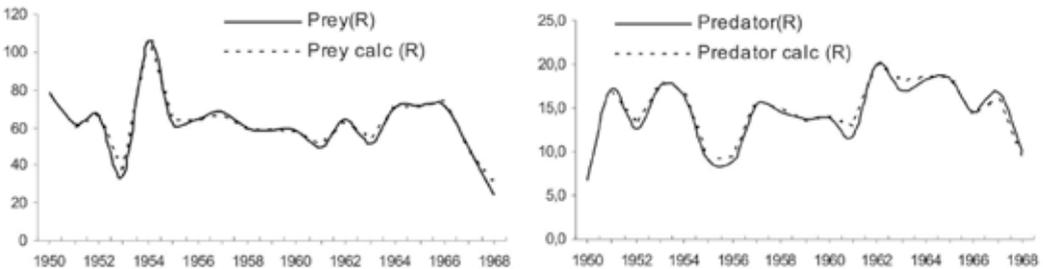


Figure 2. Observations (solid line) and Lotka-Volterra modeled data (dotted line) of the annual biomass catch in Lake Razna. X-axis represents time in years, Y-axis represents biomass in tons. Left-hand side pane presents predator data, whereas in the right-hand side pane prey data are presented.

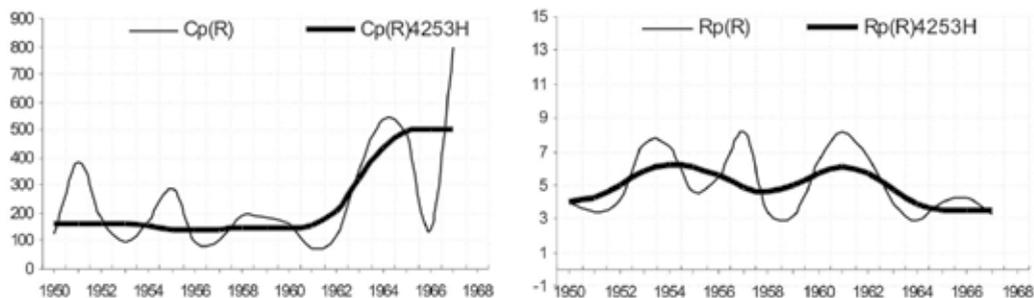


Figure 3. Dynamics of variations in coefficient values of carrying capacity $C_p(t_i)$ and growth rate $R_p(t_i)$ of prey of the general Lotka-Volterra discrete time equation. The thin line represents identifying parameters, whereas the thick line represents the filter-processed values (4253H filter).

Interpretation of carrying capacity values $C_p(t_i)$ and $C_h(t_i)$ may represent certain interest for the research. Variations in values of carrying capacity $C_p(t_i)$ over time may be caused among other factors by the nutrients level of the prey species. Unfortunately, such related observations cannot be obtained, thus leaving possible only estimation of $C_p(t_i)$ values.

Analyzing presented carrying capacity of the prey presented in Figure 3 (left-hand side pane), there can be assumed a 5-year cyclical pattern of lake capacity. Observing the filter-processed graph, it can be noted that the capacity of the lake increased more than thrice over the last years of the period considered. The same should also be observed in other related indirect measurements, which, however, currently lies outside the scope of the

present research. Should it be possible to find indirect proof of such variations, this would be a solid contribution to the verification of the model presented in the research. The 4253H filter-processed graph of the prey population growth rate (Figure 3, right-hand side) reveals presence of two peaks of prey growth rate which do not coincide with the maxima of the carrying capacity.

The carrying capacity graph for the predators (Figure 4, left-hand side pane) shows that the capacity of the lake with regard to the predator species is virtually constant for the whole period in focus. The smoothed graph of the dynamics of the predator population (Figure 4, right-hand side pane) does not feature any notable deviations, although it fluctuates around its average with the magnitude of

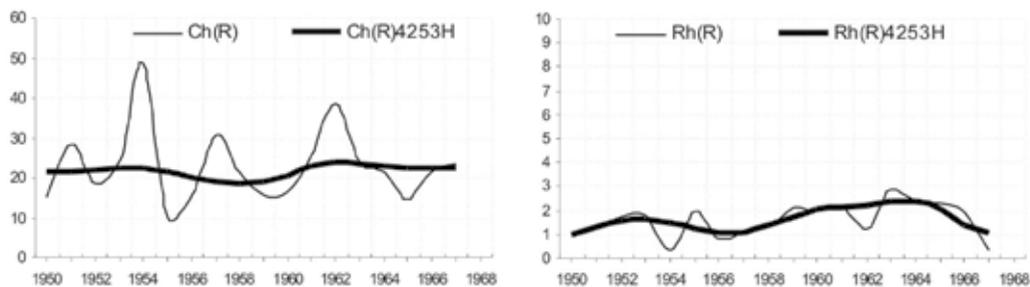


Figure 4. Dynamics of the coefficients of $Ch(t)$ and $Rh(t)$ for predators and the 4253H filter-processed values (thick line).

1.5-2 times but not exceeding the value of 3. However, it should be noted that the equation (2) for the predator population differs from the traditional Lotka-Volterra formulation when it is assumed that in the trophic chain predators are only prey-dependent.

The term $P(t_i)/C_p(t_i)=ER_p(t)$ in the equation (2) represents environmental resistance presented by the environmental conditions to limit a species from growing out of control or to stop them from reproducing at maximum rate. Environmental resistance includes a mixture of abiotic factors such as temperature to limit the organism for expressing its full capacity to reproduce.

Figure 5 illustrates environmental resistance graphs for the prey and the predators. At $ER_p(t)=1$ annual biomass increase equals zero. From Figure 5 it follows that apparently, for a long period of time the lake provided a relatively stable level of environmental resistance for the prey biomass at an average level of $ER_p=0.4$, however, by the end of the period in focus the value dropped drastically to the value of $ER_p=0.1$. This drop occurs simultaneously with the carrying capacity $C_p(t_i)$ increase observed in Figure 3.

The environmental resistance of the predators illustrates a stable pattern, as it follows from

Figure 5 (right-hand side graph). The average value of the environmental resistance of the predators lies around the value of 0.7 which indicates a weak dependency of the predator biomass on other sources of food, therefore it might be concluded that the main source of predators' biomass increase is attributable to the prey species considered in the research.

Figure 6 features graphs of the identified coefficients $a(t_i)$ and $b(t_i)$ from the equation (2). The value of the filter-processed coefficient $b(R)_{4253H}$ varies insignificantly within the range of values of 0.10-0.13, whereas its sharp peak in the earlier observations is to be explained by the edge effect in the calculations. The coefficient $b(R)_{4253H}$ represents efficiency of prey-predator biomass transformation. The most constant values of the coefficient indirectly assumes a constant predator diet, which is in turn attributable to the large area of Lake Razna. This possibility is also underpinned by the stable values of prey biomass consumed by the predators, as it follows from the biomass dynamics graph $H_p(t)$ featured in Figure 8.

In order to analyze interaction of the populations let the equation (2) to be interpreted as a sum of the two biomasses. In each of the equations the first term depicts annual growth of the prey or predator biomass,

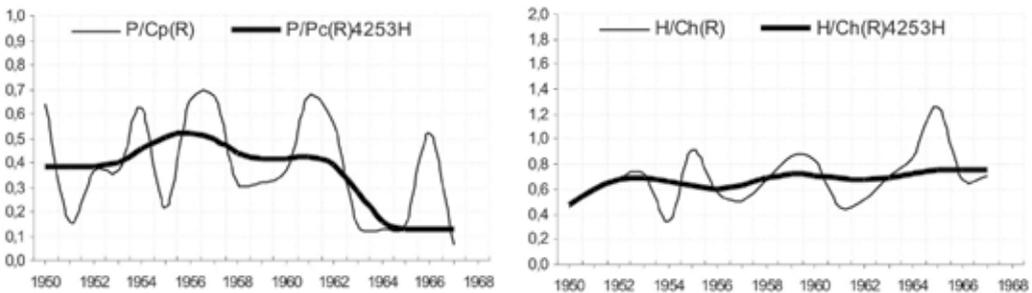


Figure 5. Left-hand side graph portrays the environmental resistance of the prey, whereas the right-hand side pane features the same of the predators. The thick line represents 4253H filter-processed values.

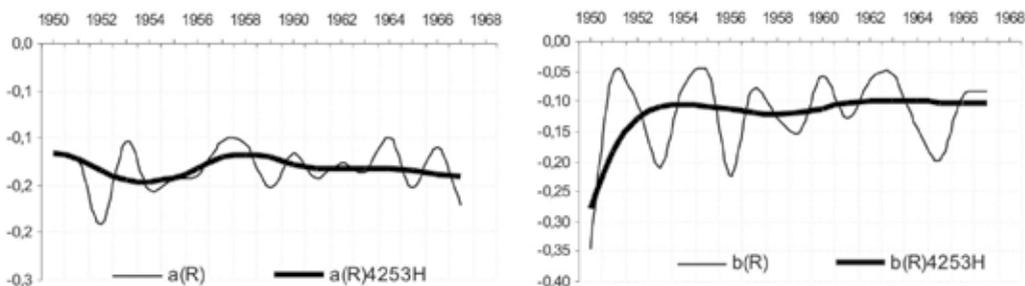


Figure 6. Coefficient $a(t)$ of prey biomass consumption by the predator (left-hand side graph) and coefficient $b(t)$ of food transformation (right-hand side pane). The thick line represents 4253H filter-processed values.

whereas the second term describes the effect of annual cross-population interaction. This is formalized in the following way:

$$\begin{aligned} P(t_{i+1}) &= P_c(t_i) + P_h(t_i), \\ H(t_{i+1}) &= H_c(t_i) + H_p(t_i), \end{aligned} \quad (4)$$

where:

$$\begin{aligned} P_c(t_i) &= R_p(t_i) \cdot P(t_i) \cdot (1 - P(t_i) / C_p(t_i)); \\ P_h(t_i) &= a(t_i) \cdot P(t_i) \cdot H(t_i); \\ H_c(t_i) &= R_h(t_i) \cdot H(t_i) \cdot (1 - H(t_i) / C_h(t_i)); \\ H_p(t_i) &= b(t_i) \cdot a(t_i) \cdot P(t_i) \cdot H(t_i). \end{aligned} \quad (5)$$

In the equation (4) above $P_c(t_i)$ stands for prey biomass which could have appeared over the period of time of $[t_i, t_{i+1}]$ in the absence of the predator species. The term $H_p(t_i)$ defines predator biomass attributable to the consumed prey $P_h(t_i)$ over the period of time

$[t_i, t_{i+1}]$. Thus, $H_p(t_i)$ stands for predator biomass which linearly depends on the consumed prey $P_h(t_i)$ with the varying over time coefficient $b(t_i)$ of predator-prey biomass transformation.

The following paragraphs present the graphs of the respective biomasses as well as brought forward a discussion on interpretation of the results. As in previous cases, for the ease of the analysis the graphs contain the filter-processed values.

The left-hand side graph in Figure 7 may be interpreted as the dynamics of the prey population biomass $P_c(R)$ in the absence of predators. The filter-smoothed line presents wave-like dynamics of prey biomass over time. The right-hand side graph in Figure 7 presents prey biomass $Ph(R)4253H$ taking

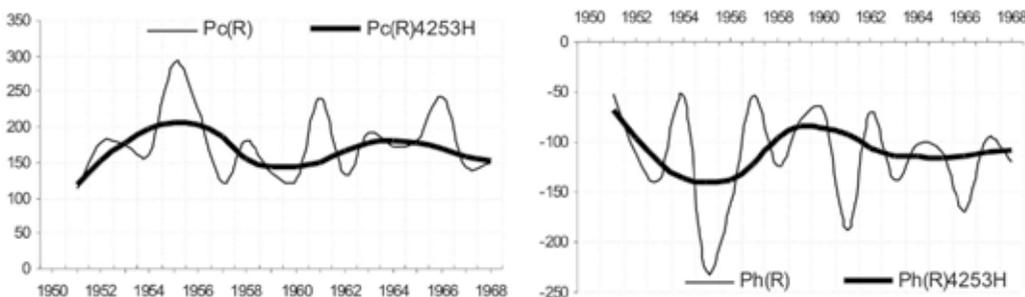


Figure 7. Left-hand side pane portrays increase in prey biomass in absence of the predator species. The right-hand side pane presents annual losses attributable to predators. Thick line represents the same data processed with 4253H filter.

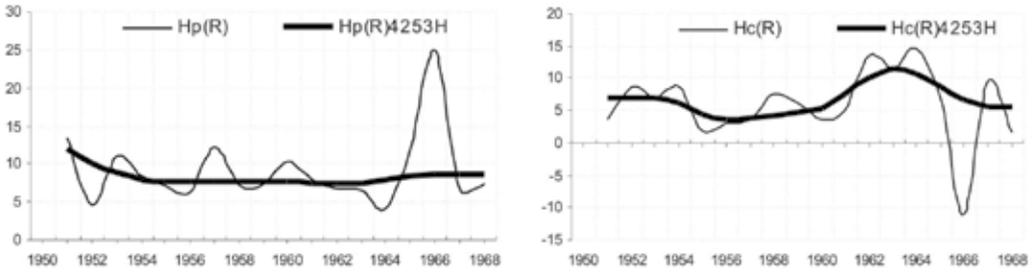


Figure 8. Left-hand side graph presents predator biomass gained for the account of the consumed prey with coefficient of biomass transformation $b(t)$. The right-hand side pane represents the predator biomass gained from other unidentified sources. Thick line represents the same data processed with 4253H filter.

into consideration biomass losses due to predators. The latter mirrors the dynamics of biomass $P_c(R)_{4253H}$.

Figure 8 illustrates the predator biomass increase obtained through sources of nutrition other than the prey. These unidentified sources account for a substantial part of total gained biomass by the predators, as it follows from the $H_c(R)_{4253H}$ plotted on the right-hand side graph in Figure 8.

In conclusion, Figure 9 presents a flowchart wrapping up the non-stationary discrete Lotka-Volterra LV33 equations (2) employed in modeling and identification of coefficients. The flowchart concisely illustrates the dynamics of predator-prey interaction in Lake Razna as modeled in the present paper.

CONCLUSIONS

The given paper presents an attempt to interpret numerical estimations of the coefficients of the general discrete Lotka-Volterra model for observation of prey and predator population catch in the lake of Razna (Latvia). Unfortunately, the scarcity of the observations does not allow performing an acceptable statistical assessment of the results. Certain difficulties represent procedures of identification of non-stationary coefficients of the general discrete Lotka-Volterra model

(Liu & Xiao, 2007; Jost & Arditi, 2000; Jost & Arditi, 2001). The principal confirmation of the adequacy of the model is compliance of its results with the historically observed data. Besides that, the features of the modeled object comply with independent research.

Since research of Lotka-Volterra model is a relatively new field of academic research (Vano et al., 2006; Liu & Xiao, 2007; Peitgen & Richter, 1986), other non-stationary models with identified coefficients of predator-prey interactions within lake habitats are unknown to the authors. Thus, it is not possible to obtain a comparative evaluation of the obtained result with alternative models. However, the results contain implications for future research as well as for indirect verification of the model. For instance, the coefficient of biomass transformation between the species $b(t)$ having the value of -0.12 may represent academic value for future experimental research.

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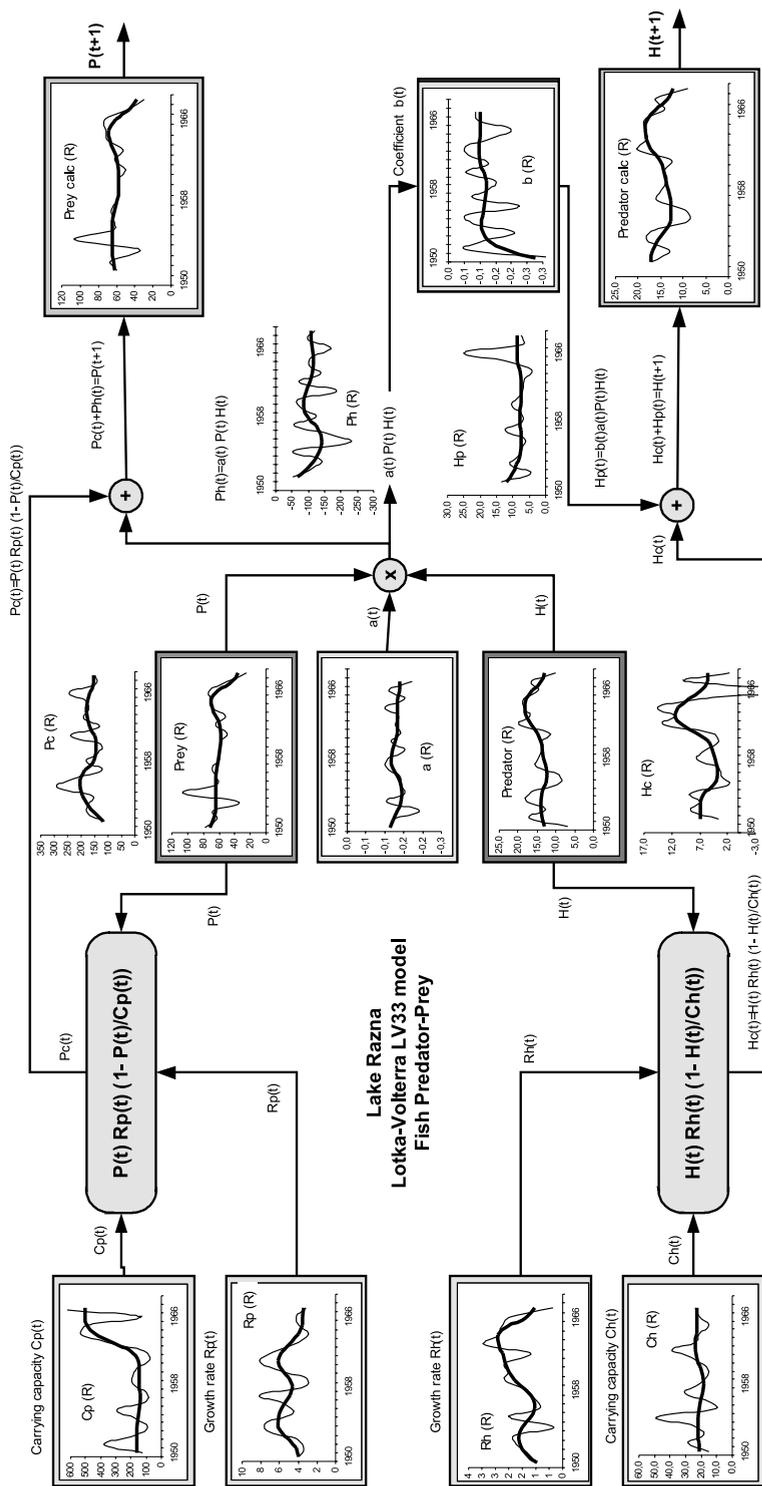


Figure 9. Visualisation of the Lotka-Volterra model of Lake Razna (Latvia).

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