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POPULATION CONSEQUENCES OF THE COMPETITION OF VARIABLE INDIVIDUALS UNDER VARIOUS REGIMES OF RESOURCE DYNAMICS

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Abstract.

Individual-based model of the dynamics of population with non-overlapping generation and explicitly introduced resources which are unequal partitioned between competing individuals is analysed. It is investigated how individual variability in assimilation of different kinds of resources influences population dynamics. Following kinds of resources are considered: unlimited resources with linear or exponential growth and limited resources growing logistically or with seasonal dynamics. When resources are unlimited population dynamics exhibits oscillations of number of individuals and resources which sooner or later end in extinction of the population. An increase of individual variability increases extinction time. Population dynamics is different when resources growth is limited. Number of individuals in the population initially increases until a certain level is reached, then fluctuates around that level. However, still greater individual variability guarantees greater persistence of the population, especially in rich environments.

Key words*: individual-based model, individual variability, population dynamics, unlimited resource growth, limited resource growth*

1. Introduction

In the single population dynamics models considered in classical theoretical ecology, the resources used by individuals do not explicitly exist in the equations (Maynard Smith 1974, May 1976, Pielou 1977, Wissel 1989, Murray 1990). Explicitly, resources do exist in the Tilman's model (Tilman 1977, 1982), which is a system of differential equations describing changes in species density and amount of resources constructed according to the principles of classical theoretical ecology. This is essentially a model of the laboratory culture of plankton organisms. Most often, however, the effect of resources on population dynamics is implicit in the density dependence of reproduction and mortality (Bazykin 1985, Begon & Mortimer 1996). Classical models have shaped ecologists' ideas about the patterns of dynamics of ecological systems. In the case of a single population, this is the type of population regulation that is represented by solutions of the logistic equation (Nicholson 1933, 1958, Petrusewicz 1978).

These types of models are called black-box models by Kalmykov & Kalmykov (2015, 2024) and distinguished from white-box models. Black-box models are those whose mathematical structure and properties of the solutions of the model equations are completely understood, while the biological interpretation is not clear. There can be a great deal of doubt as to what biological situation these models describe. In contrast, white-box models - most often individual-based models - are distinguished by the fact that they address a specific biological situation in addition to the understandable mathematical structure of the algorithm.

Including resources explicitly in a single population dynamics model involves resolving two issues. First, the nature of the resource dynamics has to be decided. Secondly, how these resources are shared between competitors. Few, but very relevant from this point of view, studies indicate that resources are partitioned between competing individuals unequally (Yamagishi 1969, Łomnicki 1988, Weiner 1990, Jobling 1993, Nakano 1995, Wyszomirski & Weiner 2009,Wyszomirski et al. 1999)). The aim of this work is to show how the number dynamics of a single population depends on the nature of resource dynamics and on the degree of individual variability in resource partitioning. The author also hopes to find in this way stronger and more biological justifications for classical patterns of single population dynamics.

To meet the requirements for white-box models, an individual-based model of a single population will be analyzed. The individuals represent a parthenogenetic species. The life cycle of individuals in this population begins with the larval stage. The larvae grow using the resources available in the environment. There is global and scramble competition for these resources between larvae (Nicholson 1954): each individual competes with all other individuals in the population by using the common resources. As stated earlier, this leads to uneven resource partitioning among competitors. The larvae complete their growth period at the same time, develop into adults and lay eggs from which the next generation starts. The adults do not consume the resources and die after laying eggs.

Among other, resources with discontinuous dynamics will be considered. At the beginning of each generation of larvae, a portion of the resource is available and later eaten by individuals. At the end of a generation, the resources that have not been used do not pass to the next generation, but there is a new portion, the same as before, exploited by the next generation. This could be a model of the dynamics of annual, herbivorous insects using plant resources with seasonal dynamics (for example, a temperate deciduous forest). If the resources have continuous dynamics, i.e. the amount that remains after the death of adults is the initial resource for the next generation of larvae, and the unexploited resources are logistically increasing, this will be a model of the dynamics of annual, herbivorous insects in an environment without seasonal dynamics (e.g. temperate zone coniferous forest or tropical forest). In both of these interpretations, we assume that there is no migration of insects between neighboring trees. A version of the model with migration would allow simulations of outbreaks of forest insects (Uchmański 2019, 2024). And finally, a version of the model with continuous resources that, unexploited, grow linearly or exponentially will be analyzed. This could be models of the dynamics of herbivorous plankton in a non-seasonal aquatic environment or in a seasonal environment, but then where the life cycle of animals is short enough that several generations can occur during a single summer season.

This work will use, in a modified form, the same model that has previously been used to analyze the effect of individual variability in the amount of resources obtained by competing individuals on the dynamics and persistence of a single population (Uchmański 1999, 2000a, 2000b, Grimm & Uchmański 2002). The modification will address resource dynamics, which in earlier versions of the model describes only continuous resources renewed linearly.

2. The Model

The model describes the population dynamics of animals with non-overlapping generations and the dynamics of resources available to them. The lifecycle of individuals starts at the beginning of the season. They grow over the season and reproduce at the end of the season, then they die. Juveniles overwinter and start growing at the beginning of the next season.

The growth rate of an individual is assessed as the difference between the rate of resource assimilation and the rate with which these assimilated resources are used for living costs. The rate of resource assimilation A and living costs as measured by the rate of respiration R are power functions of body weight w (Duncan & Klekowski 1975):

$$A = a_1 w^{b_1}, \tag{2.1}$$

$$R = a_2 w^{b_2}, \tag{2.2}$$

where a_1, a_2, b_1 and b_2 are parameters. This gives the following equation of individual growth (Majkowski & Uchmański 1980):

$$\frac{dw}{dt} = a_1 w^{b_1} - a_2 w^{b_2}. \tag{2.3}$$

The rate of resource assimilation depends on the amount of resources available. The rate of assimilation A of a single individual isolated from interactions with other individuals of the same species, as a function of the amount of resources V can be described by the equation proposed by Ivlev (1961):

$$A = a_{1,max}(1 - e^{-sV})w^{b_1}, \tag{2.4}$$

where $a_{1,max,}$ is the maximal value of parameter a_1 reached when $V = \infty$ and s is constant parameters describing the rate of reaching this maximal value.

However, if individuals live together, they may compete for resources. The resources are shared unequally between competitors. If individuals often compete, then the individual who acquired more resources in the past, will acquire more of them also in the future. A good measure of the cumulative amount of resources acquired by an individual in the past, accounting also for the energy costs of resource acquirement, is its actual weight. For this reason, the rate of assimilation of an individual in the case of a group of competing individuals is described by Eq. (2.1) with additionally added dependence on the actual body weight of the individual according to the scheme below.

The passage of time was simulated on two time scales. Large time steps described the number of individuals in the population in successive generations, and small time steps contained within each large time step were used to simulate the growth of individuals during each generation and the dynamics of resources. It was assumed that processes such as assimilation, respiration and growth of each individual within a large time step are continuous processes. For this reason, the dynamics of resources within a large time step and growth of each individual within this time step were described by an appropriate differential equations.

At each small simulation step, individuals with the lowest weight w_{min} and the highest weight w_{max} are identified. The value of the parameter a_1 for the lightest individual is described as

$$a_{min} = a_{1,max}(1 - e^{-s_{min}V}) \tag{2.5}$$

and that of the heaviest individual as

$$a_{max} = a_{1,max}(1 - e^{-s_{max}V}). \tag{2.6}$$

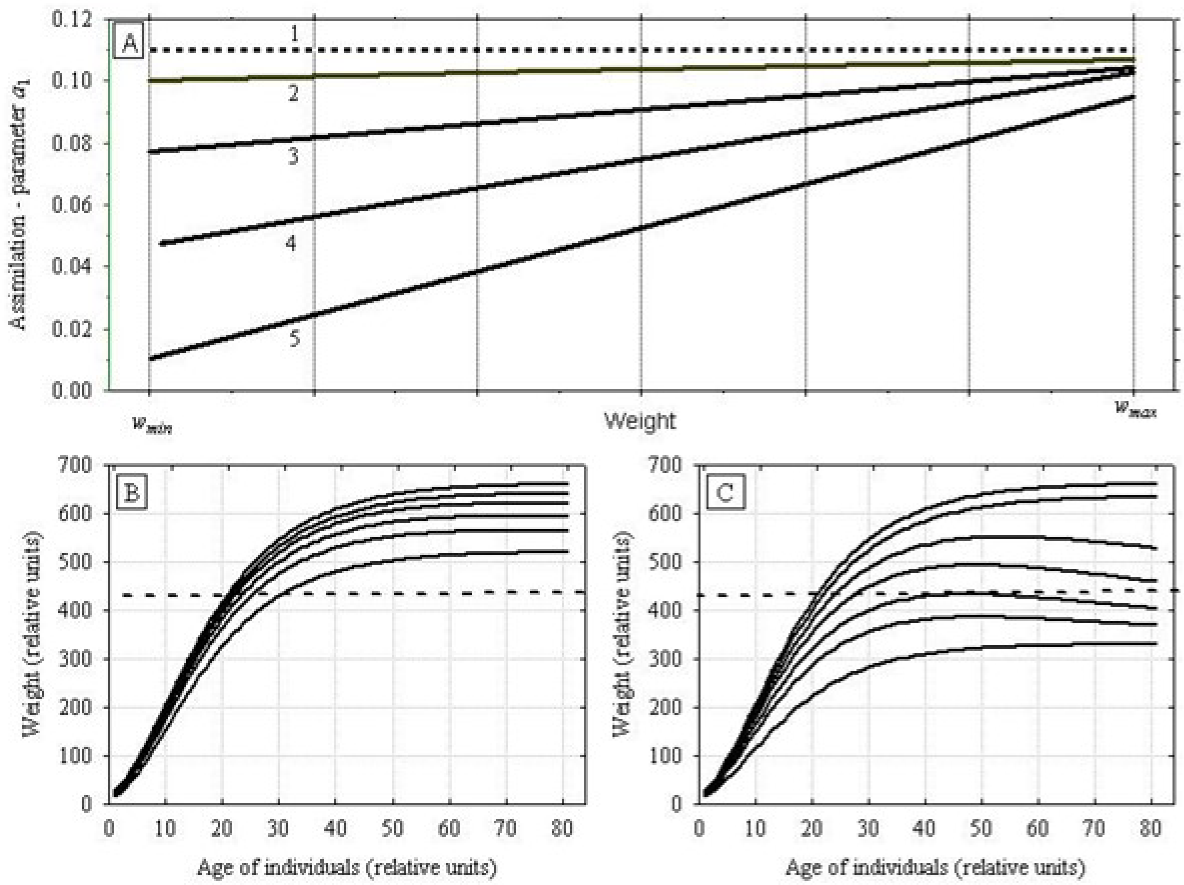

Fig 1. Resource partitioning among competing individuals and their growth in relation to the available amount of resources (Uchmański 2019). A - Shows how the values of parameter a_1 were calculated for individuals that differ in actual body weight. The w_{min} and w_{max} represent the lowest and the highest body weights in the current population. Sections of straight lines represent linear approximations to calculate the value of parameter a_1 for individuals with body weights $w_{min} < w < w_{max}$ at various amounts of resources V. (1) - amount of resources $V = \infty$. The values of parameters a_1 are the same for all individuals in the population, and equal to the maximum value a_{max}. Successive lines (2, 3, 4 and 5) show the values of a_1 for decreasing amounts of resources V. It can be seen that when V is decreasing, differences between individuals in the amount of assimilated resources are increasing. But the decrease in the amount of resources V accounts for a greater decline in assimilation for individuals with low body weights than for individuals with large weights. B and C - Growth curves of individuals obtained by the above presented method of the calculation of assimilation rate. The results of the simulation of growth are shown for several chosen individuals at a constant resource level V (B - $V = 6 \times 10^6$, C - V = 4×10^6). It can be seen that the differentiation of body weights increased with age of individuals, and a greater differentiation occurred at a lower resource level. The horizontal dashed line represents the threshold value of body weight $w_{fak}\, w_{max}^{end}$. Individuals with the final body weight greater than the threshold value can reproduce.

The parameter a_1 of individuals with intermediate weights are calculated by using interpolation between the values a_{min} for w_{min} and a_{max} for w_{max}. The analysis of the weight distributions of growing and at the same time competing individuals shows that these distributions are positively skewed (Uchmański 1985, Dgebuadze 2001). To obtain positively skewed weight distributions, a linear or convex function should be used for the above interpolation (Uchmański 1985, 1987, Uchmański & Dgebuadze 1990). The linear case has been chosen in the present model (Fig.1A).

Between the values of parameters s_{min} and s_{max} of Eqs (2.5) and (2.6), there is an inequality

$$s_{min} \leq s_{max}. \tag{2.7}$$

When $s_{min} = s_{max}$, individuals in even-aged population are equal. Assimilation of each individual depends in the same way on V. When $s_{min} < s_{max}$, individuals differ in the rate of assimilation. The degree of these differences increases with the increasing difference between s_{min} and s_{max} or decreasing V. However, the differences disappear for $V \to \infty$ (Fig. 1A).

The greatest weight w_∞ at successive small time steps of the simulation has a hypothetical individual which is growing under conditions $V = \infty$:

$$\frac{dw_\infty}{dt} = a_{1,max} w_\infty^{b_1} - a_2 w_\infty^{b_2}. \tag{2.8}$$

The maximum final weight w_∞^{end} of an individual, asymptotically reached when assimilation is equal to respiration, for the growth described by equation (2.8) is

$$w_\infty^{end} = \left(\frac{a_{1,max}}{a_2}\right)^{\frac{1}{b_2-b_1}}. \tag{2.9}$$

An individual growing under condition when $V < \infty$, after the end of growth will reach the weight $w_{end} < w_\infty^{end}$. The number of juveniles produced by an individual after the end of growth is proportional to the difference between its final weight and some threshold weight:

$$z = \begin{cases} round\left(c\left(w_{end} - w_{fak}w_\infty^{end}\right)\right) & for \quad w_{end} > w_{fak}w_\infty^{end} \\ 0 & for \quad w_{end} \le w_{fak}w_\infty^{end} \end{cases}, \tag{2.10}$$

where c is the parameter describing the intensity of progeny production, and w_{fak} ($0 < w_{fak} < 1$) says what part of the maximum end weight w_∞^{end} given by Eq. (2.9) is the threshold weight for calculation of progeny production by an individual. Individuals with body weights lower than or equal to the threshold weight die without producing progeny. The function *round* rounds a real number to the nearest integer, as the number of juveniles can be only a natural number. The initial weights of juveniles of each individual are drawn from the normal distribution with a mean value $w_{0,\,mean}$ and variance $w_{0,\mathrm{variance}}$, but only from the interval [$w_{0,min}$, $w_{0,max}$].

The number of individuals in the population N_{t+1} at large time step $t+1$ conforms to the following equation

$$N_{t+1} = \sum_{i=1}^{N_t} z_i, \tag{2.11}$$

where the summation is done over all N_t individuals present in the population at large time step t.

At the beginning of the initial large time step, the population consisted of N_0 individuals. Their initial body weights are derived from a normal distribution with a mean value $w_{0,mean}$ and variance $w_{0,\mathrm{variance}}$ and are in the range [$w_{0,min}$, $w_{0,max}$]. The initial amount of resources was V_0. Within each generation, the equations describing the growth of individuals and the resource equation were solved by using the Euler method in 80 smaller time steps. This number of smaller steps allowed a good enough fitting of the numerical solutions to the analytical solutions of the Eq. (2.8) for an individual with the maximum weight. During each small time step, resources were used by growing individuals and renewed in different ways depending on the version of the model. Weight increases at each smaller time step were calculated in the model with reference to the actual amount of resources available to individuals.

At each smaller time step, the highest and the lowest body weights were found, so that it was possible to calculate assimilation by each individual with respect to their weight differentiation in the population, corresponding to the actual resource level available. For each individual, a growth curve was assigned. When combined for all competing individuals in the population, they form a characteristic "fan" (Fig.1 B and C): differences in weights among individuals increase with growth, and their magnitude depends on growth conditions. This has been supported in many experiments and observations of the growth of competing individuals in even-aged populations (Uchmański 1985).

After the end of growth, at the end of large time step, the number of juveniles for each individual was calculated, their initial weights were assessed, and the amount of resources available for the next generation was calculated according to the assumptions regarding resource dynamics adopted for a given version of the model. This allowed for the same calculations at successive generation. The simulation was stopped when $N_{t+1} = 0$ or $V_{t+1} < 0$. Standard values of the parameters used in simulations are shown in Table 1.

3. Continuous Resources: Linear Case

The first considered version of the model was one in which resources were continuous and renewed linearly by a constant amount. Resource continuity means that the amount of resources that was available at the end of the previous generation was later the initial amount of resources in the next generation. These assumptions gives the following equation describing the resource dynamics during one generation:

$$\frac{dV}{dt} = -\sum_{i=1}^{N_t} A_i + g, \tag{3.1}$$

where V is the amount of resources, A_i is the resource assimilation by the *i-th* individual and g is the constant amount of resources added at each smaller time step. The summation is over all individuals present in the population. The initial (at the beginning of the first large generation) amount of resource V_0 was equal to 6.0×10^6 and the total amount of resource g with which the environment was renewed during the generation was equal to 2×10^6. The other parameters had standard values (Table 1).

The population dynamics produced by the model with continuous and linearly renewed resources were characterized by fairly regular oscillations in number and accompanying oscillations in the amount of resources. The population repeatedly went through phases of rapid increases in number and then rapid declines. Sooner or later, at minimum abundance, the population goes extinct. The population extinction time depends on the degree of individual variability. In all versions of the model discussed in this paper, the degree of individual variability is determined by the magnitude of the difference in the values of the parameters s_{max} and s_{min}: the larger it is, the greater the individual variability in the amount of assimilated resources and the weights of individuals. Fig. 2 shows the average

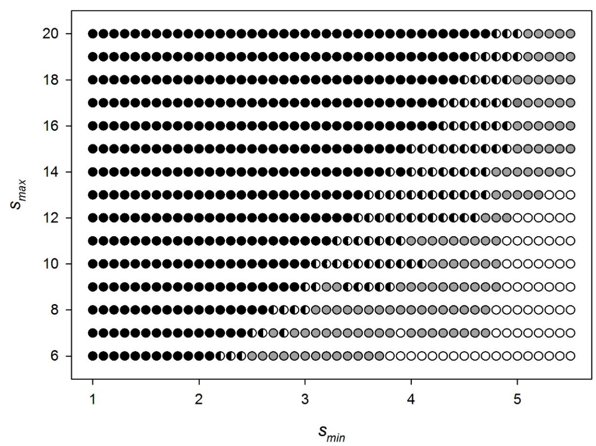

Fig. 2. Continuous resources linearly renewed. Parameter space s_{min} and s_{max}. Average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max} (the values on the axes should be multiplied by 10^{-7}). Simulations were run for a maximum of 1000 generations. Empty circles - average extinction time less than 10 generations. Grey circles - average extinction time greater than or equal to 10 generations and less than 100 generations. Half-filled circles - average extinction time greater than or equal to 100 generations and less than 1000 generations. Fully filled circles - extinction time greater than or equal to 1000 generations. The remaining parameters had standard values (Table 1).

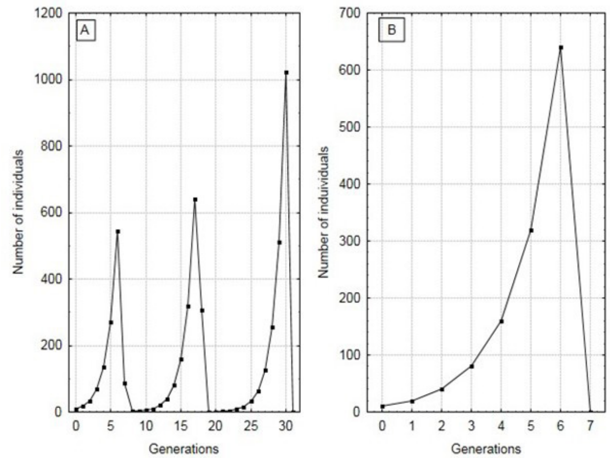

Fig. 3. Continuous resources linearly renewed. Types of population dynamics corresponding to those areas of the parameter space s_{min} and s_{max} from Fig. 3, which are characterized by short population extinction times. A - average extinction time greater than or equal to 10 generations and less than 100 generations, $s_{min} = 0.45\text{x}10^{-6}$ and $s_{max} = 1.0\text{x}10^{-6}$ (grey circles in Fig. 2). B - average extinction time less than 10 generations, $s_{min} = 0.55\text{x}10^{-6}$ and $s_{max} = 1.0\text{x}10^{-6}$ (empty circles in Fig. 2).

from 100 simulations extinction times of a population for different values of the parameters s_{min} and $s_{max.}$ Figs. 3 and 4 illustrate the dynamics of the population in more detail. The highest individual variability takes place in the upper left corner of the parameter space s_{min} and s_{max}. Here, the population size repeatedly goes through phases of growth and decline without extinction on the time scale adopted in the simulations (1000 generations). The smallest individual variability corresponds to the parameter values in the lower right corner of the parameter space s_{min} and s_{max}. Here the population goes extinct most often after the first maximum and this happens after only a few generations. Between these two areas with extreme population extinction times we have dynamics with intermediate extinction times.

4. Continuous Resources: Exponential Case

In this version of the model, the equation that describes resource dynamics has the form:

$$\frac{dV}{dt} = -\sum_{i=1}^{N_t} A_i + rV, \tag{4.1}$$

where r is a parameter characterizing the rate of resource renewal. The initial amount of resources was equal to V_0 (Tab. 1).

The types of population dynamics in the case of continuous and exponentially renewed resources are shown in the parameter space s_{min} and s_{max} for $r = 0.001$ in Fig. 5. For a larger value of $r = 0.002$, the parameter space s_{min} and s_{max} is illustrated in Fig. 6. In all areas of the parameter space in Figs. 5 and 6, the dynamics of population looks as in the earlier case of continuous and linearly renewed resources: population number and amount of resources are characterized by periods of increase and decrease until, at some generation, the population at minimum number goes extinct (see Figs 3 and 4). However, in the case of faster renewing resources (r = 0.002, Fig 6), the range of parameters for which the population persists longer than 1000 generations disappears.

5. Continuous Resources: The Logistic Case

In this version of the model with continuous resources, these were consumed during the season by growing individuals and renewed according to the logistic equation. The equation describing the resource dynamics was of the following form:

$$\frac{dV}{dt} = -\sum_{i=1}^{N_t} A_i + r\left(1 - \frac{V}{V_k}\right)V, \tag{5.1}$$

where r and V_k are constant parameters describing the logistic regeneration of resources. The initial amount of resources was equal to V_0 .

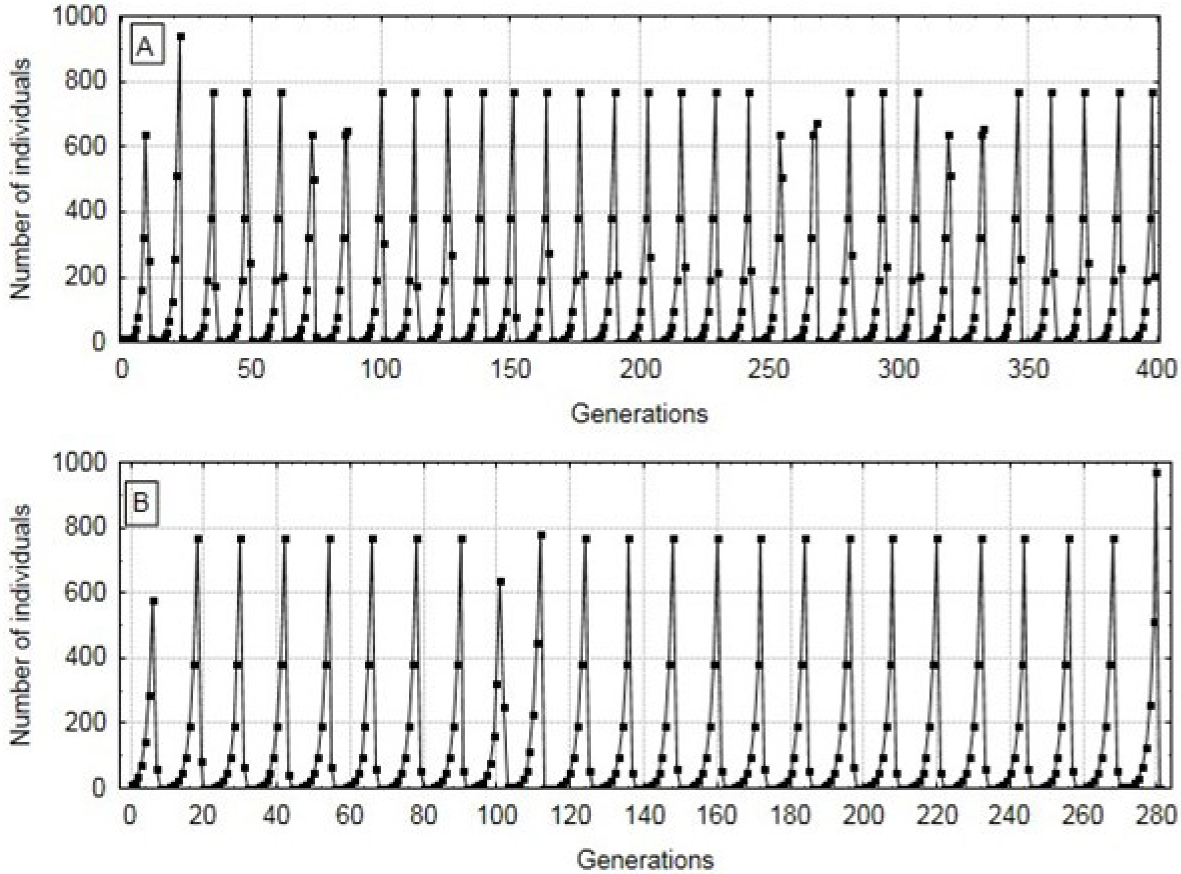

Fig. 4. Continuous resources linearly renewed. Types of population dynamics corresponding to those areas of the parameter space s_{min} and s_{max} from Fig. 2, which are characterized by large population extinction times. A - extinction times greater than or equal to 1000 generations, s_{min} = 0.30x10^{-6} and s_{max} = 1.5x10^{-6}, only 400 first generations are shown (fully filled circles in Fig. 2). B - average extinction time greater than or equal to 100 generations and less than 1000 generations, s_{min} = 0.45x10^{-6} and s_{max} = 1.5x10^{-6} (half-filled circles in Fig. 2).

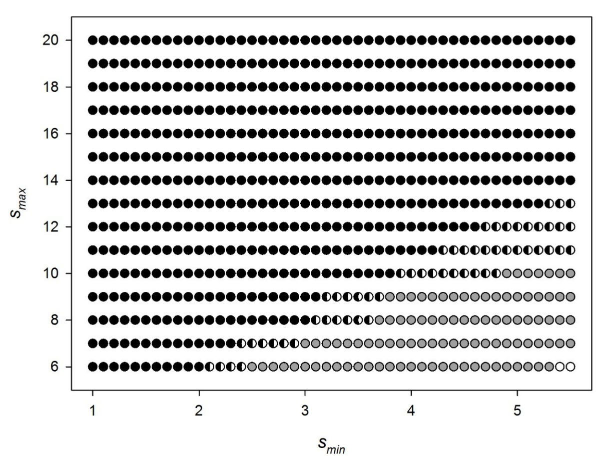

Fig. 5. Continuous resources exponentially renewed. Parameter space s_{min} and s_{max} for r = 0.001 (the values on the axes should be multiplied by 10^{-7}). Average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max}. Simulations were run for a maximum of 1000 generations. Empty circles - average extinction time less than 10 generations. Grey circles - average extinction time greater than or equal to 10 generations and less than 100 generations. Half-filled circles - average extinction time greater than or equal to 100 generations and less than 1000 generations. Fully filled circles - extinction time greater than or equal to 1000 generations. The remaining parameters had standard values (Table 1).

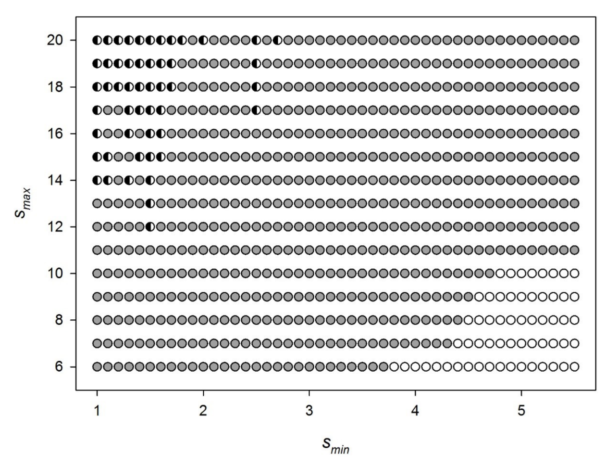

Fig. 6. Continuous resources exponentially renewed. Parameter space s_{min} and s_{max} for r = 0.002 (the values on the axes should be multiplied by 10^{-7}). Average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max}. Simulations were run for a maximum of 1000 generations. Empty circles - average extinction time less than 10 generations. Grey circles - average extinction time greater than or equal to 10 generations and less than 100 generations. Half-filled circles - average extinction time greater than or equal to 100 generations and less than 1000 generations. The remaining parameters had standard values (Table 1).

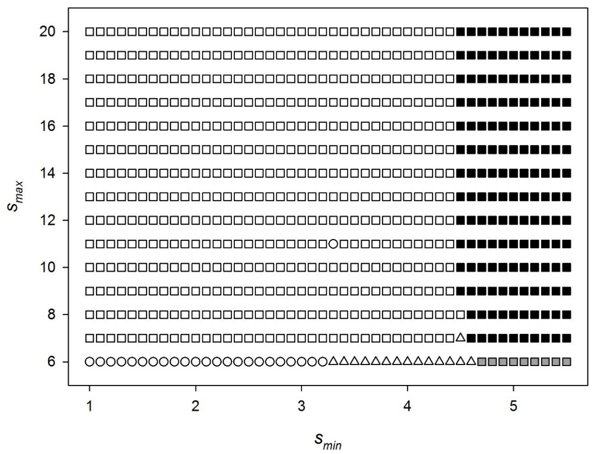

Fig. 7. Continuous resources logistically renewed. Parameter space s_{min} and s_{max} for r = 0.05, V_0 = 6x10^6 and V_k = 6x10^6 (the values on the axes should be multiplied by 10^{-7}). Average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max}. Simulations were run for a maximum of 1000 generations. Empty squares - fixed point type population dynamics. Number of individuals is fixed at values 2 and shows no fluctuation. Fully filled squares - population number fluctuates around some larger values. Grey squares – fixed point type dynamics. The number of individuals is fixed at value greater than 2 (it is equal to 10 for greater values of s_{min}). Empty triangles - fixed point type dynamics. The number of individuals is fixed at value equal to 1. No population extinction was observed at any point of the above parts of the parameter space. Empty circles - the population goes extinct at generation 2 or 3. The remaining parameters had standard values (Table 1).

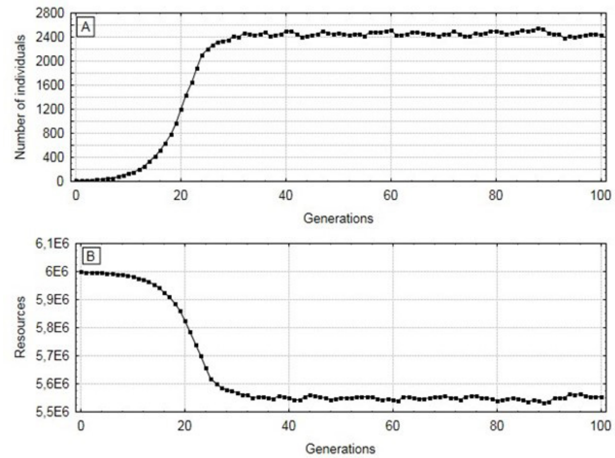

Fig. 8. Continuous resources logistically renewed. Example of population (A) and resource (B) for s_{min} = 048.x10^{-6}, s_{max} = 1.1x10^{-6} (fully filled squares region in Fig. 7), r = 0.05, V_0 = 6x10^6 and V_k = 6x10^6. The other parameters had standard values (Table 1).

Fig. 7 shows how the different types of population dynamics described by the model with continuous logistically renewed resources for V = 6x10^6 and r = 0.05 are distributed in the parameter space s_{min} and s_{max}. The dynamics of the population now has a different character than in the case of linearly or exponentially renewed continuous resources.

The right-hand part of the parameter space is dominated by the population dynamics, which is characterized initially by an increase, which then slows down and the population number settles showing small fluctuations (Fig. 8). The level at which population number is fluctuating does not depend on the initial population size (Fig. 9). However, it linearly depends on the value of the parameter r (Fig. 10). In the right-hand side of parameter space shown in Fig. 7 large values of the parameter r do not lead to population extinction. For r greater than about 0.08, the population number is fixed at 2. Very small values of the r parameter (of the order of 0.0001) still give fluctuations in the number, although around very small values (a few individuals) and of very small ranges.

In the left-hand side of the parameter space s_{min} and s_{max} shown in Fig. 7 different types of population dynamics exist. In the lower left corner of the parameter space quick population extinction will be observed. However, population dynamics of the fixed point type dominates in the left-hand side of the parameter. Most often the population

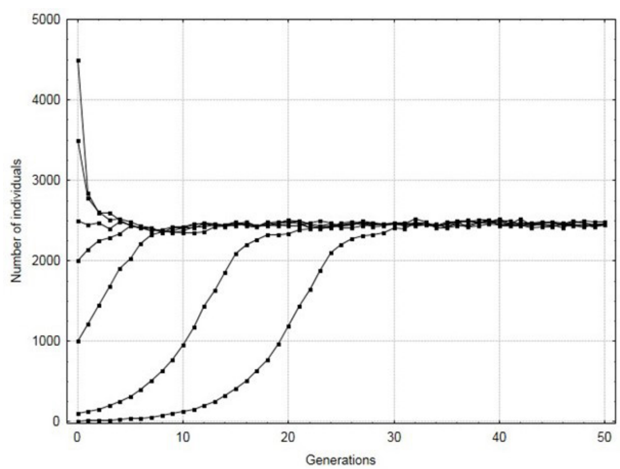

Fig. 9. Continuous resources logistically renewed. Dependence of population dynamics on initial population size. Following case are illustrated: N_0 = 10, 100, 1000, 2000, 2500, 3000 and 4000 individual. Simulation results for s_{min} = 048.x10^{-6}, s_{max} = 1.1x10^{-6}, r = 0.05, V_0 = 6x10^6 and V_k = 6x10^6. The other parameters had standard values (Table 1).

number fixes at value 2 and persists in this state.

Changing of V_k parameter value modifies details of population dynamics in all points of the parameter space s_{min} and s_{max} and changes the distribution of its different types across this parameter space. Fig. 11 shows this parameter space for V_k = 12x10^6. The area where the population number is fixed at 2 still exists, although it is much smaller. The area where the population number fluctuates around a certain value after an initial increase is greater, but has shifted significantly to the left. On the right side of the parameter space, there is an area where the population goes extinct. It happens most often, after the first maximum in less than twenty time steps. Only on the left border of the area of population extinction, population has

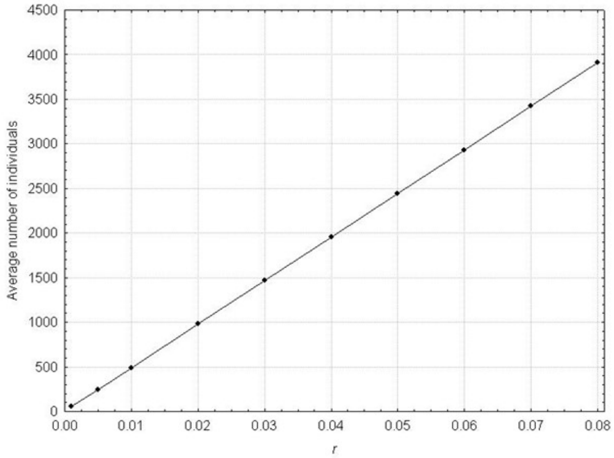

Fig. 10. Continuous resources logistically renewed. Dependence of average number of individuals in this phase of population dynamics when the population is not systematically increasing (for the 160 generations following the 40 initial generations) on vale of the parameter r for s_{min} = 048.x10^{-6}, s_{max} = 1.1x10^{-6}, V_0 = 6x10^6 and V_k = 6x10^6. The other parameters had standard values (Table 1). Standard deviations were not shown because they are very small.

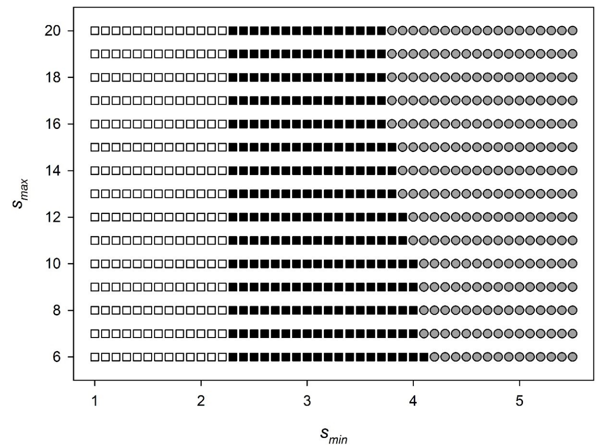

Fig. 11. Continuous resources logistically renewed. Parameter space s_{min} and s_{max} for r = 0.05, V_0 = 6x10^6 and V_k = 12x10^6 (the values on the axes should be multiplied by 10^{-7}). Average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max}. Simulations were run for a maximum of 1000 generations. Empty squares - fixed point type population dynamics. Number of individuals is fixed at values 2 and shows no fluctuation. Fully filled squares - population number fluctuates around some larger values. No population extinction was observed at any point of the above parts of the parameter space. Grey circles - average extinction time greater than or equal to 10 generations and less than 100 generations. The remaining parameters had standard values (Table 1).

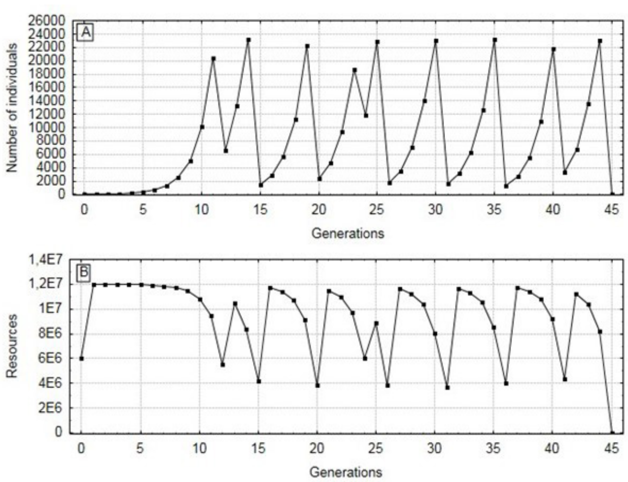

Fig. 12. Continuous resources logistically renewed. Example of population (A) and resource (B) for s_{min} = 048.x10^{-6}, s_{max} = 1.1x10^{-6} (grey circles region in Fig. 12), r = 0.05, V_0 = 6x10^6 and V_k = 12x10^6. The other parameters had standard values (Table 1).

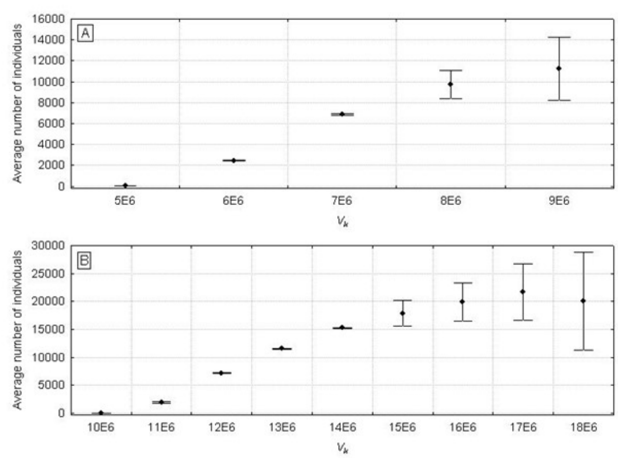

Fig. 13. Continuous resources logistically renewed. Dependence of average number of individuals in this phase of population dynamics when the population is not systematically increasing (for the 160 generations following the 40 initial generations) on vale of the parameter V_k for: A - s_{min} = 0.48x10^{-6} and s_{max} = 1.1x10^{-6} (fully filled squares region of the parameter space show in Fig. 7), B - s_{min} = 0.25x10^{-6} and s_{max} = 1.1x10^6 (empty squares region of the parameter space shown in Fig. 7). V_0 = 6x10^6 and r = 0.05, the other parameters had standard values (Table 1). Average values of number of individuals together with standard deviations around them are shown.

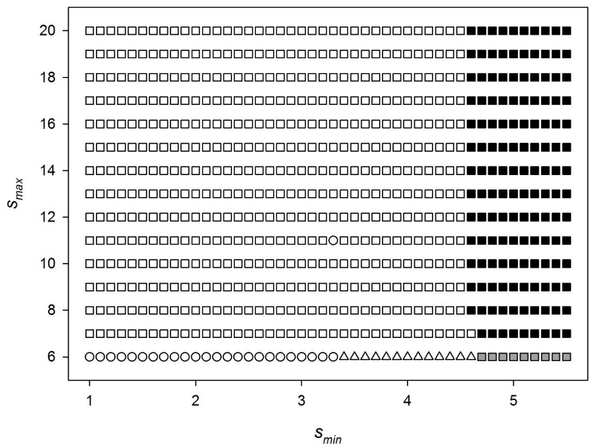

Fig. 14. Discontinuous resources renewed to constant value at the beginning of each generation. Parameter space s_{min} and s_{max} for α = 1.0 (the values on the axes should be multiplied by 10^{-7}). Average for 100 simulations of population extinction times for different values of parameters s_{min} and s_{max}. Simulations were run for a maximum of 1000 generations. Empty squares - fixed point type dynamics. The number of individuals is fixed at value equal to 2. Fully filled squares – number of individuals fluctuates around some larger values. Grey squares – fixed point type dynamics. The number of individuals is fixed at value greater than 2 (it is equal to 10 for greater values of s_{min}). Empty triangles - fixed point type dynamics. The number of individuals is fixed at value equal to 1. No population extinction was observed at any point in above parts of the parameter space. Empty circles – population goes extinct in the second generation. The other parameters had standard values (Table 1).

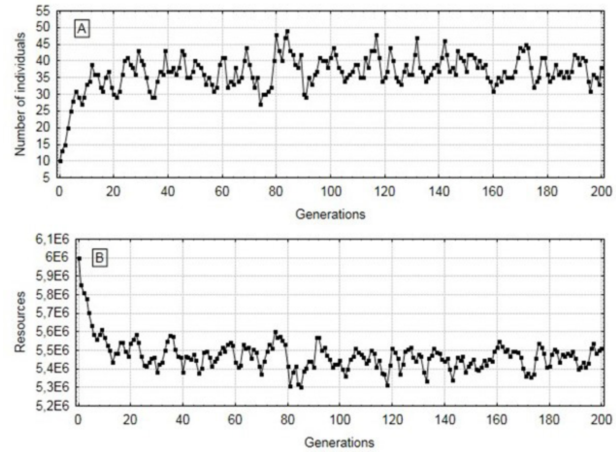

Fig. 15. Discontinuous resources renewed to constant value at the beginning of each generation. Example of population (A) and resource (B) dynamics for parameter values s_{min} and s_{max} from the right side of the parameter space shown in Fig. 14 (fully filled squares region - s_{min} = 0.48x10^{-6} and s_{max} = 1.1x10^{-6}). The other parameters had standard values (Table 1). Resources are shown at the end of each generation.

several maxima, and then goes extinct after several dozen time steps. An example of such population dynamics is shown in Fig. 12.

Let us follow how changes in the value of the parameter V_k affect the nature of the population dynamics at two points in the parameter space s_{min} and s_{max}: one corresponds in Fig. 7 to the point where for V_k = 6x10^6, the population fluctuates around a certain value (Fig. 13A), and the other to the point where the number settles at a value of 2 (Fig. 13B). At the first point, the nature of the dynamics persists over a relatively small range of changes in the value of V_k. The value around which the population fluctuates and the range of these fluctuations increase as V_k increases. For V_k of order 10x10^6, the population goes extinct. At the second point for V_k of order 10x10^6 the nature of the dynamics changes. It ceases to be a fixed point type dynamics. It starts to be characterized by fluctuations around a certain value, which increases significantly as V_k increases. The range of fluctuations around this value also increases, until it becomes so large that for V_k of the order of 20x10^6 the population goes extinct. This is because, as V_k increases the area of fixed point type dynamics in s_{min} and s_{max} parameter space (for high individual variability) disappears, and the area of fluctuation around a certain value (for higher individual variability) and population extinction (for low individual variability) shifts to the left.

6. Discontinuous Resources and Renewed to Constant Amount at the Beginning of Each Generation

In the model with discontinuous resources, the resources were consumed by growing individuals during each generation and not renewed during it. The resources at the beginning of the next generation V_{t+1} were assumed to have nothing to do with the amount of resources at the end of the previous generation. At the beginning of each generation the resources were renewed to some constant value according to equation:

$$V_{t+1} = \alpha V_0, \tag{6.1}$$

where α is a fixed parameter. In the basic version of the model α = 1, which means that at the beginning of each generation resources are renewed to the value they had at the beginning of the first generation.

Fig. 14 shows the parameter space s_{min} and s_{max} for α = 1.0. As in the case of logistically renewed resources two types of solutions dominate in the parameter space. In the right-hand side of the parameter space we observe an increase in the number of individuals and then smaller or larger fluctuations within a certain range of values (Fig. 15). For the values of s_{min} and s_{max} from the left-hand side of the parameter space, fixed point type dynamics is observed. Except for the bottom line, where s_{max} is the smallest, the value at which the population size settles is 2. Population extinction appears in the lower left corner of the parameter space for the smallest s_{max} and s_{min} values. Increasing the value of s_{min} in this region of the parameter space leads to fixed-point dynamics. First, the population

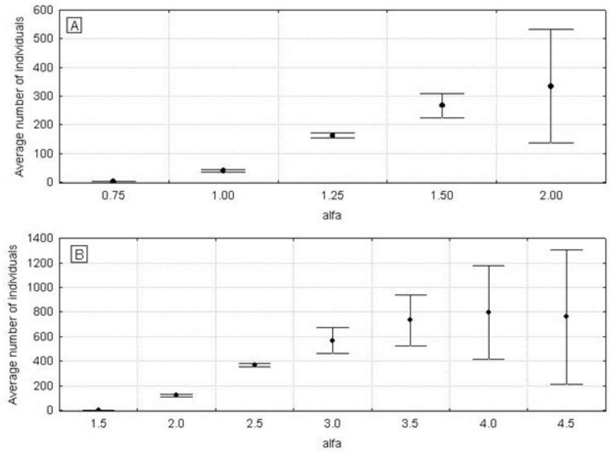

Fig. 16. Discontinuous resources renewed to constant value at the beginning of each generation. Dependence of average number of individuals in this phase of population dynamics when the population is not systematically increasing (for the 160 generations following the 40 initial generations) on vale of the parameter α for: A - s_{min} = 0.48x10^{-6} and s_{max} = 1.1x10^{-6} (fully filled squares region of the parameter space show in Fig. 14), B - s_{min} = 0.25x10^{-6} and s_{max} = 1.1x10^{-6} (empty squares region of the parameter space shown in Fig. 14). The other parameters had standard values (Table 1). Average values of number of individuals together with standard deviations around them are shown.

size is set to 1, and then for larger values of the s_{min} parameter to 10.

In this part of parameter space s_{min} and s_{max}, where for α = 1.0 population fluctuates, the level of these fluctuations and their range depend on the amount of resources at the beginning of each generation (Fig. 16A). In the another part of parameter space, where for α = 1.0 population number is fixed, increase in the value of the parameter α results in transition of population dynamics: it is fixed-point type dynamics for small α and fluctuations of number for greater values of parameter α (Fig.16B). In both cases an increase in the value of the parameter α results in an increase in the size of the population, but also significantly increases the range of its fluctuations, which, with a sufficiently high value of the parameter α (of the order of 2.5 in Fig. 14A and of the order of 5 in Fig. 14B), leads to extinction. On the other hand, low values of parameter α (of the order of 0.75 and 1.0 respectively) are not the causes of population extinction. The population size is then set to 2. The reason for the above dependence of population dynamics on the value of the parameter α is due to the same changes in the geometry of the s_{min} and s_{max} parameter space as previously observed for logistically renewable resources and different values of the parameter V_k.

7. Discussion

The dynamics of a single population with non-overlapping generations described by the above models depends significantly on two factors. One is the individual variability in the amount of resources obtained from the environment, the main cause of which is intraspecific global competition for common for all individuals resources. The second factor is the nature and the amount of the resource. This two factors are intertwined and in each version of the model they determine differently the number of individuals that reproduce and their characteristics. Also important is at what point in the history of the population what individuals, and how many of them, become important for the continued persistence of the population.

The population dynamics described by the above model with continuous and linearly renewed resources is characterized by oscillations of the population number and the amount of resources, which sooner or later end in the extinction of the population. The details of these dynamics very much depend on the degree of individual variability. Population dynamics of identical or almost identical individuals is very simple. It starts with a low number of individuals and a relatively high resource level. In this situation, each individual can produce more than one juvenile, and the population number increases in successive generations. This pattern of the initial dynamics of the population and its resources does not depend on the initial population number or on the rate of resource growth. Only the number of individuals at a maximum and the rate at which this maximum is reached depend on the model parameters. The resources which are exploited by increasing number of individuals start shrinking. Thus, the production of juveniles is declining. At a certain time step, an individual can produce only one juvenile, and this is the case of all individuals in the population, as they are identical. Because progeny production can be expressed only as natural numbers or zero, with a further decline in the resources progeny production drops to zero. The population goes extinct.

When individuals are variable the population dynamics will be significantly different, although the initial phases will be similar. After the first maximum, the population size and resources start declining. However, now the population does not go extinct after reaching the first minimum. This is so because in the population comprising variable individuals also at a low resource level there will be at least one individual whose weight will be sufficient for the production of at least one juvenile. As the number of individuals is low, then resources are exploited at a low rate and, renewed constantly, they start increasing. This is followed by an increase in the population number, and the cycle is repeated. The population can go through several cycles of growth and decline. However, sooner or later, it will happen that in the phase of a low number of individuals and low resource level there will be no individual able to reproduce, and the population will go extinct.

The above pattern of population and resource dynamics is repeated for resources that are continuous but renewed exponentially. This shows that in order to achieve this type of population dynamics important is that resources are continuous and have the possibility of unlimited growth. The details of the resource dynamics are not important. In both cases of resource dynamics (linear and exponential), the importance of their continuity allows for a systematic decrease or increase in resources over many generations. Unlimited growth of resources means that when resources are poorly exploited by a small number of individuals in the initial phase of the above population cycles, they grow to such values that systematically increase the population number and results in the appearance of the maximum in population number. When resources are consumed intensively by a large number of individuals, this results in a systematic deterioration of resources in subsequent generations. This happens until a small number of individuals are present in the population and then individual variability comes into play. What becomes important at this point is whether there is at least one individual in the population capable of reproducing. If so, the population starts to grow and the whole cycle repeats itself. Such population dynamics is sustained by the continuity of resources, their unlimited growth when not exploited and individual variability.

For resources that are discontinuous and renewed at the beginning of each generation to some constant value or are continuous but renewed logistically, the number dynamics looks very different. This shows that in these cases it is not the continuity or discontinuity of the resources that is important, but the fact that they grow in a limited way when they are not exploited.

These differences manifest themselves in two types of dynamics. For those ranges of s_{min} and s_{max} parameters values which are responsible for the greatest individual variability (left side of the parameter space of s_{min} and s_{max}), we have fixed point dynamics - the size of the population is set to 2. For areas with lower individual variability (right side of the parameter space of s_{min} and s_{max}), we have an initial increase in population size, and then its fluctuations around a certain level.

Let us trace the development of this type of population dynamics in the case of resources being renewed to the same value at the beginning of each generation. The initial population and resource dynamics are similar to those of continuous resource with unlimited growth - the population increases and the resources decrease. At the beginning the renewal rate of resources is sufficient for most individuals in the generation to produce more than one offspring and population number to increase. Later with some relatively high population number, the amount of resource that occurs at the beginning of the generation is too small to ensure that all individuals in that generation have good conditions for growth and reproduction. During this generation, as a result of the growth of individuals using the resources, their growth conditions become worse and worse. Since this generation is characterized by more or less variable individuals, at its end only a certain number of individuals will be able to reproduce, and their offspring will form the next generation. This next generation will encounter the same conditions in terms of resources - their amount at the beginning of the next season will be the same as those encountered by their mothers. A kind of quasi-equilibrium is created between the amount of resources at the beginning of the generation and their dynamics within this generation, the variability of individuals in terms of the amount of resources obtained, which influences the number of individuals in the current generation able to reproduce and the number of individuals in the next generation. These conditions begin to repeat themselves in subsequent generations. As a result, we start to observe a more or less constant number of individuals in successive generations. In the earlier models with continuous linear or exponential resources that unlimited resource growth pulls the population up in a sense when it is small. It will not be the case for resources with limited growth.

Also in this version of the model, in which continuous resources are renewed logistically, a similar mechanism is working. Here, too, a balance is established between the process of recruiting individuals to the next generation and the nature of the resource dynamics. Unlike the case with discontinuous resources renewed to a constant value, this mechanism, because of their continuity, works now more precisely, resulting in less fluctuations in population and resources. Their logistic growth rate allows smooth increases and decreases in population size.

The extent of population fluctuations once these quasi-equilibrium conditions are established depends on the degree of individual variability measured by the difference between s_{max} and s_{min}. If individual variability is low, fluctuations are greater. When individual variability is high, number of individuals in the population is the same from generation to generation. In the case of high individual variability, when s_{min} is much smaller than s_{max}, a strict hierarchy of individuals capable of reproduction is established, which, because the conditions for the growth of individuals are the same from generation to generation, is also repeated in subsequent generations. The greater the variability of individuals, the tighter this hierarchy is and the smaller the number of individuals capable of reproduction. A strict elite of individuals is formed, which is less numerous the greater the variability of individuals. This gives a fixed point type population dynamics. The population dynamics is different when the individual variability is smaller, that is, when the difference between s_{min} s_{max} is smaller. Then the recruitment to the elite of individuals capable of reproduction is more open and their number in successive generations can vary with the accompanying fluctuations in the amount of resources. As a result of this, the population number will also fluctuate.

The degree of individual variability depends not only on the difference between the values of the s_{max} and s_{min} parameters, but also on the level of resources. When it is small, the same difference in s_{max} and s_{min} causes greater individual variability in the amounts of acquired resources than when there are more resources. Therefore, changes in the value of the parameter α in the case of discontinuous resources renewed to a constant value and the parameter V_k in the case of logistically renewed continuous resources cause characteristic changes in the distribution of different types of population dynamics in the parameter space s_{min} and s_{max}. This has been illustrated on the example of a model with logistic resources, but judging from the model's response to changes in the value of parameter α, it will also take place in the case of a model with discontinuous resources. When the environment is poor (for relatively small values of the V_k parameter, for example for $V_k = 6x10^6$), the entire parameter space analyzed in the model is covered with solutions that give a persistent population dynamics. Increasing the level of resources ($V_k = 12x10^6$) gives sufficient individual variability for the persistence of the population only in the left part of the parameter space, where the differences between s_{max} and s_{min} are sufficiently large. In the right part of the parameter space, individual variation is too small to ensure this. Here we begin to observe the dynamics leading to the extinction of the population.

Increasing the value of parameter V_k in the version of the model with logistic resources or of parameter α in the model with discontinuous resources for a given values of s_{min} and s_{max}, also increases the value around which the population number fluctuates and the range of these fluctuations. If the number of individuals in a certain generation is small, the growth of individuals in conditions where resources are high during that generation results in a large production of offspring at the end of that generation. This large number of individuals will be confronted with the same or similar resources in the next generation, but because there are more competing individuals, offspring production will be smaller. This will cause a rapid decline in numbers in the next generation and, as a result, will lead to fluctuations in number of individuals. For a small individual variability and a sufficiently large value of parameter α or V_k, these fluctuations may be so large that the question arises about whether, in the case of a small number, there are individuals in the population capable of reproducing or whether, in the case of high number, the resource level is sufficiently high to support consumption of all individuals. If not, the population goes extinct because resources have been exhausted. This will happen with a lower level of resources for discontinuous resources than for continuous resources, as the latter are the cause of a more precise regulation of the system.

The significance of individual variability depends not only on the difference between s_{max} and s_{min}, but also on the absolute values of these parameters. Therefore, on the left side of the bottom line in the parameter space shown in Figs 7 and 14, there is an area where the population, despite the difference in the values of the parameters s_{max} and s_{min}, goes extinct within a few generations. This is because with sufficiently low resources, the value of the s_{max} parameter is so small that even the heaviest individual is unable to produce offspring.

Individual variability in the amount of resources obtained by competing individuals is very rarely studied by ecologists. For this reason, it is difficult to decide how large the range of individual variability is in actual populations. So, too, it is unclear what type of population dynamics should be expected in real populations. On the other hand, the pattern of responses of individual variability to changes in the amount of resources for which individuals compete, proposed in this work, is supported by the shapes of the distributions of weights of individuals in even-aged populations (Uchmański 1985, Wyszomirski 1992). In any case, the analysis of population dynamics provided by the model presented in this work shows at least a spectrum of potential solutions to the model.

8. Conclusions

The same mechanism describing the emergence of differences between individuals in the amount of acquired resources when the competition for common resources is global gives different population dynamics depending on the dynamics of the resources. This is also related to the different meanings of the term population persistence. For a resource that grows indefinitely as the population goes through phases of low abundance many times, an increase in persistence will mean an increase in the time to extinction of the population. When the resources grow in a limited way, the increase in persistence will mean a transition from the population dynamics which produces extinction of population to dynamics characterized initially by an increase in numbers and then by its fluctuations around a certain value or to the fixed point type dynamics.

In both of the above situations, individual variability is important for population persistence - population persistence increases with increasing individual variability.

As already mentioned in the introduction, unlimited growth of resources is characteristic of organisms such as, for example, herbivorous plankton using phytoplankton or bacteria. In this type of organism, little individual variability can be expected, for example in the case of asexual reproduction (Kaliszewicz et al. 2005). The problem of extinction of such a population then arises, which will be particularly relevant in the case of an environment with poorly expressed seasonality (tropical zone lakes). Several mechanisms can be identified that increase the persistence of such populations such as, for example, different types of mortality (Uchmański 2023). The problem of extinction of a population with small individual variability seems to be less relevant in environments with well-expressed seasonality (temperate zone lakes). Here, usually a couple of summer population maxima are followed by winter, forms of organisms that are able to overwinter emerge, the eco-

Table 1. Standard values of the model parameters used in the simulation of population dynamics. For s_{min} and s_{max} the maximal range of their values is shown, as the results of simulations will be presented for different values of this parameter.

	Parameter	Value
Growth equation parameters	$a_{1,max}$	0.11
-	a_2	0.03
-	b_1	0.7
-	b_2	0.9
Parameters of initial weight distribution	$w_{0,min}$	14
-	$w_{0,max}$	26
-	$w_{0,mean}$	20
-	$w0_{,variance}$	5
Parameters of resource partitioning function	s_{min}	0.10×10^{-6} - 0.55×10^{-6}
-	s_{max}	0.60×10^{-6} - 2.00×10^{-6}
Threshold for reproduction	w_{fak}	0.65
Progeny production	c	0.01
Initial number	N_0	10
Initial resources	V_0	6×10^6

logical mechanism that previously controlled the population size ceases to function, so that the next spring everything starts all over again. This effect will not be observed in regions without clear seasonality.

It is also worth noting that in ecosystems with increased primary production due to, for example, higher temperatures (Uvarov 1931), maintaining the same extinction time for a population whose individuals use resources with unlimited dynamics will require an increase in individual variability, as was shown in the example of populations of organisms using resources with exponential type dynamics. Thus, better food conditions do not necessarily automatically mean greater population persistence.

I the case of resources with limited growth greater population persistence is also achieved when individual variability is greater, but population persistence is already possible for less individual variability than in the case of unlimited resources. However, population persistence then means, as we already know, completely different population dynamics. If we refer to the example with annual insects, we can say that in the case of a resource with limited growth, we will observe what to some extent resembles the dynamics known from the classical logistic equation. After an initial phase of growth, the population will more or less fluctuate around a certain fixed value. Moreover, disturbed out of this state, it will return to it. The insects will thus form a somewhat stable population, although the dynamics will not be as smooth as those given by the differential or difference version of the classical logistic equation. This is a natural result of the individual-based model. Such population dynamics will be observed regardless of whether resources have continuous or discontinuous dynamics. What is important is that their dynamics is limited. Thus, both insects from the evergreen forest of the tropical zone, the coniferous forest of the temperate zone and the deciduous forest of this zone will have similar dynamics.

For resources with limited dynamics, too little individual variability leads to population extinction. However, the cause is now different. When the resource has limited dynamics, the population becomes extinct due to too large range of fluctuations in number. This will occur more often with sufficiently low individual variability in a resource-rich environment than in a resource-poor environment. In the latter, even a population with low individual variability can be characterized by ‘logistic equation’ type dynamics. Thus in the rich, evergreen forests of the tropical zone (Pianka 1966), the individuals of a persistent population must be characterized by a sufficiently high degree of individual variability, while in the poorer coniferous forests of the temperate zone (Striganova & Porjadina 2005), populations composed of less variable individuals may produce persistent dynamics. On the other hand, in regions without seasonality and with high primary production, a population of sufficiently diverse individuals can reach a higher number than in a seasonal environment and persist despite its significant fluctuations.

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