

Dynamic model and simulation analysis of the genetic impact of population harvesting

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ABSTRACT

In this paper the impact of exploitation of a sexually reproducing population is investigated by means of a selection model. Our aim is to find genetic systems for which the fishing results in selection effect, provided that the growth and reproduction rates of individuals are genetically determined. To this end a complex dynamic model is presented, providing long-term predictions both on the size structure and on the genetic composition of the population. For a minimal nontrivial model, the two-locus two-allele case is considered, where the survival, transition and reproduction rates depend on size and genotype. For each size class and genotype the corresponding density is a state variable. The mating system is supposed to be totally panmictic and the gamete production is described in terms of the meiosis matrix.

Based on the above model, an *in silico* analysis is carried out. The simulation results show that the long-term behaviour of the genetic structure can be characterized by a cyclic convergence, which means that the state sequences corresponding to different phases of the reproduction cycle tend to an asymptotic genotype distribution. For an illustration of the effect of exploitation on the genetic composition the “fishing effort” model is considered. If the *totally homozygous* genotype possesses the best phenotype, fishing does not seem to influence the genetic distribution in the long term. The same is true in case of heterozygote advantage. In some situations, however, fishing modifies the genetic distribution of the population. Meanwhile there is a significant change in the size of the harvested individuals. This result points out to the importance of the genotype–phenotype correspondence while building up fishing strategies.

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1. Introduction

The possibility of the selection effect (evolutionary consequence) of human exploitation of populations is widely accepted [1]. In this paper we will study the selection effect of human fishing activity on the fish population. By now many observations have been accumulated on the possible selection for a trait (e.g. growth rate, sexual maturation, egg number, etc.) of fish species both in fish farms (see e.g. [2,3]) and under ocean conditions [4,5]. Thus there is no doubt that, for instance, the growth rate is genetically determined and there is a genetic variation of this trait within the fish populations. In general, in

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the long run, fishing removes the largest individuals from the population. Therefore, the slow-growing phenotypes survive with a greater possibility; moreover, the phenotypes having earlier sexual maturation have selective advantage because the older (i.e. larger) individuals are less likely to survive to reproduce (see e.g. [4,6,7] and their references).

There are a few possible model approaches to study this kind of phenomenon. First, there is a phenotypic model, in which the genetic determination of the traits is neglected [6,7]. The second one is a multi locus model, in which the large number of loci additively determine the trait under selection [8,9]. Although we are aware of the fact that quantitative traits are usually determined by many loci, in the present paper, to begin with, we assume that two loci determine the traits, but not in an additive way. In this investigation the main question is: What is the role of the genotype-phenotype correspondence in the selection process induced by harvesting?

In Section 2 we introduce a discrete-time dynamical system that combines a population genetics model with an appropriate size dynamics and also includes intraspecific competition. Indeed, for the study of the selection effect of harvesting such a model is needed since, for example in fishery, the net mesh size influences the survival rate of individuals. In fact, we combine the following three basic models of mathematical biology: The first one is the well-known Leslie model describing the dynamics of the age structure of a population (see e.g. [10,11]). In our model, a size-classified version of the Leslie type dynamics is considered where in unit time, for each genotype, a part of the individuals at a genotype-dependent rate grow into the next size class, the rest of them remain there or die. During this unite time, the individuals of each class, according their genotype produce individuals entering the first size class. The second model is the simplest standard limited growth population dynamics, assuming that due to the intraspecific competition, the biological parameters (death and transition rates are density-dependent, as well [10]. For simplicity, we assume that each coefficient depends on the total density of all genotypes. The third model is the standard two-locus population genetics model, in which the meiosis determines the proportions of the gamete types produced by a zygote individual of a panmictic population. Of course, the productivity of the individuals breaks at small population density, according to the fact that at very low density it is more difficult to find a sexual partner for breeding. This phenomenon, called *bottle-neck effect* [12] can also be built into our model.

In Section 3 the case is studied when the totally homozygous genotype is distinguished among all genotypes. Section 4 is devoted to the biological case when the totally heterozygous genotype is “the best.”

In our model, the activity of harvesting above a given size (defined by net mesh size in fisheries) decreases the density regardless to the genotype of the individuals. Therefore, harvesting selection is based on the size of the individuals. Both in Sections 3 and 4, we will consider only the *fishing effort model*, when the catch is proportional to the actual densities [12].

Finally we note that in an earlier paper, in the one-locus case we *analytically* pointed out that the genotype-phenotype correspondence is crucial when in the knowledge of the asymptotic state of evolution in a sexual population, we want to predict what would happen in the corresponding phenotypic model [13]. Now, using simulations, we investigate a similar question in the two-locus case, and find such genotype-phenotype correspondences in which fishing selection results in the same and different final states, respectively.

2. Dynamic model

2.1. The basic model

Consider two independent loci, with m_1 and m_2 alleles, respectively. In this two-locus model let the type of a gamete be $A_\mu B_\nu$, or briefly $\mu, \nu (\mu \in \overline{1, m_1}, \nu \in \overline{1, m_2})$. Let i denote the i -th gamete type in the lexicographic order (i.e., $i := 1$ for $A_1 B_1, i := 2$ for $A_1 B_2, \dots, i := m_2$ for $A_1 B_{m_2}, i := m_2 + 1$ for $A_2 B_1, \dots, i := m := m_1 m_2$ for $A_{m_1} B_{m_2}$). Then the genotype of a zygote is given by an ordered pair (k, l) or shortly kl ($k, l \in \overline{1, m}$). Let us divide the population into N size classes. Let $x_{kl}^n(t)$ denote the number of individuals of genotype kl , size class n , at time t . In a time unit (say a month) a part of n -th size class of genotype dies at rate a_{kl}^n , the b_{kl}^n part of it passes to the next size class ($a_{kl}^n, b_{kl}^n > 0, a_{kl}^n + b_{kl}^n < 1$). Then the size dynamics for genotype kl is

$$x_{kl}^n(t + 1) = (1 - a_{kl}^n - b_{kl}^n)x_{kl}^n(t) + b_{kl}^{n-1}x_{kl}^{n-1}(t) \quad (n \in \overline{2, N}, t \in \mathbf{N}_0). \tag{1}$$

In this model the relation between time scale and size scale is such that the growth rate is slow enough to guarantee that no individual can jump two size classes in unit time. Due to the intraspecific competition, the model parameters may also depend on the total density $x := \sum_{n=1}^N \sum_{k,l=1}^m x_{kl}^n$. This dependence may be e.g. of the following form (where $K > 0$ is an appropriate constant):

$$a_{kl}^n(x) := \left(1 - \frac{1 - a_{kl}^n}{1 + Kx}\right), \quad b_{kl}^n(x) := \frac{b_{kl}^n}{1 + Kx}. \tag{2}$$

2.1.1. Dynamics for the first size class

Let $m_{i,kl}$ be the probability of the event that a kl -zygote produces an i -gamete. Then the n -th row of the *meiosis matrix* M is defined as

$$[m_{i,11} \quad \dots \quad m_{i,1m} \quad m_{i,21} \quad \dots \quad m_{i,2m} \quad \dots \quad m_{i,mm}].$$

Clearly, the meiosis matrix strictly depends on the genetic situation, e.g. the loci location at chromosomes and probabilities of crossing-over between loci etc. For the simplicity in this paper we only consider the most simple genetic situation, where the loci are located at different chromosomes, and the number of alleles in both loci is $m_1 := m_2 := 2$. In this case the meiosis matrix is

$$M = \begin{bmatrix} 1 & \frac{1}{2} & \frac{1}{2} & \frac{1}{4} & \frac{1}{2} & 0 & \frac{1}{4} & 0 & \frac{1}{2} & \frac{1}{4} & 0 & 0 & \frac{1}{4} & 0 & 0 & 0 \\ 0 & \frac{1}{2} & 0 & \frac{1}{4} & \frac{1}{2} & 1 & \frac{1}{4} & \frac{1}{2} & 0 & \frac{1}{4} & 0 & 0 & \frac{1}{4} & \frac{1}{2} & 0 & 0 \\ 0 & 0 & \frac{1}{2} & \frac{1}{4} & 0 & 0 & \frac{1}{4} & 0 & \frac{1}{2} & \frac{1}{4} & 1 & \frac{1}{2} & \frac{1}{4} & 0 & \frac{1}{2} & 0 \\ 0 & 0 & 0 & \frac{1}{4} & 0 & 0 & \frac{1}{4} & \frac{1}{2} & 0 & \frac{1}{4} & 0 & \frac{1}{2} & \frac{1}{4} & \frac{1}{2} & \frac{1}{2} & 1 \end{bmatrix}. \tag{3}$$

We note that in this paper we only consider case of two independent loci, and case of linkage loci will not studied, where the meiosis matrix is more complicated, according to the recombination between chromosomes.

Let us now assume that the reproduction cycle starts every T time units, and each individual of the n -th size group with genotype (k, l) , at average produces α_{kl}^n gametes. Then, for any $t \in \mathbf{TN}$, the $x_{kl}^n(t)$ zygotes of genotype kl and size class n , produce $\alpha_{kl}^n x_{kl}^n(t)$ gametes (\mathbf{TN} denotes the set of all multiples of T).

Supposing the mating is panmictic over the whole population and gametes are produced at Hardy–Weinberg proportions, we get

$$x_{kl}^1(t+1) = \frac{1}{2} \frac{\left[\sum_{n=1}^N \sum_{r,s=1}^m m_{k,rs} \alpha_{rs}^n x_{rs}^n(t) \right] \left[\sum_{n=1}^N \sum_{r,s=1}^m m_{l,rs} \alpha_{rs}^n x_{rs}^n(t) \right]}{\left[\sum_{i=1}^m \sum_{n=1}^N \sum_{r,s=1}^m m_{i,rs} \alpha_{rs}^n x_{rs}^n(t) \right]} + (1 - a_{kl}^1 - b_{kl}^1) x_{kl}^1(t) \quad (t \in \mathbf{TN}). \tag{4}$$

For time moments different from the reproduction periods, we have

$$x_{kl}^1(t+1) = (1 - a_{kl}^1 - b_{kl}^1) x_{kl}^1(t) \quad (t \in N_0 \setminus \mathbf{TN}). \tag{5}$$

2.2. The effect of harvesting

The harvesting will be built into dynamics (1)–(5) will be analyzed on the basis of the fishing effort model (see e.g. [12]).

2.2.1. Fishing effort model

In the *fishing effort* system the intensity of the fishing activity determines the catch, the latter is proportional to the density, and in case of differentiate (size-dependent) fishing, the proportionality constant also depends on the size, but does not depend on the genotype. The effort is given by an N -dimensional vector h . Assume the population is harvested from size class n_0 on. Hence $h_n = 0$ for $n < n_0$, and $h_n \in]0, 1]$ for $n \geq n_0$. In this case (1) becomes

$$x_{kl}^n(t+1) = (1 - h_n) \left[(1 - a_{kl}^n - b_{kl}^n) x_{kl}^n(t) + b_{kl}^{n-1} x_{kl}^{n-1}(t) \right]. \tag{6}$$

2.3. The bottle-neck effect

The productivity of the individuals breaks at small population density, according to the fact that at very low density it is more difficult to find a sexual partner for breeding. This phenomenon, called *bottle-neck* effect (see e.g. [12]), may be built into the model by replacing the original parameters α_{kl}^n with

$$\alpha_{kl}^n \frac{\lambda x(t)}{1 + \lambda x(t)}, \tag{8}$$

where $x(t)$ is the total density and $\lambda > 0$ is a constant. Obviously, smaller λ means stronger bottle-neck effect.

2.3.1. Model parameters

During simulations we consider meiosis matrix (3) and set $m := 4$, $N := 7$ and $T := 4$. We start from the following coefficient set and later on we will change this according to the particular genetic cases. Suppose that death rates a_{kl}^n , transition rates b_{kl}^n and gamete production rates (or fitness parameters) α_{kl}^n depend only on the size class, and the corresponding concrete parameters are given by the following vectors:

$$\begin{aligned} a &:= [0.99, 0.3, 0.1, 0.1, 0.2, 0.4, 0.7], \\ b &:= [0.007, 0.3, 0.5, 0.5, 0.3, 0.15, 0], \\ \alpha &:= [0, 0, 500, 3000, 8000, 9500, 10000], \end{aligned} \tag{9}$$

which are the same for all genotypes. We have taken into account the biological fact that death rates have a minimum in the middle size classes, in general the first class has the highest death rate, the transition rates have a maximum at the middle size classes and the egg number strictly increases with the size class. Of course, these parameters are different for different

animals, but in the case of fish usually the largest fish produce more eggs than the smaller ones, independently of the age of the fish. Thus fitness parameter is supposed to increase with size. Furthermore, the effect of intraspecific competition is taken into account with $K = 0.000002$.

Now we will assume that the phenotype of an individual is uniquely determined by its genotype. In the following we will consider different genotype–phenotype correspondences. Now this correspondence generates a classification of genotypes where each class contains such genotypes that have the same phenotype. In our case, the phenotypes are defined by parameters of the dynamics. Using simulation we will examine whether the selection process is affected by the genotype–phenotype mapping or not.

3. A totally homozygous genotype is distinguished

In this section we suppose that some properties of genotype (1,1) (having A_1B_1 , A_1B_1 gametes) are different from those of the other 15 types. Various situations will be studied, when the original parameters in (9) are modified for the type (1,1), while they are unchanged for the other types.

We find in each situation that the 16 genotypes can be classified into the following groups according to their long-term dynamics. The colours assigned to the groups will be used on subsequent figures, in which the proportions of different genotypes as functions of time are plotted. The degree of resemblance of a genotype to the type (1,1) shows the number of the alleles which are identical to those in type (1,1).

Number	Zygotes	Degree of resemblance
I	(1,1)	4
II	(1,2), (1,3), (2,1), (3,1)	3
III	(1,4), (4,1)	2
IV	(2,2), (2,3), (3,2), (3,3)	2
V	(2,4), (3,4), (4,2), (4,3)	1
VI	(4,4)	0

3.1. Total homozygote genotype (1,1) is “the best”

Suppose that genotype (1,1) dominates over the other 15 genotypes in the sense that it is better survivor, grows faster and produces more gametes. This is ensured by the following choice of the parameter values for the type (1,1):

$$\begin{aligned} a_{11}^n &= 0.9a_{kl}^n, \\ b_{11}^n &= 1.1b_{kl}^n, \\ \alpha_{11}^n &= 1.1\alpha_{kl}^n, \end{aligned} \quad (10)$$

for each $n > 1$ and $(k,l) \neq (1,1)$.

For $n = 1$ we set $a_{11}^1 = 0.98$, $b_{11}^1 = 0.01$ and for simplicity we suppose that, except for the first size class, the initial size distribution is uniform for all genotypes (k,l) , say

$$x_{kl}^n(0) = [1000, 10, 10, 10, 10, 10].$$

One can see in Figs. 1 and 2 that the “good” genotype becomes dominant on the long term, while the other types die out, even without fishing. (In all figures the curves are labeled with I–VI, in correspondence with the table of the previous section.)

From a biological point of view, this means that, when a total homozygote has an absolute selective advantage (i.e. is the best in competition, in growth and in number of eggs) then the other genotypes will die out, and finally a genetically monomorphic population is obtained.

We also studied this case with fishing and for the genotype proportions we got the same results as shown in Figs. 1 and 2. Fishing, of course, changes the equilibrium total density of fish population.

3.2. Total homozygote genotype (1,1) is dwarfish

Suppose that the growth of an individual of the type (1,1) stops at a medium size. Thus we set

$$b_{11} = [0.007, 0.3, 0.5, 0, 0, 0],$$

for the type (1,1), i.e., its maximal size class is $n = 4$. All other parameters (a, α) are the same for all genotypes, and are chosen as in (9). The dynamics of the 6 groups in this case is represented in Fig. 3, where there is density-dependent competition and no fishing.

Type (4,4) seems to become dominant. The dwarfish (1,1) type will die out. This is also true for other types, whose genetic structure resembles to that of (1,1).

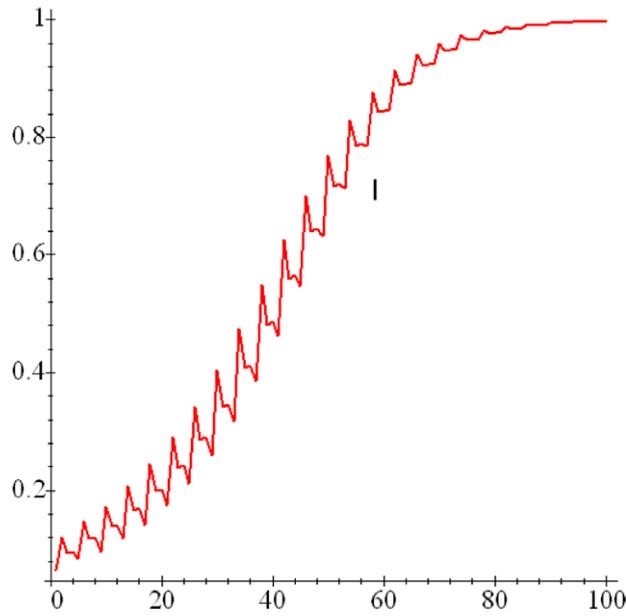


Fig. 1. Proportion of genotype (1,1) as function of time.

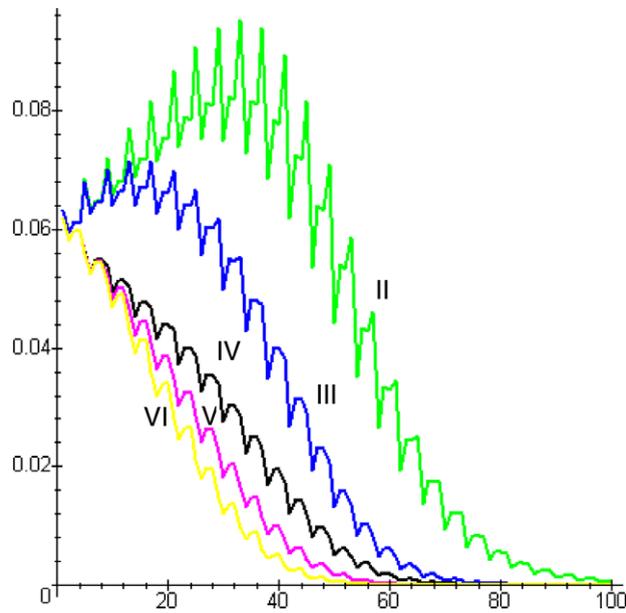


Fig. 2. Proportions of genotypes other than (1,1) as function of time.

From biological point of view this is the case when A2 and B2 alleles are dominant and the presence of one of them ensures the growing process.

3.3. Zygote (1,1) is dwarfish, the other types are harvested

With the same parameter setting, we suppose that the large-size classes are harvested with the fishing effort method, varying the intensity vector. In particular, $h = 0$ gives the original situation of the previous section.

We can conclude that fishing influences the genetic structure in the long term in the considered situation. Intensive fishing results in the dominance of the dwarfish type (Fig. 4). Furthermore, there exists a fishing intensity, which maintains a uniform genetic distribution (unstable equilibrium, see Fig. 5.)

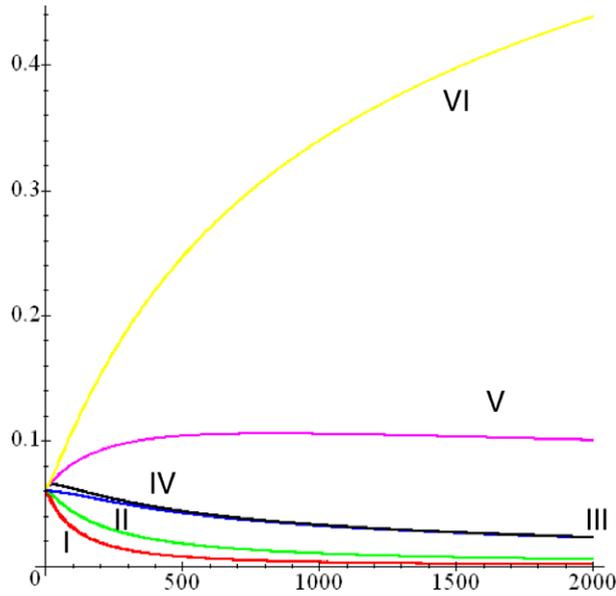


Fig. 3. Long term dynamics in the “dwarffish case”.

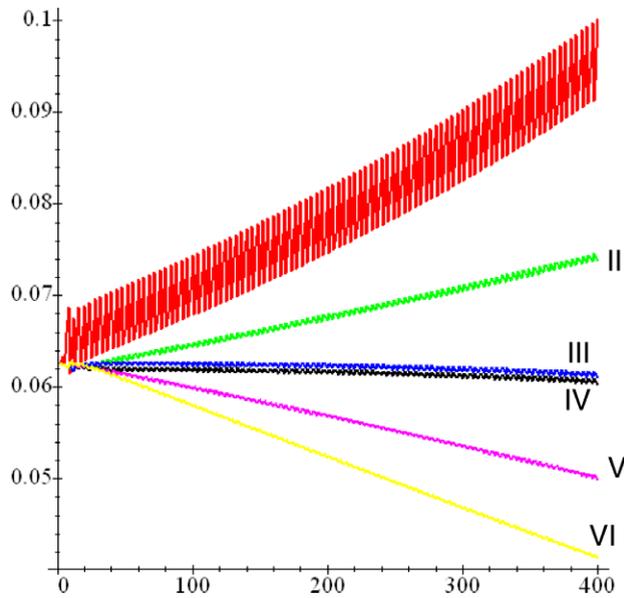


Fig. 4. Dynamics with fishing intensity $h = [0, 0, 0, 0, 0.25, 0.25, 0.25]$.

From the point of view of fishery, intensive fishing in this genetic situation does not only destroy the “quality of catching” but also decreases the “biomass output” of this kind of fish population.

3.4. Total homozygote genotype (1, 1) is dwarffish but more productive

Now “we compensate” the dwarffish feature of zygote (1, 1) by an increased fitness parameter of its maximal size class, that is, we increase parameter α_{11}^4 . (The other parameters are the same as in Section 3.2. In particular, $\alpha_{11}^4 = 3000$ gives the original situation.) The graphs below (Figs. 6 and 7) show the dynamics for the choices $\alpha_{11}^4 = 4000$ and $\alpha_{11}^4 = 3907$, respectively.

One can see from Fig. 4 that if the full-sized zygote (1, 1) is much more productive than the other types in the same size class, then (1, 1) will dominate and some other types will dye out. Fig. 7 tells us that there exists an (unstable) equilibrium state, in which all groups of genotypes will survive. In this case the system displays a limit cycle.

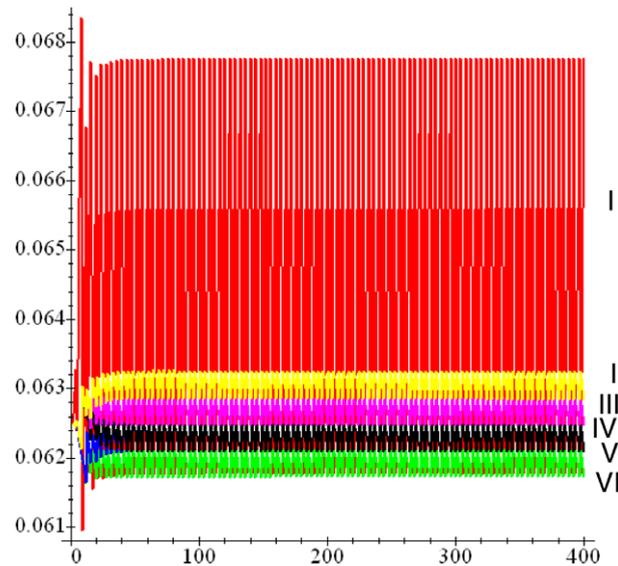


Fig. 5. Dynamics with fishing intensity $h = [0, 0, 0, 0, 0.229, 0.229, 0.229]$.

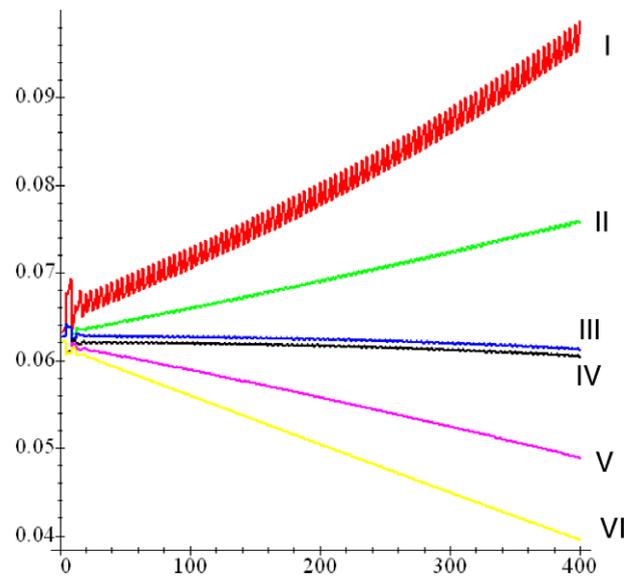


Fig. 6. Dynamics in case $\alpha_{11}^4 = 4000$.

Simulations also show that fishing influences the long-term genetic composition in the same way as in Section 3.3. That is, fishing can destabilize the cyclic coexistence and only the dwarffish phenotype can survive. Thus in this situation, the fishing also destroys its own benefit.

In a well-known phenotypic model, intensive harvesting for a long period selects this phenotype [2].

4. The totally heterozygous genotype (1,4) is “the best

For the study of the genetic distribution suppose that the “mixed” genotypes (1,4), (4,1), (3,2), (2,3) are better than the other 12 genotypes, which can be expressed by relations similar to (10). This is the case of heterosis, when the totally heterozygote (having $A_1 B_1, A_2 B_2$ alleles) perform better than the other genotypes.

From dynamical viewpoint, the genotypes are classified into the following two groups:

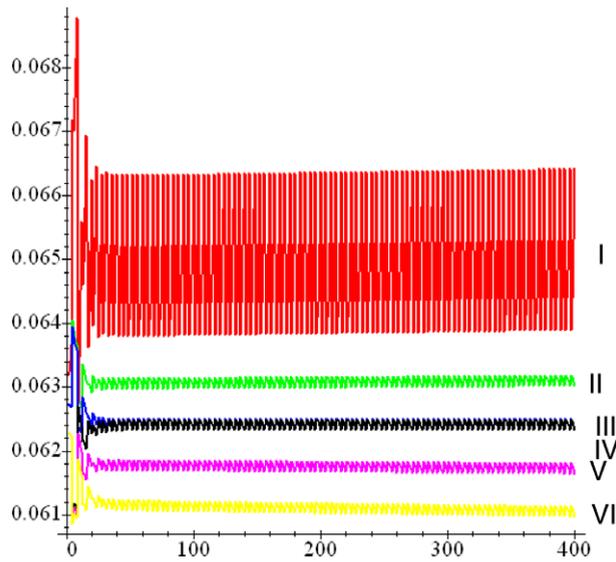


Fig. 7. Dynamics in case $\alpha_1^1 = 3907$.

Number	Zygotes
I	(2,3), (3,2), (1,4), (4,1)
II	all others

4.1. No harvesting

Firstly, we study the case when the population is not harvested. Then in the long term a cyclic behaviour according to the reproduction period $T=4$ occurs (Fig. 8). In technical terms, the system displays a limit cycle, which is obtained from arbitrary initial state. We remark that for the size distribution a similar cyclic behaviour was found.

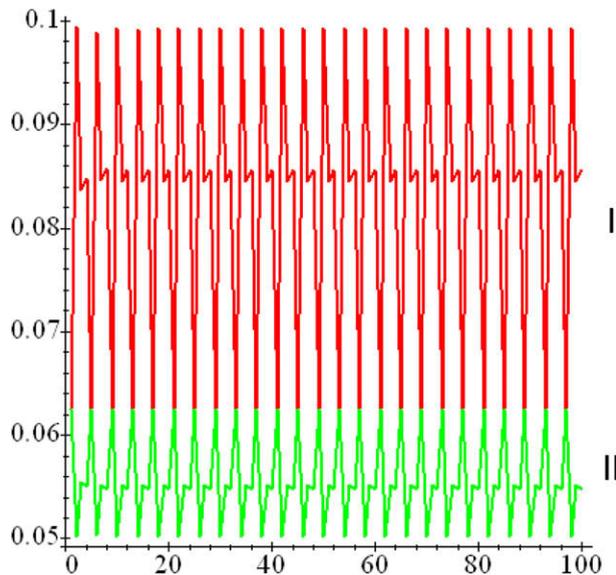


Fig. 8. Cyclic behaviour of the genetic distribution for two genotype classes.

4.1.1. The case of limited growth

Suppose that because of intraspecific competition we have density-dependent rates of type (2), setting rates a_{kl}^n and b_{kl}^n as in the previous section, and $K := 0,000002$.

The simulation shows that not only the vector sequence of proportions but that containing the absolute numbers of individuals of the different genotypes also will converge in the cyclical sense.

4.2. Moderate harvesting

Suppose now that the population is harvested with the fishing effort system. The smaller size classes are not harvested, while the fishing intensities of the large classes are not “too great”. The intensity vector may be e.g.

$$h = [0, 0, 0, 0, 0.2, 0.2, 0.2].$$

We obtained, that the sequence of the proportion vectors converges cyclically to the same limit vectors as in the case of unharvested population. This means harvesting does not seem to influence the genetic distribution of the population.

4.3. Intensive fishing

In this section the sustainability of fishing is studied. Leaving all biological parameters unchanged and varying the intensity vector h , the following limit densities of zygote (1,4) (considering time moments $4t+1$) are obtained:

h	$\lim_{t \rightarrow \infty} \sum_n x_{14}^n(4t+1)$
(0, 0, 0, 0, 0, 0, 0) (no fishing)	102255
(0, 0, 0, .7, .7, .7, .7)	8454
(0, 0, 0, .8, .8, .8, .8)	0
(0, 0, 0, .75, 0, 0, 0)	24854
(0, 0, 0, .75, 1, 1, 1)	2369
(0, 0, 0, .9, 0, 0, 0)	6262
(0, 0, 0, .9, .3, .3, .3)	0
(0, 0, 0, .95, 0, 0, 0)	0
(0, 0, .9, 0, 0, 0, 0)	0

One can conclude that the limit density is a decreasing function of the fishing intensity. The population dies out, if it is harvested above a certain intensity. (The fishing is not sustainable.) The most important observation is that sustainability is sensitive only to the harvesting of the *medium size classes*. Large-sized individuals can be harvested with arbitrary intensity.

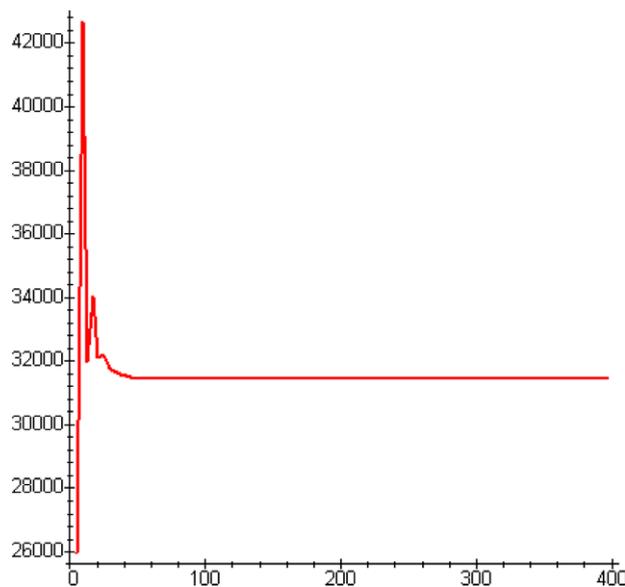


Fig. 9. Density of type (1,4) at time moments $4t+1$, with $\lambda = 0,0003$.

4.4. The bottle-neck effect

The impact of the bottle-neck effect is also studied in the case when genotype (1,4) is “the best”. We set the parameters as in Section 4.1, and run the model with different λ values. The following graphs show the density of the genotype (1,4) at time moments $4t+1$, with bottle-neck effects of different degrees.

Fig. 9 shows the case when the bottle-neck effect is not substantial, the population is sustained. The population, however, dies out at a strong bottle-neck effect. Equivalently, it dies out, if it decreases below a critical density (Fig. 10).

If there is fishing, we have two possibilities according to the intensity. With moderate fishing effort all the genotypes coexist, though at a reduced density. Intensive fishing can destroy fish population. Both cases could be illustrated by figures similar to Fig.9 and Fig. 10, respectively.

Summarizing the above results, in the case of heterosis (when the total heterozygote is the “best”), fishing modifies the total density of the population, but does not affect its genotypic composition on long term.

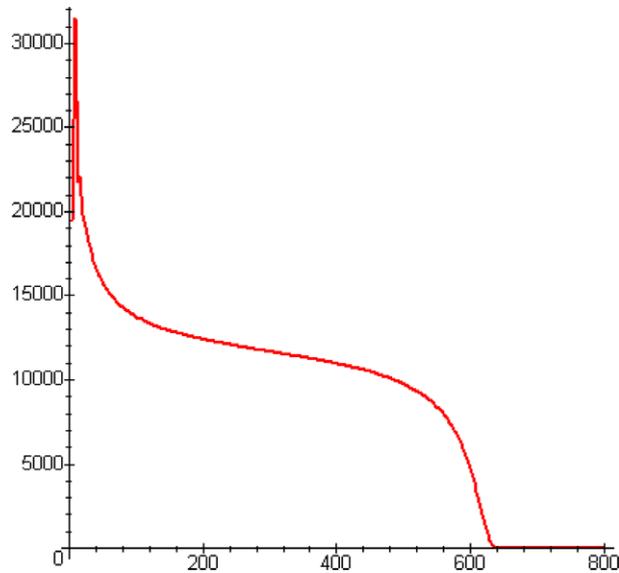


Fig. 10. Density of type (1,4) at time moments $4t+1$, with $\lambda = 0,0002$.

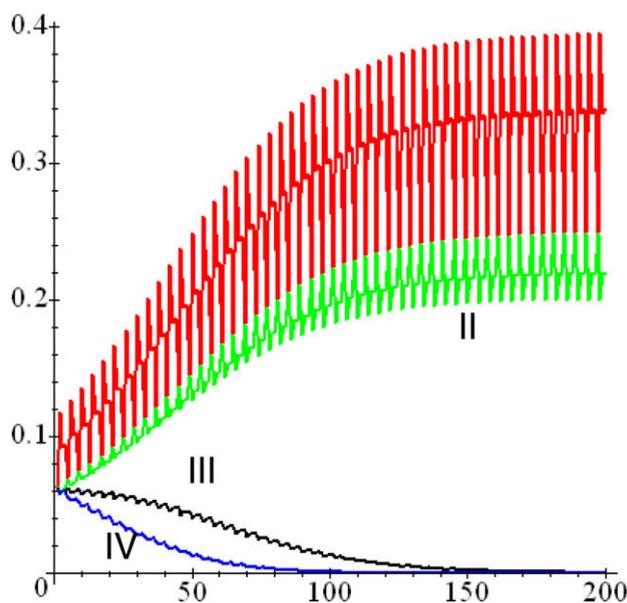


Fig. 11. Complex behaviour for the “semi-mixed” genotype (1,2).

5. The heterozygote (1,2) is “the best”

Finally, let us assign dominance to the so-called “semi-mixed” (1,2)-type zygote by setting parameters similarly as in (10). From the dynamical aspect, genotypes are classified as follows:

Number	Zygotes
I	(1,2)
II	(1,1), (2,1), (2,2)
III	(1,3), (1,4), (2,3), (2,4), (3,1), (3,2), (4,1), (4,2)
IV	(3,3), (3,4), (4,3), (4,4)

The long-term dynamics is shown in Fig. 11. This behaviour reflects the features of both of the (1,1) homozygote and the (1,4) heterozygote case. Namely, there are two classes of dominant types, whose proportions are cyclically convergent, while the other types die out.

We also studied this case with fishing and we obtained the same long term results as shown in Fig. 11.

6. Conclusions

Even in the case of the simplest dynamic model the analytical study of the long-term effect of harvesting on the genetic composition of a population faces technical difficulties. However, simulation methods provide well-interpretable predictions on the asymptotic behaviour of the population and the selection effect of the widely applied fishing effort model. In fact, for the different biological situations (without harvesting) we can conclude the following:

1. If the totally homozygous genotype dominates, the other types gradually die out.
2. If the totally heterozygous genotype dominates, then the limit densities are different for the saturation model, but the limit genotype distribution remains unchanged (cyclic behaviour).
3. If a partially heterozygous genotype performs best, then the combination of the above two phenomena takes place at the same time, i.e. “bad” genotypes die out, the other genotypes display cyclic behaviour.
4. Fishing modifies the genetical distribution as well as the phenotypic properties in the long term, provided that the (1,1) homozygote is “dwarfish”.
5. If the totally heterozygous genotype is the “best one”, then moderate harvesting does not seem to influence the genetic distribution of the population. An intuitive explanation to this fact may be that the best genotypes have all possible alleles and high fitness, thus, according to panmixy, they continuously reproduce all possible genotypes. However, the population cannot be sustained, if medium size classes are intensively harvested.
6. If the bottle-neck effect is included in the model, the population dies out provided that it decreases below a critical density.

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