International Environmental Modelling and Software Society (iEMSs)
2012 International Congress on Environmental Modelling and Software
Managing Resources of a Limited Planet, Sixth Biennial Meeting, Leipzig, Germany
R. Seppelt, A.A. Voinov, S. Lange, D. Bankamp (Eds.)
http://www.iemss.org/society/index.php/iemss-2012-proceedings

Dynamics of Genetic Structure of Population with Age Structure during Optimal Harvest with Constant Quota

Oksana Zhdanova[1] and Efim Frisman[2]

[1]*Institute of Automation and Control Processes FEB RAS, Laboratory of Mathematical Modelling of Ecological Sistems, Vladivostok, Russia*
[1]*axanka@iacp.dvo.ru*
[2]*Institute of Complex Analysis of Regional Problems, Birobidzhan, Russia*
[2]*frisman@mail.ru*

Abstract: Ecological and genetic consequences of optimal equilibrium harvest with constant quota in uniform and two-aged populations have been considered in this work. It has been shown analytically that maximum of equilibrium harvest income is unreachable when both age groups are harvested simultaneously. The optimal strategy of harvest is the catch of fixed portion from single age group. In addition, optimal harvest may result not only in a change in the dynamic mode of the system, but also in a considerable change in the genetic composition of the population.

Keywords*:* optimal harvest; structured population; evolution; genetic structure dynamics.

1 INTRODUCTION

1.1 Modelling of evolution in exploited population

Dynamical theory of populations is traditionally considered as an adjacent section of theoretical population ecology and of populations' biophysics (for example, in [Bazykin 1985, Vol'kenshtein 1988, Romanovskij et al. 2004]). The main problem, which is formed around a dynamic theory, - the description of the nature and explanation of the mechanisms of fluctuating (quasi-periodic and chaotic) behaviour of populations. This problem borders is related to an important applied problem, namely, the development of an optimal strategy for exploitation of commercial species (optimization of harvesting). It is clear from the very essence of these problems that theoretical population ecology studies the dynamics of limited populations developing under the conditions of limited resources of vital activity.
Since the 30s of the XXth century, another branch of the population dynamic theory - the mathematical population genetics is rapidly developing. A Number of models of evolutionary change of populations' genetic structure are constructed and studied. Features of population dynamics in this case are usually not analyzed. The number was considered either "enough" large (in fact, infinitely, in deterministic models) or unchanged (the models used to analyze the effects of genetic drift).
The combining of population-ecological and population-genetic approaches has highlighted two types of problems that may be considered under this theory.
First, there was a natural development of the study of evolutionary factors (in the first place, natural selection) to change the genetic structure and the behavior of population dynamics living in conditions of limited environmental resources. The development of these ideas were received in many studies, and formulated in the form of the conception of K and r-selection (for example, in [Rougharden 1971, Charlesworth 1971, Evdokimov 1999]).

The second one is necessity of analyses of harvest consequences. The conception of maximal equilibrated catch asserts that harvested populations are not in the same ecological conditions as non-harvested ones. So the conditions of selection and hence fitnesses of genotypic groups can changes in harvested populations.
Nearly catastrophic reduction of the effective population size and loss of genetic diversity resulting from human impact is reported in a large series of modern research. And these negative trends for the species are observed not only in the exploited populations (for example, changing the genetic structure of rock-forming trees in the regeneration of forests after harvesting [Norton 1996, Lee et al. 2002, Finkeldey and Ziehe 2004], and of fish species [Hindar et al. 2004]. But even in populations that do not harvested directly, but rather are influenced by anthropogenic impacts due to the fragmentation and reduction of habitat (eg, genetic changes in populations of salamanders, mentioned by Curtis and Taylor [2004]). The final decision of the question, what happens with the adaptive variability due to human impact, it is not obvious, and also attracted the interest of researchers.
The aim of this study is revealing of some non-obvious consequences of optimal harvest by mathematical modeling. We consider the simple model situations, when exploited population is uniform or it has two age groups.

2 THE EVOLUTIONARY MODEL OF HOMOGENOUS EXPLOITED POPULATION

The simplest model case where mechanisms of interconnected changes in genetic structure and in population size induced by interaction of ecological (that limit the population size growth) and evolutionary (generally selective) factors become apparent is considered by Frisman et al. [2010].
The model of homogenous Mendelian diploid organisms' population dynamics is investigated. The genetic variety is controlled by single diallelic locus (with *A* and *a* alleles):

$$\begin{cases} x_{n+1} = \overline{W}_n(x_n)x_n \\ q_{n+1} = q_n\left(W_{AA}(x_n)q_n + W_{Aa}(x_n)(1-q_n)\right)/\overline{W}_n(x_n), \end{cases} \qquad (1)$$

where x_n is the population number in *n*-th generation, q_n - is the frequency of allele A in n-th generation, $\overline{W}_n = W_{AA}(x_n)q_n^2 + 2W_{Aa}(x_n)q_n(1-q_n) + W_{aa}(x_n)(1-q_n)^2$ is the average fitness of the population in *n*-th generation.
Ecological limitation is implemented by genotypes fitnesses (W_{ij}) decreasing dependence from population size:

$$W_{ij} = \exp\left(R_{ij}\left(1-\frac{x_n}{K_{ij}}\right)\right) \text{ or } W_{ij} = 1 + R_{ij} - \frac{R_{ij}}{K_{ij}}x, \qquad (2)$$

where R_{ij} and K_{ij} is the Malthusian and resort parameter of ij-genotype respectively.

The influence of harvest includes the removal of constant portion from population size each generation:

$$\begin{cases} x_{n+1} = x_n\overline{W}_n(1-u) \\ q_{n+1} = q_n\left(W_{AA}q_n + W_{Aa}(1-q_n)\right)/\overline{W}_n, \end{cases} \qquad (3)$$

Where *u* is the the proportion of catch from population number. So value of removal ("yield") in the *n*-th generation is $R = x_nW_nu$.

If removal fraction from population is sufficiently small, then there is a small yield and harvesting does not significantly affect the dynamics of the population.

Increased percentage of catch reduces the population size. At the initial stage it is accompanied by corresponding increase in the yield, and possibly stabilization of the population dynamics. A further increase in the proportion withdrawal such reduces the population number that the volume of yield falls. So, it is necessary to determine that level of harvesting from population in which the mode of its exploitation would be optimal. By now a concept has formed in which the optimum harvesting [Skaletskaya et al. 1979, Abakumov 1993, Srinivasu and Ismail 2001, Braumann 2002, etc.] refers to a fraction of catch from the population, which provides a stable equilibrium level of the maximum commercial "yield", provided non-extinction population. Present model illustrates the effect of optimal harvesting on the genetic structure of population.

The results of the analytical study of the model of an exploited population (3) show that harvesting with an optimal catch proportion may change the type of stability of equilibrium states as compared to the stability of similar equilibriums of free (unexploited) population; i.e., it may result not only in a change in the dynamic mode of the system, but also in a considerable change in the genetic composition of the population. In one case (at small reproduction potentials), the optimal harvesting only decreases the population size and does not change its dynamic mode or genetic composition, whereas in other cases (when the genotypes have high reproduction potentials), the consequences of harvesting may be quite unexpected, and not only the withdrawal proportion, but also initial parameters of the population may be the key factors. Let us illustrate the above considerations by some examples of numerical modeling.

On Figure 1 one can see an example of polymorphic population that may completely loose genetic diversity as a result of optimal harvesting, and its size and genetic composition are stabilized. In this example, the monomorphic equilibrium $q = 0$, $x = 0.84$ with a stable harvest $R = 7.61$ is achieved at the maximum of the three possible catch proportions ($u_{AA} = 0.863$, $u_{Aa} = 0.862$, and $u_{AA} = 0.900$), and the allele *A* is replaced by, approximately, the 210-th generation. The exploitation of the population with a smaller intensity ($u_{AA} = 0.863$ or $u_{Aa} = 0.862$) helps to maintain the genetic diversity and even increase a little the harvest, $R = 7.63$; in this case, the polymorphic equilibrium $q = 0.896$, $x = 1.22$ is achieved.

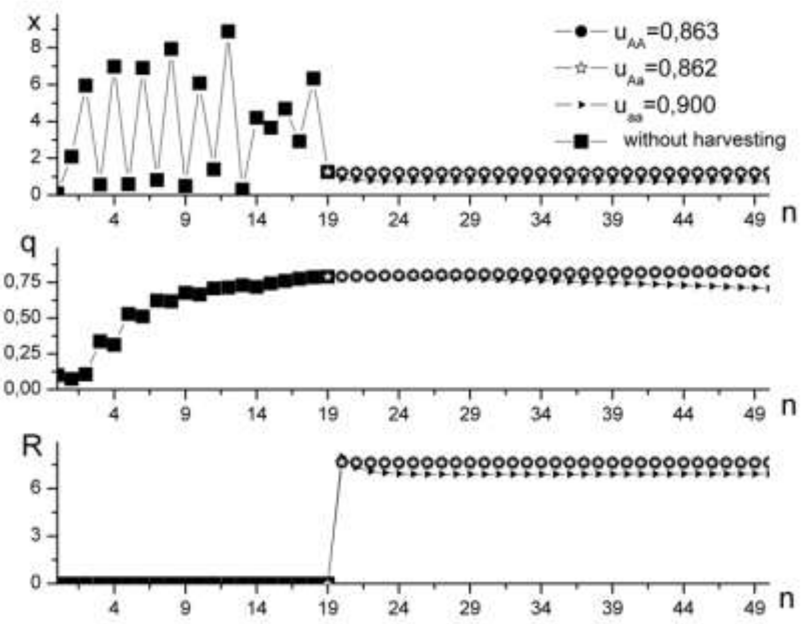

Figure 1. The dynamics of the population size (*x*), allele *A* frequency (*q*), and catch rate (*R*) at constant proportions corresponding to the polymorphic and two monomorphic stationary states. Exploitation begins after the 19-th generation of free development. Chaotic dynamics of the population size and genetic composition are typical for the situation in the absence of harvesting.

Figure 2 shows an example of the dynamics of a population that looses genetic diversity in the case when it is not exploited; depending on the initial conditions, only one monomorphic equilibrium is achieved: q = 1 (Figure 2a) or q = 0 (Figure 2b). Exploitation of this population with the highest optimal intensity (u_{Aa} = 0.991) maintains the genetic diversity: a stable polymorphic equilibrium q = 0.498, x = 0.31 and maximum equilibrium harvest R = 34.81 are achieved. Selection of the minimum optimal catch (u_{AA} = 0.433) results in the elimination of one of alleles and stabilization of yield at a level of R = 1.48 (for monomorphism *aa*) or R = 1.65 (for monomorphism *AA*). Exploitation of the population with an intensity of u_{aa} = 0.623 destabilizes the dynamics of the size, genetic composition and, as a consequence, yield from harvesting. In this case, polymorphism is maintained and the average harvest achieves R = 5.29.

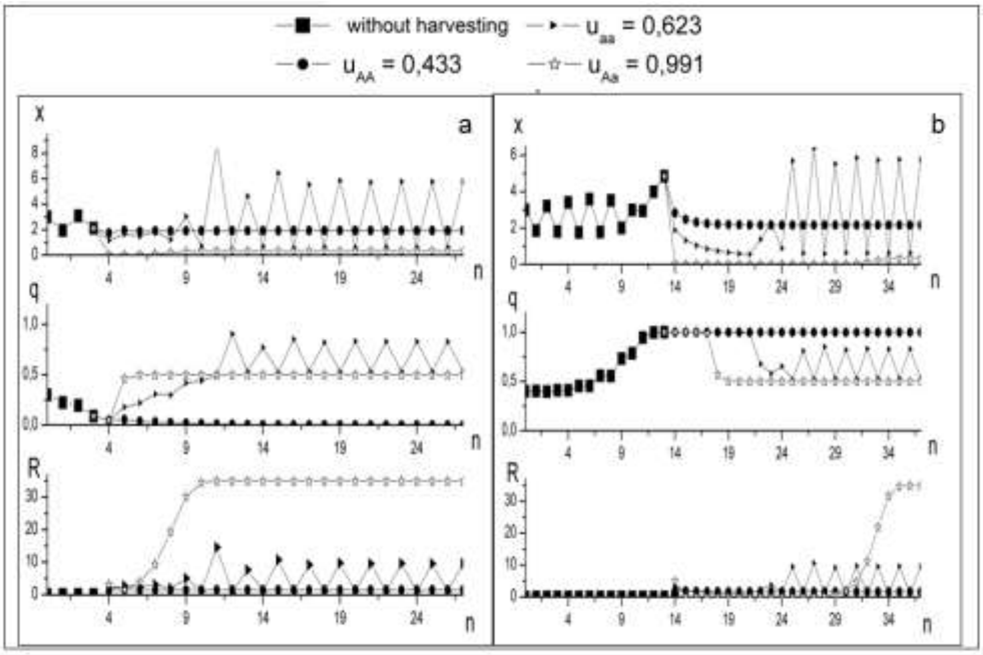

Figure 2. A population approaching monomorphic equilibrium in the absence of harvesting. Cases (a) and (b) differ only in the frequency of allele *A* at the initial state (q_0): (a) q_0 = 0.4, an unexploited population achieves the monomorphic equilibrium {q = 1, x = 5}; exploitation begins after the 13-th generation, when the population parameters almost achieve the stationary level; q_{13} = 0.99999, x_{13} = 4.85; (b) q_0 = 0.3, the monomorphic equilibrium {q = 0, x = 3} is achieved in the absence of harvesting; in this case, exploitation begins after the 3-rd generation: q_3 = 0.088, x_3 = 2.11.

It has been shown that whereas in unexploited population the optimization of its genetic structure flows in accordance with resource parameter; namely the genotypes giving greater equilibrium population size in conditions of limited vital resources have advantage; and in exploited population the rate of its growth is optimized and those genotypes which give greater progeny size (i.e. which having greater reproductive potential) became the most adapted ones and factor of vital resources limitations draws back.

3 THE EVOLUTIONARY MODEL OF EXPLOITED TWO-AGED POPULATION

Previous population dynamic model considers changes of whole population number only, assuming that different generations of the population do not overlap. However, such conception is incorrect, when the lifetime of each generation is essentially longer than the time between breeding seasons. In this case, each local population consists of individuals from different age groups during the breeding season.

Therefore, the number of each separated age group is naturally considered as the model's variable. The treatment for clustering the population is defined by the characteristics of biological species.
The model with age structure is considered. This model may be presented by the set of two age classes: junior and elder. The junior age class consists of immature individuals, and the reproductive part consists of individuals participating in the breeding process.
Let x_n be the number of individuals in the junior age class in n-th breeding season and y_n be the number of individuals in the reproductive part of the population. The breeding season ends by the appearance of newborn individuals in the next generation. During the time between two reproductive periods, the individuals from the junior age class are assumed to reach the age of reproductive part, whereas newborns (or larvae) are assumed to reach the junior age class. Moreover, fitness and the reproductive potential of reproductive individuals are assumed to be independent of their ages. These assumptions are correct for organisms with not great lifetime consisting of two or three breeding periods, such as insects, fishes, small mammals, biennials or triennials, and others.
The mechanism for the regular evolutionary complication of the dynamics of a structured population is illustrated by considering the effect of natural selection in one of the simplest model situations, when the adaptive character *a* is encoded by one diallelic locus. The following dynamic equations relate the sizes of the age classes to their genetic structure in neighboring generations [Frisman and Zhdanova 2009]:

$$\begin{cases} x_{n+1} = \overline{w}_n y_n \\ y_{n+1} = x_n f(x_n) + c y_n \\ q_{n+1} = \dfrac{p_n (W_{AA} p_n + W_{Aa}(1-p_n))}{\overline{w}_n} \\ p_{n+1} = \dfrac{x_n f(x_n) q_n + c y_n p_n}{x_n f(x_n) + c y_n} \end{cases}, \qquad (4)$$

where p_n is the allele *A* frequency in the reproductive part of the population, q_n is the allele *A* frequency in the immature part of the population, and $\overline{w}_n = W_{AA} p_n^2 + 2W_{Aa} p_n (1-p_n) + W_{aa}(1-p_n)^2$ is the reproductive potential (or the average fitness of embryos).
It is usually assumed that limitation of junior age class's number is realized by linear ($f(x) = 1 - x$) or exponential ($f(x) = e^{-x}$) rule.
Let some portion is removed from population one-time before reproduction period; catch portion from reproductive part of population is u_1 and those from immature part is u_2. Then sizes of age groups and population genetic structure will be following to the next reproduction period:

$$\begin{cases} x_{n+1} = \overline{w}_n y_n (1-u_1) \\ y_{n+1} = x_n (1-u_2) f(x_n(1-u_2)) + c y_n (1-u_1) \\ q_{n+1} = \dfrac{p_n (W_{AA} p_n + W_{Aa}(1-p_n))}{\overline{w}_n} \\ p_{n+1} = \dfrac{x_n(1-u_2) f(x_n(1-u_2)) q_n + c y_n (1-u_1) p_n}{x_n(1-u_2) f(x_n(1-u_2)) + c y_n (1-u_1)} \end{cases} \qquad (5)$$

Income from harvest is:

$$R(u_1, u_2) = c_1 u_1 y_n + c_2 u_2 x_n, \qquad (6)$$

where c_1 is cost of reproductive age individual, c_2 is cost of immature age individual.

Aside from the trivial stationary point (x = 0, y = 0), model (5) has two monomorphic stationary points: {p = 0, q = 0} and {p = 1, q = 1} and a polymorphic one {p = q = (w_{Aa} - w_{aa})/(2w_{Aa} - w_{aa} - w_{AA})}.
All non-trivial models' equilibriums and income function for each of the equilibriums were found for linear and exponential limitation of immature group size.
Then investigating of income function extremums was conducted for each of equilibriums. It has been shown analytically that maximum of equilibrium harvest income is unreachable inside the region $\{0 \le u_1 \le 1, 0 \le u_2 \le 1\}$. So further search of maximum values of income function from harvest for each equilibriums was conducted on the region boundaries $\{u_1 = 0, u_2 = 1\}$ and $\{u_2 = 0, u_1 = 1\}$. The local maximum of income function is reachable for each boundary.

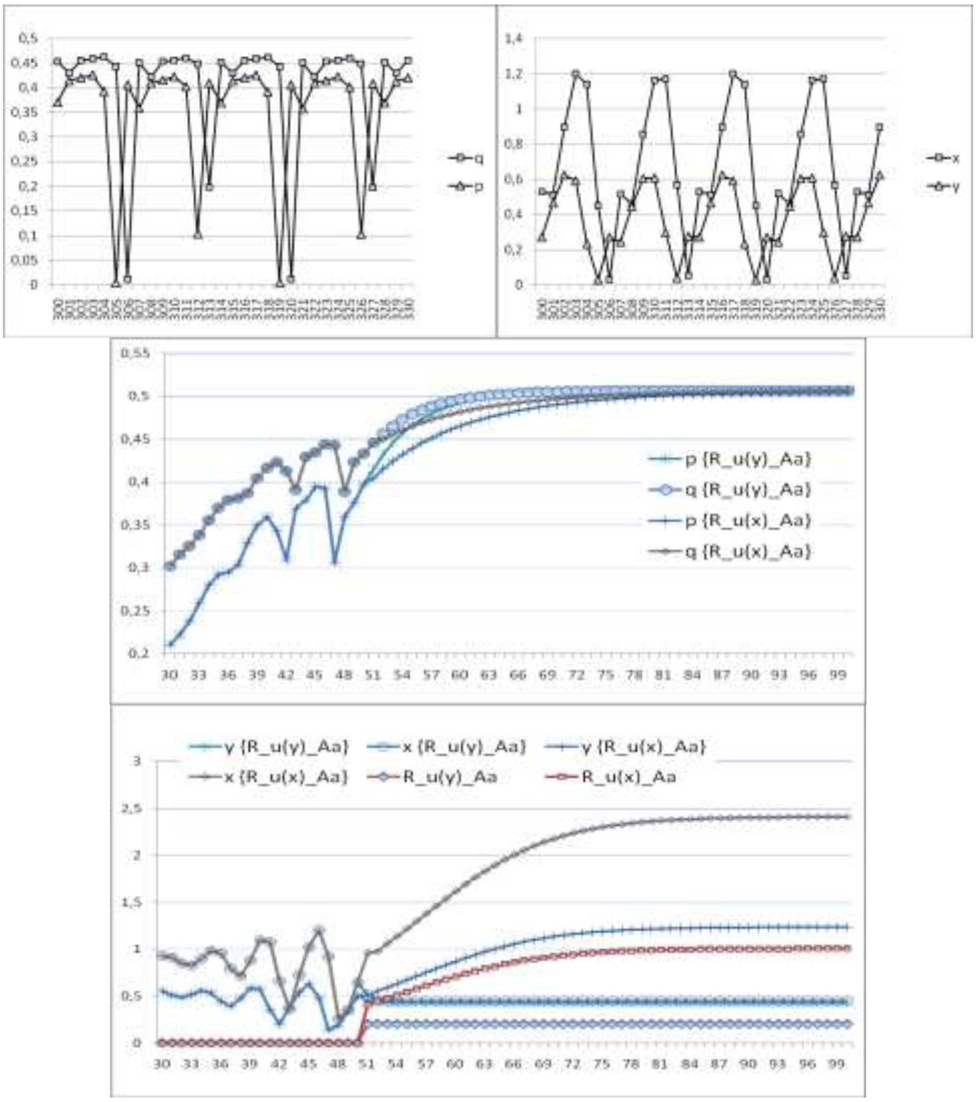

Figure 3. In the top row the dynamics of genetic structure (p and q) and groups' numbers (y and x) for non-exploited population. On the following charts the stabilization of genetics structure and groups numbers dynamics due to optimal harvest. Also the bottom chart illustrates income from harvest of reproductive group (*R_u(y)_Aa*) and immature part (*R_u(x)_Aa*), provided equal cost of individuals from two age groups ($c_1 = c_2$). Exploitation begins after the 50-th generation, when the population dynamics is markedly fluctuating. Population parameters are: c = 0.8, W_{AA} = 1.1, W_{Aa} = 2.8234, W_{aa} = 1.05.

In general case when all three non-trivial equilibriums exist in the model there are six different catch portions ensuring the local maximum of income function. Therefore the comparison of local maximums of income function for each of

equilibriums on each boundary was made for the purpose to define what kind of catch from which age group and equilibrium type is most profitable.
In all considered cases optimal harvest stabilizes the dynamics of age-group numbers and genetic structure. Figure 3 illustrates this stabilization. The harvest in polymorphic equilibrium only is illustrated to avoid the charts overflow; this catch volume is most profitable in presented case. Depending on the costs ratio on reproductive and immature individuals the harvested part of population will be determined: it may be immature (*R_u(x)_Aa*) or reproductive individuals (*R_u(y)_Aa)*.

It appears that there is set of population parameters values with which maximum income is reached for immature and reproductive part in different genetic types of equilibrium (Figure 4).

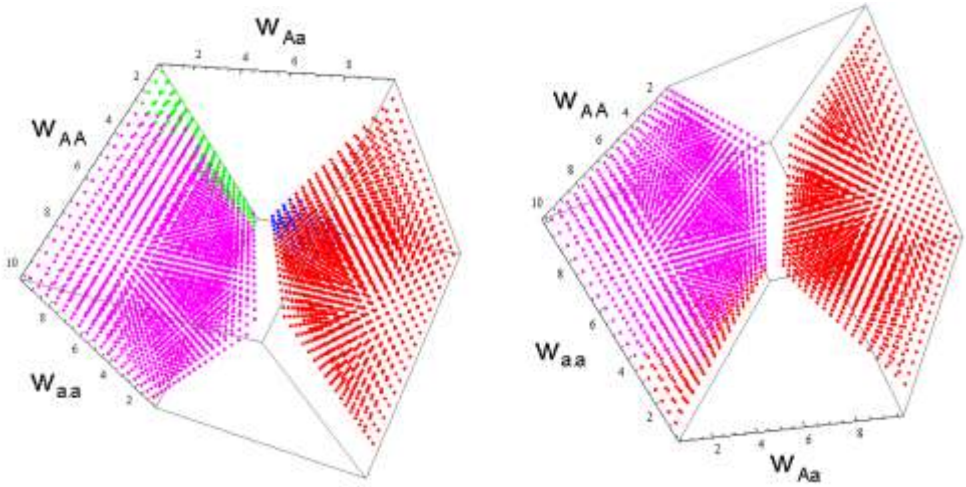

Figure 4. Comparison of income from harvest in various equilibriums and population age-groups. The situations when income from population reproductive part harvest is the greatest, and type of equilibrium with optimal income of harvest from reproductive part is the same as those from immature part are marked by blue points. If types of optimal equilibriums are not the same then points are green. The situations when income from immature part harvest is the greatest and types of optimal equilibriums from both parts of population are the same are marked by red points. If types of optimal equilibriums are not the same then points are pink. At the left figure c = 0.4, c_1/c_2 = 5; at the right figure c = 0.6, c_1/c_2 = 1.3.

4 CONCLUSIONS

The conducted research for uniform population shows that harvesting with an optimal catch proportion may change the type of stability of equilibrium states as compared to the stability of similar equilibriums of free (unexploited) population; i.e., it may result not only in a change in the dynamic mode of the system, but also in a considerable change in the genetic composition of the population. It has been shown that whereas in unexploited population the optimization of its genetic structure flows in accordance with resource parameter; namely the genotypes giving greater equilibrium population size in conditions of limited vital resources have advantage. In exploited population the rate of its growth is optimized and those genotypes which give greater progeny size (i.e. which having greater reproductive potential) became the most adapted ones and factor of vital resources limitations draws back.
The questing about optimal strategy of harvesting arises when age structured population is exploited. Namely, whether should to catch from single age group or from several? This study shows that optimal strategy of harvest is the catch of fixed portion from single age group.

ACKNOWLEDGMENTS

The present work was supported by the Russian Foundation for Basic Research (project 11-01-98512) and the Far Eastern Branch of Russian Academy of Sciences in the framework of Program 28 of Presidium of RAS (project FEB RAS 12-I-P28-02, 12-II-CO-06-019, 12-I-P15-02)

REFERENCES

Abakumov, A.I., *Control and Optimization in Models of Experimental Populations*, Dal'nauka, 129 pp., Vladivostok, 1993.

Bazykin, A.D., *Mathematical biophysics of interconnecting populations*, Nauka, 181 pp., Moskow, 1985.

Braumann, C.A., Variable effort harvesting models in random environments: generalization to density-dependent noise intensities, *Mathematical Biosciences* 177-178, 229-245, 2002.

Charlesworth, B., Selection in density-regulated populations, *Ecology,* 52, 469-474, 1971.

Chernavskij, D.S., *Synergetics and information (dynamic theory of information)*, Editorial URSS, 288 pp., Minsk, 2004.

Curtis, J.M.R., and E.B. Taylor, The genetic structure of coastal giant salamanders (Dicamptodon tenebrosus) in a managed forest, *Biological Conservation,* 115(1), 45-54, 2004.

Evdokimov, E.V., Problems of Regular Behavior and Determined Chaos in the Basic Models of Population Dynamics: Theory and Experiment, Extended Abstract of Doctoral (Biol.) Dissertation, Krasnoyarsk, 1999.

Finkeldey, R., and M. Ziehe, Genetic implications of silvicultural regimes, *Forest Ecology and Management,* 197(1-3), 231-244, 2004.

Fjodorov, V.D., and T.G. Gil'manov, *Ecology,* MGU, 464 pp., Moskow, 1980.

Frisman, E.Ya., and O.L. Zhdanova, Evolutionary transition to complex population dynamic patterns in a two-age population, *Russian Journal of Genetics,* 45(9), 1124–1133, 2009.

Frisman, E.Ya., O.L. Zhdanova, and E.A. Kolbina, Effect of harvesting on the genetic diversity and dynamic behavior of a limited Mendelian population, *Russian Journal of Genetics,* 46(2), 239 – 248, 2010.

Hindar, K., J. Tufto, L.M. Sættem, and T. Balstad, Conservation of genetic variation in harvested salmon populations, *ICES Journal of Marine Science,* 61(8), 1389-1397, 2004.

Lee, C.T., R. Wickneswari, M.C. Mahani, and A.H. Zakri, Effect of selective logging on the genetic diversity of Scaphium macropodum, *Biological Conservation,* 104(1), 107-118, 2002.

Norton, T.W., Conserving biological diversity in Australia's temperate eucalypt forests, *Forest Ecology and Management,* 85(1-3), 21-33, 1996.

Romanovskij, Yu.M., N.V. Stepanova, and D.S. Chernavskij, *Mathematical modeling in biophysics. Introduction in theoretical biophysics,* Institute of computer investigations, 471 pp., Izhevsk, 2004.

Rougharden, J., Density dependent natural selection, *Ecology,* 52, 453-468, 1971.

Skaletskaya, E.I., E.Ya. Frisman, and A.P. Shapiro, *Discrete Models of Population Dynamics and Optimization of Exploitation*, Nauka, 166 pp., Moscow, 1979.

Srinivasu, P.D.N., and S. Ismail, Global dynamics and controllability of a harvested prey-predator system, *Journal of Biological Systems,* 9(1), 67-79, 2001.

Vol'kenshtein, M.V., *Biophysics*, Nauka, 592 pp., Moskow, 1988.