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Mathematical modeling of the evolutionary dynamics of plankton community

The paper proposes and studies a model of the evolutionary dynamics of plankton community. Phytoplankton is assumed to consist of two genetic groups competing for resources and differing by the trait of toxicity. Zooplankton consumes non-toxic phytoplankton due to its selective choice of food. The evolutionary scenario of the development of two different phytoplankton genotypes is shown to depend significantly on competitive intensity between them.

Key words: *prey — predator community, competition, Holling type II function, evolution, dynamics modes.*

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1 Introduction and statement

Evolution may be a key cause in the emergence of population cycles in prey-predator systems that include planktonic communities as a prominent example. The cycle phase between interacting species is shown to be an indicator of eco-evolutionary dynamics [1]. In non-evolutionary cases, predator-prey cycles run counter-clockwise on the phase plane, and prey peaks precede those of the predator. In turn, the dependence of the dynamics on evolutionary processes often generates a reverse or clockwise cycle where the peak in the population number (or density) of the consumer precedes that of the resource. In particular, experiments with algae populations showed that their dynamics were in antiphase to their consumer, while interspecific cycles were clockwise with the algal defense mechanisms evolved dropping their competitiveness [2]. Such a phenomenon, referred to as the reverse cycle, occurs in about half of the time series of protozoa dynamics that make up the resource-consumer system [3]. Note that although not all clockwise cycles are driven by evolution [3], evolution can be a definite cause of cyclical behavior in natural systems, especially for organisms with short generation times that have the potential for rapid evolution [1], which is typical for many phytoplankton species.

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To study the evolution in the plankton community, we propose a discrete-time model of the phytoplankton and zooplankton dynamics. The reason for applying such models to phytoplankton dynamics analysis is the day-night rhythm. Indeed, many processes occurring in the phytoplankton community are consistent with a circadian rhythm that is cyclic fluctuations in the intensity of various biological processes due to the alternation of day and night. To describe the dynamics of genetically different groups (phenotypes) of phytoplankton, we use the Ricker competition model with two components taking into account both interspecific competition of interacting species and their intraspecific competition in form of self-limitation [4]. In addition, the Ricker model quite well describes the change in the biomass/abundance of phytoplankton that occurs due to cell division. The phytoplankton defense from zooplankton impact decreasing consumption of toxic phytoplankton by zooplankton is considered by the proposed evolutionary model to be an adaptive trait. Accordingly, phytoplankton consists of two genetically different groups (phenotypes): toxic and non-toxic ones. Note that the change in toxicity depends on the interaction between phytoplankton and consuming it by zooplankton. Phytoplankton release toxic chemicals when they sense the presence of a zooplankton population around them. In response, zooplankton reduces predation rates due to the adverse effects of the chemicals on the zooplankton population. Such an impact decreases phytoplankton consumption (demonstrating its selectivity in the choice of food or stopping the consumption of phytoplankton-producing toxins), egg production, and zooplankton survival. In this context, “stopping consumption by zooplankton” or low consumption of a toxic phenotype practically does not affect the densities of phytoplankton and zooplankton, just leads to the fixation of a phenotype with toxicity, the evolution and development of which are largely determined by self-regulation and competition for resources with the second non-toxic phenotype. It is natural to assume that in the group of non-toxic phenotypes during cell division, mutations arise and increase the protective mechanisms by toxicity. However, in this model, we do not consider mutational processes since they are very slow, and their influence during short times is not significant. In turn, the evolution and development of the second phytoplankton genotype are determined by trophic interactions with zooplankton. To describe the feeding process of zooplankton, we use the Holling type II function taking into account the predator saturation. Thus, the ecological-genetic model describing the evolutionary dynamics of such a system has the following form:

$$\begin{cases} x_a(n+1) = B_a x_a(n) \exp(-g_a x_a(n) - d_A x_A(n)(1-u(n))), \\ x_A(n+1) = B_A x_A(n)(1-u(n)) \exp(-d_a x_a(n) - g_A x_A(n)(1-u(n))), \\ y(n+1) = \alpha_0^{-1} w \cdot x_A(n) \cdot u(n) \exp(-\gamma \cdot y(n)), \end{cases} \quad (1)$$

where x_a is the density of the first genotypic group of phytoplankton with toxicity trait, x_A is the density of the second genotypic group without toxicity trait. The day number is denoted by n , parameters B_a and B_A characterize birth rates of phenotypes x_a and x_A , accordingly; g_a and g_A are selflimitation coefficients, d_a and d_A characterize competitiveness intensity phenotypes x_a and x_A , accordingly; $u(n) = \alpha_0 \cdot y(n)/(X_A^* + x_A(n))$ denotes the share of non-toxic phytoplankton consumed by zooplankton ($u(n) < 1$), α_0 is the biomass conversion coefficient ($\alpha_0 \gg 1$), X_A^* is the half saturation constant, y is the zooplankton density, γ is its self-limitation coefficient, w is the maximal value of the zooplankton reproductive potential.

2 Results and discussion

Model (1) has six fixed points. Trivial one corresponds to the community extinction. Four solutions are semi-trivial, two of them describe the free existence of one of the phytoplankton genotype groups without its competitor and predator; the other two are the coexistence of two competing genotypic groups of phytoplankton or the coexistence of a non-toxic phenotype of phytoplankton with zooplankton. The sixth fixed point is non-trivial and corresponds to the complete community existence. We have analytically and numerically studied model (1). The local stability of system (1) fixed points has been analyzed using its Jacobian. Next, we have considered the semi-trivial fixed point, which is two competing genotype coexistence, and non-trivial solution; because they are the most meaningful from the evolution point of view. Moreover, comparison of their stability loss scenarios allows us to analyze the zooplankton influence on the phytoplankton evolution taking into account trophic relationships.

We use dynamic mode maps to study changes in dynamics of two competing phytoplankton genotypes without zooplankton with different parameter values (see fig. 1). Figure 1 shows all features of the analytical study of model (1) at $y = 0$ or $\alpha_0 = 0$.

With $\rho_A \rho_a < 1$, the system (1) at $\alpha_0 = 0$ has 4 fixed points, which are separated from each other by transcritical bifurcation lines, the transition through which is accompanied by an exchange of stability between neighboring solutions. The stability loss of the fixed points corresponding to one of genotypes elimination or their coexistence occurs via a period-doubling scenario when a cascade of period-doubling bifurcations complicates the dynamics from the emerging 2-cycle to chaos. A lower $\rho_A \rho_a$ value expands the area with two competing genotypes' coexistence. However, at small values of $\rho_A \rho_a$, in the irregular dynamics region, there is a stable 2-cycle domain that wedges into the area of

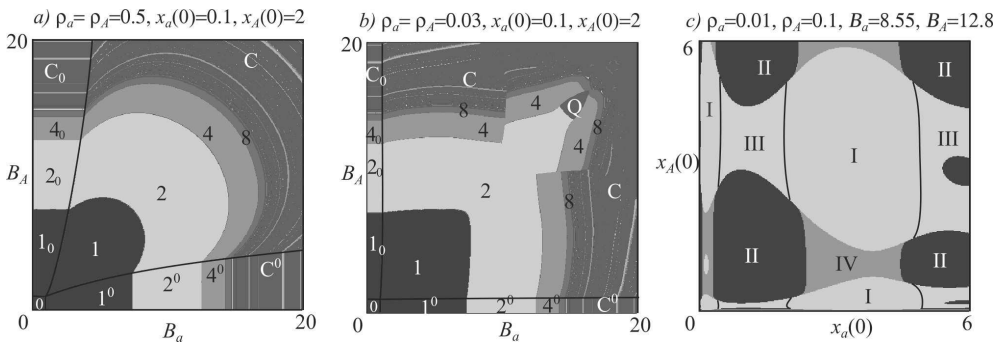


Fig. 1: a, b) Dynamic mode maps of model (1) for different values of parameters $\rho_A = d_A/g_A$ and $\rho_a = d_a/g_a$. Figures are the period of observed cycles; Q and C are quasiperiodic and chaotic dynamics, respectively; 0 stands for the extinction of both genotypes. The subscript and superscript 0 correspond to the elimination of x_a and x_A genotypes, respectively. c) Attraction basins of two antiphase 2-cycles (I and III) and asynchronous to them (II and IV) for the case of coexistence of genotypes x_a and x_A .

2-cycle arisen due to the stability loss of nontrivial fixed point via the period-doubling bifurcation. The appearance of this 2-cycle changes the expected dynamic behavior and leads to multistability [4]. The resulting antiphase 2-cycle loses its stability according to the Neimark-Sacker scenario, when an closed invariant curve is born around each element of the 2-cycle. The key point here is that different 2-cycles can simultaneously exist in a community with the low interspecific competition, as a result, the initial conditions determine which of them will be attracted (see fig. 1 c).

In general, in the absence of zooplankton, depending on the values of the model parameters that characterize the fitness of different genotypic groups of phytoplankton and the intraspecific and interspecific competition between them, the following evolutionary scenarios for the phytoplankton development can be distinguished: 1) Genotype x_A displaces genotype x_a if $\rho_A\rho_a < 1, B_a < B_A^{\rho_A}, B_A > 1$ or $\rho_A\rho_a > 1, B_A > B_a^{\rho_a}, B_A > 1$; 2) Genotype x_a displaces genotype x_A if $\rho_A\rho_a < 1, B_A < B_a^{\rho_a}, B_a > 1$ or $\rho_A\rho_a > 1, B_a > B_A^{\rho_A}, B_a > 1$; 3) Genotypes x_a and x_A coexist if $\rho_A\rho_a < 1, B_A B_a > B_A^{\rho_A} B_a^{\rho_a}, B_a > 1, B_A > 1$; 4) The displacement of a genotype by another one depends on the values of initial conditions with $\rho_A\rho_a > 1, B_A B_a < B_A^{\rho_A} B_a^{\rho_a}, B_a > 1, B_A > 1$.

Figure 2 shows dynamic mode maps with consumption of non-toxic phytoplankton by zooplankton. As can be seen, the nature of the dynamic behavior is the same as in fig. 1, but a vast domain of parameter values occurs where all the community components exist and develop.

An increase in the growth rate of zooplankton expands the parametric area with the complete community that evolves via the period-doubling scenario with higher phytoplankton birth rates. At the same time, the increase in the parameter w values narrows

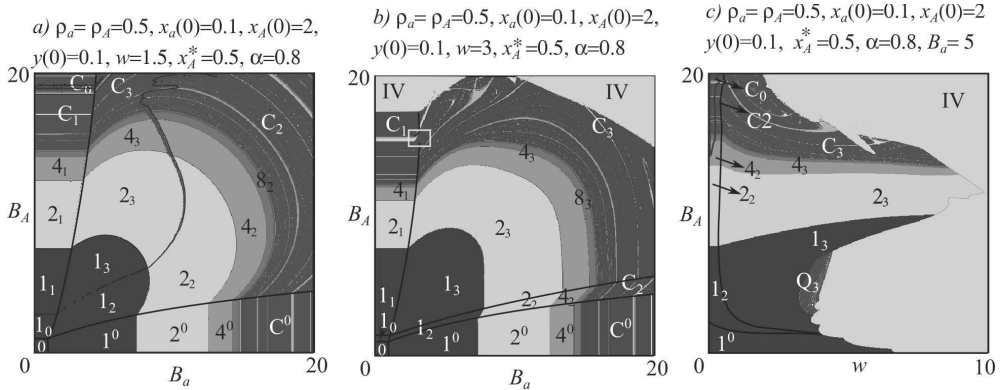


Fig. 2: Dynamic mode maps of model (1) with $x_A^* = g_A X_A^*$ and $\alpha = g_A \alpha_0$. Figures correspond to the period of observed cycles; Q stands for quasiperiodic dynamics; C is chaotic dynamics; 0 corresponds to the community extinction. The subscript and superscript 0 correspond to the survival of the x_a and x_A genotype, respectively. Index 3 is the complete community existence. Index 1 corresponds to the community without toxic phytoplankton. Index 2 corresponds to the community without zooplankton. IV is infeasible parameter value area where the model loses its meaning.

the parameters' domain, corresponding to a reduced community with non-toxic phytoplankton and zooplankton. Accordingly, a phytoplankton toxicity trait fixes due to the vital activity of zooplankton decreasing competition between different phytoplankton genotypes. In particular, in the multistability area highlighted by a rectangle in fig. 2 b, the toxicity trait can either be eliminated or fixed depending on the current ratio of phytoplankton genotypes. Note that an increase in the zooplankton growth rate can lead to quasi-periodic oscillations: the nontrivial fixed point of system (1) loses its stability through the Neimark-Sacker bifurcation. This scenario is not possible in a reduced community without a predator.

Thus, this study shows changes in the current densities of different phytoplankton genotypes caused by environmental factor influence or zooplankton's consumption can change the evolution direction with accompanying dynamic mode shift. In this context, the consumption of phytoplankton by zooplankton can play a key role during the evolution of the plankton community.

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АННОТАЦИЯ

В работе исследуется модель эволюционной динамики планктонного сообщества. Предполагается, что фитопланктон представлен двумя генетически группами, которые конкурируют за ресурсы и отличаются наличием признака токсичности. При этом зоопланктон проявляет избирательность при выборе пищи и потребляет нетоксичный фитопланктон. Показано, что эволюционный сценарий развития двух разных генотипов фитопланктона существенно зависит от уровня конкурентных взаимоотношений между ними.

Ключевые слова: *система хищник — жертва, конкуренция, функция Холлинга II типа, эволюция, режимы динамики.*