

Simulation of Cladoceran Survival Strategy under Conditions of Food Depletion

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Abstract—Competition between several cladoceran species has been studied with the use of simulation. The results have demonstrated that, in most cases, one or two species survive. Under conditions of the minimum food supply, the most competitive species have the selective advantage. With an increase in food supply, the survival of low-competitive species was observed more often. The mean body size of surviving species increases with an increase in food reproduction.

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INTRODUCTION

The problem of the coexistence of competing species under natural conditions is closely related to the problem of biodiversity, as well as to the possibility of the invasion of foreign species into communities. Whether the invader species will be displaced or will coexist with the aboriginal species is an important question, because competitive relationships are one of the factors determining the ecosystem structure (Montague *et al.*, 1982; Gilyarov, 1987; Hu and Tessier, 1995). Seeking to learn to predict the outcome of interspecific competition, researchers have put forward a number of hypotheses on the specific characteristics of “strong” competitors.

According to the size efficiency hypothesis (Brooks and Dodson, 1965), large crustaceans are stronger competitors than small ones because, in the authors’ opinion, the former species filter food resources more efficiently. Indeed, there is evidence (Gliwicz, 2003) that large crustaceans dominate in the absence of predator pressure. However, some other researchers believe that small species have a higher competitiveness, because they require less energy to grow and mature (Neill, 1975; Lynch, 1978; Romanovsky, 1984, 1985).

Equilibrium concentration, i.e., the threshold concentration of the resource at which the birth and death rates in the given population are equal to each other, is another criterion that is important for predicting the outcome of competition. Tilman (1981) demonstrated that a species with a lower equilibrium concentration of the resource was more competitive; therefore, species with lower equilibrium concentrations are expected to dominate under the conditions of food depletion. This parameter was taken into account as a criterion of com-

petitiveness in studies on the invasion of alien species into communities (Shea and Chesson, 2002).

Finally, the “paradox of the plankton” hypothesis (Hutchinson, 1961) is no less popular and has stimulated many studies on species competition. According to this hypothesis, phytoplankton contains many competing species because they are ecologically similar to one another. The coexistence of similar competing species was also observed in zooplankton (den Boer, 1980; Riley, 1963). The “paradox of the plankton” contradicts Gause’s principle of competitive exclusion, according to which a “weak” species will inevitably be replaced by a “stronger” one if they are competing for a common resource.

In this study, we investigated the causes of contradictions in the aforementioned hypotheses. The necessity of seeking out approaches to the prediction of the outcome of interspecific competition is largely accounted for by the fact that the structure and functions of many aquatic ecosystems are being considerably altered by the invasion of alien species. For example, cladoceran crustaceans are successfully invading some ecosystems where they have not been found previously (MacIssac *et al.*, 1999; Laxton *et al.*, 2003; Makarewicz *et al.*, 2003). It is possible to prevent this process or, at least, alleviate its consequences, if the invasion is predicted at its initial stage.

The purpose of this study was to test the size efficiency hypothesis, assess the possibility of predicting the outcome of competition on the basis of equilibrium concentration, and estimate the probability of the coexistence of species competing for a common resource, with the use of simulation methodology.

Table 1. Population parameters of simulated species

Parameter	Minimum	Maximum
Maximum ingestion rate of juveniles ¹ , cells/ml	16000.00	132000.00
Ingestion rate threshold, cells/ml	5000.00	80000.00
Juvenile mortality threshold ² , cells/ml	4000.00	40000.00
Adult mortality threshold, cells/ml	1000.00	6000.00
Minimum juvenile mortality ^{2*}	0.01	0.02
Minimum adult mortality*	0.01	0.06
Maximum juvenile mortality ^{2*}	0.10	0.30
Maximum adult mortality*	0.10	0.30
Maximum fecundity of an adult female, number of eggs*	1.60	11.20
Lower threshold of fecundity, cells/ml*	1000.00	20000.00
Maximum duration of postembryonic development ³ , days	2.50	22.50
Threshold of postembryonic development, cells/ml	10000.00	100000.00
Adult life span, days	25.00	63.00

¹ The maximum ingestion rate of juveniles at the first stage. At the second stage, it was two times higher (in adults, four times higher).

² This parameter was the same in juveniles at the first and second stages.

³ The maximum duration of the postembryonic development of juveniles at the first stage. At the second stage, it was two times higher.

* The population parameters that are linearly related to the maximum ingestion rate.

DESCRIPTION OF THE MODEL

For solving these problems, we developed a model of cladoceran population dynamics under conditions of food depletion. Species, in our model, were specified by a set of dependences of population parameters on the concentration of food determined as a result of its reproduction and consumption.

The simulated species differed from one another in the following parameters: the lower and upper threshold concentrations of food, the functions of ingestion rates (separately for the juvenile and adult stages), mortality (the juvenile and adult stages), fecundity, and the duration of postembryonic development, as well as the maximum values of the above parameters themselves. The dependences of these parameters on food concentration were piecewise rectilinear functions. The model took into account the delays in the responses of the fecundity, mortality, and duration of postembryonic development to changes in food concentration.

The body size was determined by the maximum ingestion rate: the larger the maximum size, the higher the maximum ingestion rate (Sushchenya, 1975). Body size was related to the upper threshold of the ingestion rate, maximum fecundity, upper and lower thresholds of fecundity, minimum and maximum mortality, minimum and maximum durations of postembryonic development, and the threshold concentration of food at which the postembryonic development was the shortest (Table 1).

Figure 1 shows the general pattern of the dependences of population parameters on the concentration of food (the resource). The change in food concentra-

tion with time ($K(t)$) was described by the following equation:

$$K(t+1) = K(t) + P/BK(t) - kK^2(t) - \frac{\sum_i \sum_l R_i(K(t), l) N_i(t, l)}{V}, \quad (1)$$

where t and $t+1$ are the present and the next moments of time; k is the coefficient of the logistic growth of the food concentration in the absence of its consumption; P is daily production; B is biomass; $R_i(K(t), l)$ is the ingestion rate of individuals of size l from species i ; $N_i(t, l)$ is the number of individuals of size l from species i at moment t ; and V is the volume of the medium.

The changes in the numbers of crustaceans depending on food concentration were specified by the following set of difference equations:

$$\left. \begin{aligned} N(t+1, l+\Delta l) &= N(t, l) - M(K(t-\tau), l)N(t, l), \\ N_n(t+1) &= N_f(t)F(K(t-\tau))/D_e, \\ N_j(t) &= \sum N_i(t, l), \\ N_f(t) &= \sum N_f(t, l), \\ N(t) &= N_j + N_f, \\ \text{where } \Delta l(t) &= \frac{L_j}{D_j(K(t))}, \\ \Delta l_f(t) &= \frac{L_{\max} - L_j}{D_{\max} - D_j(K(t))}, \end{aligned} \right\} \quad (2)$$

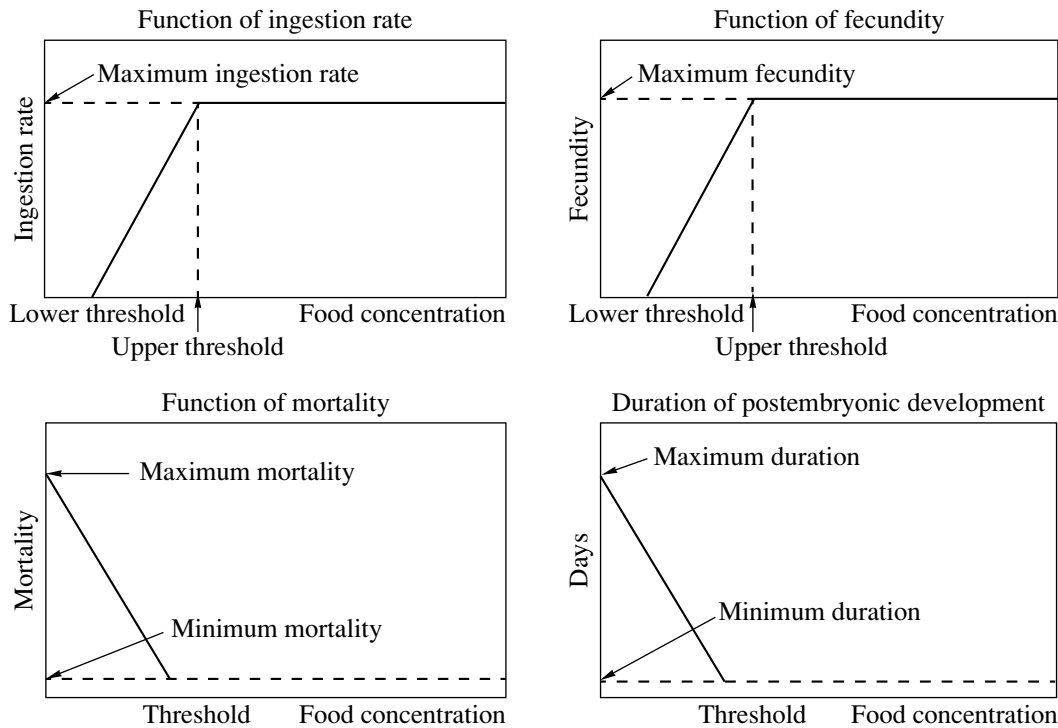


Fig. 1. General pattern of the dependences of population parameters on food concentration in simulated species.

where t and $t + 1$ are the present and the next moments of time; $N(t)$ is the total number at moment t ; $N_j(t)$ is the number of juvenile individuals; $N_f(t)$ is the number of females; $N_n(t)$ is the number of newborn individuals; $N_j(t, l)$ is the number of juvenile individuals of size l ; $N_f(t)$ is the number of adult females; $M(K(t-\tau), l)$ is specific mortality as a function of body length and food concentration with a delay of τ ; $F(K(t-\tau), l)$ is fecundity as a function of food concentration with a delay of τ ; D_e is the duration of egg development; $\Delta l(t)$ is the increment in the body size of juveniles during the model time step; $\Delta l_f(t)$ is the increment in the body size of adults during the model time step; $D_f(K(t))$ is the duration of postembryonic development; L_j is the increment in body size during postembryonic development; L_{\max} is the maximum body size; and D_{\max} is the maximum life span.

SIMULATION METHODS

The simulation model described above was implemented in the form of a computer program written in GNU Fortran in the Linux operating system. A set of the values of parameters (fecundity, mortality, ingestion rate, and development duration as functions of food concentration) (Table 1) were input to the program, and the population dynamics and changes in food concentration with time were output. The simulation was performed for a period of 180 days at a step of one-eighth of a day. For repetitive simulation cycles with

different parameters, scenarios were written in the Bash and Python languages.

Table 1 shows the variation range of population parameters (fecundity, mortality, and the duration of postembryonic development). In different simulation cycles, we randomly varied these parameters according to the law of normal distribution within their actual ranges in cladocerans (Romanovsky and Feniova, 1985; Semenchenko, 1990).

At the first stage of the study, we analyzed the population dynamics of the simulated species in monocultures. For this purpose, 2000 simulation cycles were performed. The population dynamics was used to determine the equilibrium concentration of food, which served as an estimate of competitiveness (Tilman, 1981).

At the second stage, we determined the outcome of competition for a common resource. For this purpose, we formed mixed cultures of five species differing from one another in equilibrium concentration and maximum body size. In different simulation cycles, we varied the initial concentration of food (5000, 10000, 25000, 50000, 100000, 300000, and 600000) and the P/B coefficient (0.2, 0.4, 0.6, and 0.8). We simulated all possible combinations of these initial food concentrations and P/B coefficients. Twenty-five simulation cycles were performed for each combination. In different combinations, species were put together randomly and independently.

The simulation yielded data on species population dynamics under the conditions of interspecific compe-

tion for a common resource. The following parameters of species that had survived competition were analyzed.

(1) The deviation of the maximum ingestion rate of the surviving species from the mean value in a group of five competing species reduced to the standard scale (with the mean value equal to zero and the standard deviation equal to unity). If more than one species survived, we averaged the maximum ingestion rate over the survivors and calculated its deviation from the mean value for all five species. This parameter reflects the difference in maximum ingestion rate between the surviving and replaced species.

(2) The deviation of the mean food concentration characterizing the competitiveness of the surviving species from the mean value for a group of five competing species reduced to the standard scale (with the mean value equal to zero and the standard deviation equal to unity). If more than one species survived, we averaged the mean equilibrium food concentration over the survivors and calculated its deviation from the mean value for all five species. This parameter reflects the difference in equilibrium food concentration between the surviving and replaced species.

Wichmann and Hill's (1982) procedure was used for generating random numbers. Correlation and regression analyses were used for statistical treatment of the data.

RESULTS AND DISCUSSION

The simulation of species population dynamics in monoculture yielded an array of data on species differing from one another in population parameters and allowed us to estimate the equilibrium concentration of food. Analysis of the population dynamics of five species competing for a common resource showed that one or, at most, two species usually survived, irrespective of the initial food concentration or the P/B coefficient (Table 2). To test the possible effect of the number of interacting species, we performed similar simulation experiments where 10 or 20 species were combined. However, the results of these experiments were practically identical to the results of simulation with five species.

The standardized deviation of the equilibrium food concentration characterizing the surviving species depended on both the P/B coefficient ($r_s = 0.53$, $t_{26} = 3.15$, $p < 0.05$) and the initial food concentration ($r_s = 0.59$, $t_{26} = 3.69$, $p < 0.05$). Under the conditions of the smallest food reserves ($P/B = 0.4$ and an initial food concentration of 50000 cells/ml), the most competitive species (those with the lowest equilibrium food concentration in monoculture) predominantly survived (Fig. 2). If the food reserves were the largest ($P/B = 0.8$ and an initial food concentration of 600000 cells/ml), the species with a high competitiveness (and low equilibrium food concentrations) also had advantage; however, the number of cases when species with higher food equilibrium concentrations survived also increased (Fig. 2).

Table 2. Frequencies of survival of one or two species under conditions of competition at different P/B coefficients and initial food concentrations

Number of surviving species	Initial food concentration, cells/ml							Total
	5000	10000	25000	50000	100000	300000	600000	
$P/B = 0.2$								
1	8	12	11	14	9	8	7	69
2	0	1	1	0	0	0	0	2
$P/B = 0.4$								
1	18	17	18	15	15	13	9	105
2	0	0	0	0	1	0	0	1
$P/B = 0.6$								
1	18	13	13	16	16	12	10	98
2	1	4	1	1	0	1	3	11
$P/B = 0.8$								
1	19	16	16	13	13	13	13	103
2	2	3	4	6	3	1	1	20

The population size of surviving species estimated by the maximum ingestion rate depended most strongly on the P/B coefficient ($r_s = 0.64$, $t_{26} = 4.25$, $p < 0.001$) and did not depend on the initial food concentration ($r_s = 0.21$, $t_{26} = 1.07$, $p > 0.2$) (Fig. 2). At a low resource productivity (P/B coefficient), most survivors were species with a low maximum ingestion rate, i.e., a small body size; with an increase in food production rate, the mean body size of surviving species increased.

Researchers studying interspecific competition in freshwater plankton have often attempted to determine the life-history strategies favoring survival under the conditions of food depletion. For example, Alan (1976) characterized rotifers as r -strategists, copepods as K -strategists, and cladocerans as an intermediate group according to Pianka's (1981) theory of r - and K -selections. However, these two strategies are not sufficient to explain the entire diversity of the competitive replacement of species.

Yu.E. Romanovsky (1984, 1985), having analyzed the life-history strategies of cladocerans, distinguished three general categories: violents, large species that rapidly grow and slowly decrease their numbers due to a high survivability of adults (they are competitive at the stage of mature animals); patients, small species that slowly grow, slowly reproduce, and can survive periods of food depletion due to a high survivability of juveniles (they are competitive at the stage of juvenile animals); and explerents, very rapidly growing and rapidly reproducing species that cannot survive food depletion (they are noncompetitive). Most explerents are species inhabiting temporary bodies of water, e.g., species from the genus *Moina*. V.P. Semchenko (1990) found similar groups of cladocerans when analyzing field data.

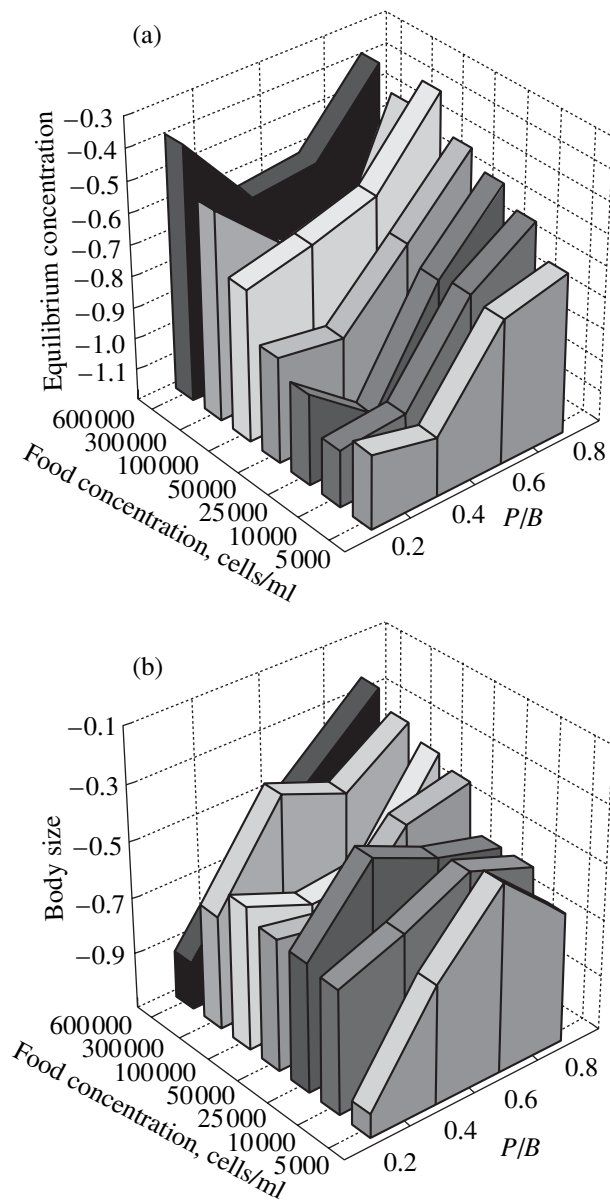


Fig. 2. Dependences of (a) equilibrium food concentrations and (b) body size of surviving species on the initial food concentration (measured as the number of cells per milliliter) and the P/B coefficient shown as a standardized deviation from the mean value.

Romanovsky (1984) suggested that the threshold food concentration at which the rate of the weight increment of juveniles with unit weight is the lowest should be used as a measure of competitiveness. The lower is the threshold concentration, the more competitive is the species. Calculation of this parameter for 12 species of cladocerans showed that it increased with an increase in body size (Romanovsky, 1985). Therefore, Romanovsky considered small species (e.g., *Diaphanosoma brachyurum*, *Bosmina coregoni*, and *Daphnia cucullata*) to be the most tolerant to a lower concentration of food and large species, such as *Daphnia magna*

and *Simocephalus vetulus*, to be less competitive. However, this contradicts the earlier size-efficiency hypothesis (Brooks and Dodson, 1965). It is impossible to give preference to any of the two hypotheses concerning the relationship between the species competitiveness and body size, because there is evidence in favor of both Brooks and Dodson's hypothesis (Gliwicz, 2003; Goulden and Hornig, 1980; Kreuzer and Lampert, 1999) and Romanovsky's hypothesis (Frank, 1952; Frank, 1957; Lynch, 1978; Neill, 1975).

Apparently, the contradiction between the two hypotheses is explained by the possibility that, depending on food reserves, small species may become more competitive than large ones. It has been demonstrated that large crustaceans usually have the selective advantage at high initial food concentrations and small ones, at low concentrations. The effect of the resource amount on the outcome of interspecies competition has also been demonstrated for representatives of other taxa, namely, protozoa (Deihl and Feissel, 2000) and fishes (McCann, 1998).

Our study confirmed that the outcome of competition depended on the rate of food reproduction, in particular, on the P/B coefficient. At extreme values of P/B , the competition outcome was related to body size. At the lowest P/B values and low initial food concentrations (an analogue of oligotrophic waters), most survivors were small species. At high P/B coefficients and initial food concentration (an analogue of eutrophic conditions, where competition occurs only periodically), some larger species survived along with small ones. Therefore, if the conditions are changing from oligotrophic to eutrophic in the absence of predators, an increase in the mean body size of the surviving species should be expected. However, there was no strict, direct dependence of the competition outcome on body size, which would be expected according to the size-efficiency hypothesis. In addition, as the body size increased, larger species acquired competitive advantage at the expense of small species.

In natural waters with an insignificant predator pressure, differences in the ratio between large and small cladoceran species are related to trophic conditions, which confirms our results. For example, the small species *Daphnia rosea* is dominant in the oligotrophic Lake Placid (Canada), whereas a larger species, *D. pulex*, is absent from this lake but is abundant in neighboring eutrophic bodies of water (Neill, 1978). Conversely, the large *D. pulex* is a dominant species in shallow ponds of Colorado, whereas the small *D. rosea* is absent there altogether (Sprules, 1972).

When testing the effect of the equilibrium food concentration, which is a measure of the species competitiveness according to Tilman, we found that this rule was true only at low food concentrations and low rates of the food resource reproduction (Fig. 2). As the amount of the food resource increases, species with a higher equilibrium concentration may also gain an

advantage. Apparently, species can employ some other competitive advantages at higher rates of food reproduction. A high survivability of mature individuals may serve as an example of such a competitive advantage: at a higher equilibrium concentration, a species may win if the proportion of mature individuals in its populations is sufficiently high.

It can be seen from Table 2 that whether or not competing species can coexist also depends on the food reproduction rate, i.e., on the P/B coefficient. An increase in the food reproduction rate optimizes conditions for the survival of competing species. However, we did not observe the "paradox of the plankton," i.e., coexistence of many species competing for a common resource. In our model of a combination of five species competing for the same resource, no more than two species could coexist. Most of the model situations complied with Gause's principle, i.e., only one species won in the interspecific competition. This was observed in 97% of cases at low food reproduction rates. At high P/B coefficients, one competitor was left in 84% of cases, and two species coexisted in 16% of cases.

A similar ratio between the numbers of coexisting competitors was observed in field studies on the species composition of cladocerans living in temporary mountain water bodies in the absence of predators (Ranta, 1979). In only 20 out of 199 ponds did two species of *Daphnia* coexist. In 90 bodies of water, only the large *D. magna* was found; in 60, only the small *D. longispina*; and in 22, only *D. pulex*. Both in the simulation experiment and in the field studies, no more than two species competing for a common resource coexisted; all other species were replaced in the course of competition.

The results of simulation indicate that the probability of the coexistence of competing species depends on the resource reproduction rate. As the conditions change from oligotrophic to eutrophic, the coexistence of competing species becomes more frequent. The coexistence of more than two competitors for food apparently requires additional interspecific differences, such as different feeding spectra, avoidance of competition via vertical migrations, different predator pressures, or difference in temperature factor. Therefore, possible factors other than the food reproduction rate should be taken into account for predicting the outcome of interspecific competition, including community invasion by alien species, as well as for explaining the cases when more than two competing species coexist.

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