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**The Effect of Food Concentration  
on the Juvenile Somatic Growth Rate of Body Length,  
Fecundity and the Production of Resting Eggs  
by *Moina brachiata* (Crustacea: Cladocera)  
Single Females**

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*The study addresses the effect of different food concentrations of green alga *Chlorella vulgaris* on the life cycle parameters (the body length, specific juvenile somatic growth rate of body length, the number of offspring in the first clutch of parthenogenetic females and the number of females producing resting eggs) of the individually cultivated females of *M. brachiata*. The lowest food concentration used in the experiment, 100 thousand cells/ml, had a limiting effect on such parameters as the size of females at the first reproduction, juvenile somatic growth rate of body length and fecundity; it also induced the production of resting eggs by females. With food concentration increase, the size of females at the first reproduction, their somatic growth rate of body length and fecundity also increased, and the number of females that produced resting eggs decreased. Under maximal food concentrations (400 and 800 thousand cells/ml) the size of females at the first reproduction, the somatic growth rates of body length and the number of hatched offspring were the largest, and there were no females producing ephippial eggs. We also tested the effect of food concentration under which the maternal generation was kept on the ability of the offspring generation to produce resting eggs. The production of resting eggs failed to occur only at the highest food concentrations for maternal females and their offspring (400 thousand cells/ml). Thus, we concluded that food concentration above 400 thousand cells/ml is favorable concentration for parthenogenetic reproduction of *M. brachiata*. Since there are no literature data on what food concentration induces the production of resting eggs for this species, the results define the trophic conditions that induce production of resting eggs in *M. brachiata*.*

*Keywords: cladocerans, food concentration, maternal effect, resting eggs, species coexistence.*

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## Introduction

Cladocerans play an important role in functioning of lake ecosystems (Chen et al., 2010). Cladocerans are among the most widespread and fertile freshwater consumers of phytoplankton and detritus that connect primary producers with higher links of trophic chain such as fish (Smyntek et al., 2008). Variations in population density of crustaceans can have a significant effect on biotic interactions in aquatic ecosystems; thus, mechanisms and factors that determine their population dynamics need to be carefully studied. The ability to switch between reproductive modes is one of the factors that control the population dynamics of Cladocera. Under favorable conditions, females reproduce by parthenogenesis. Unfavorable conditions induce a switch to gametogenesis (Carvalho, Hughes, 1983). Cyclic parthenogenesis is typical for many taxonomic units (for example, trematodes, wasps, mosquitoes, aphids, rotifers, etc.). Cyclic parthenogenesis is interesting because it combines the advantages of asexual (rapid population growth) and sexual (genetic diversity) reproduction. Usually sexual reproduction in Cladocera begins when the environmental conditions deteriorate or shortly before that and results in development of resting stages (diapausing eggs for cladocerans) (Koch et al., 2009). Diapause evolved as an adaptation allowing the population to develop in accordance with changes in environmental factors. Among the factors inducing the production of resting eggs by cladocerans, the most commonly reported are temperature, photoperiod, trophic conditions (Alekseev, 1990; Zadereev, 1998; Madhupratap, 1996), and infochemicals (Zadereev, 2003).

The effect of trophic conditions on growth and reproduction of crustaceans evokes considerable interest among researchers. The quantity and quality of food influences the somatic growth and diapause induction in many

species of crustaceans (e.g., Benider et al., 2002; Vrede et al., 2002; Rinke, Petzoldt, 2003; Bunioto, Arcifa, 2007; Koch et al., 2009; Smith et al., 2009). In general, the decrease in the food availability stimulates production of resting eggs by cladocerans (D'Abramo, 1980). However, it would be reasonable to assume that the threshold food concentration that stimulates females to the production of resting eggs will be different for different species.

We previously studied the effect of food concentration and other factors on the reproductive parameters of *Moina macrocopa* (Straus, 1820) (Zadereev, Gubanov, 1995; Zadereev et al., 1998), a widespread model species of Cladocera. This species often coexists in natural habitats with another similarly sized cladoceran *Moina brachiata* (Jurine, 1820) (Petrušek, 2002). Little is known about the ecophysiology of this species. However, different requirements for food quantity observed in natural populations of zooplankton can be considered as a mechanism enabling species coexistence (Hopp, Maier, 2005).

The purpose of this work was to study the effect of trophic conditions on the growth rate, fecundity and the ability to produce resting eggs of single females of *Moina brachiata* (Jurine, 1820). Another aim was to compare food concentrations that induce the production of resting eggs in *M. brachiata* and *M. macrocopa* females. We made the tentative assumption that two species that share the same ecological niche and are similar in size, will differ in their food requirements.

## Materials and Methods

The study species was cladoceran *M. brachiata* living in temporary water bodies and having a short life cycle and a high rate of asexual reproduction. The resting eggs of *M. brachiata* were isolated from sediment samples of

an ephemeral pond near the Institute of Biology of Inland Waters RAS (the village of Borok) provided by V. Tchugunov. After the animals emerged from resting eggs, they were kept under laboratory conditions for several months prior to experiments.

In experiments with single females 20 ml vessels were used. Experiments were carried out in a thermostat at a constant temperature of 26° C and under photoperiod (16 hours of light and 8 hours of dark). Unicellular green alga *Chlorella vulgaris* Beijerinck was used as food in all experiments. The dry weight of  $10^9$  cells of algae used in the experiments was 0.012 µg. The algae were cultivated in batch mode in 500-ml flasks on Tamiya medium. Before being used as food, the algae were separated from culture medium by centrifugation at 3000 rpm. The resultant suspension was kept in a refrigerator. The algae cell concentration in the suspension was determined using a CASY TTC particle counter (CASY, Germany).

Equally sized parthenogenetic females were cultivated individually under food conditions that did not limit their growth and development (the cultivation medium volume was 20 ml/female, the food concentration in the medium was > 800 thousand cells/ml (ca. 10 mg/l dry weight) (Zadereev, Lopatina, 2006). As laboratory experiments with individual females of *M. macrocopa* that had been previously carried out with the neonates from the first clutch enabled determination of the optimal conditions for growth and reproduction of the species (Zadereev, Gubanov, 1995), in the experiments with the closely related species, *M. brachiata*, we also used neonates from the first clutch of the females cultivated under conditions described above. Aged (ca. for 24 hours) tap water was used as a medium for cultivation of animals and for all experiments.

Two series of experiments were carried out.

*The effect of food concentration on somatic growth and reproduction of M. brachiata*

Equally sized juvenile females (0.6–0.7 mm) were selected from the first clutch of several females cultivated under the conditions described above and were placed individually (15 individual females per treatment) in 20 ml culture medium, with food concentration 100, 200, 400 or 800 thousand cells/ml.

An experiment was continued until the hatching of the first parthenogenetic clutch (hatched offspring were counted) or formation of resting eggs. The formation of resting eggs in *Moina* can be easily detected by the visual observation of cloudy white thick structures in the brood pouch which coincides with the initial stage of the formation of the ephippium (Makrushin, 1971). The medium was changed and algae were added daily to maintain the necessary food concentration. The linear size of the animals was recorded daily using a binocular magnifier with 16x magnification. Linear size was determined as the length from the top of the head to the base of the caudal spine. Based on daily measurements, we calculated the somatic growth rate of body length of each animal:

$$g = (\ln L_{fin} - \ln L_0) / t,$$

where  $g$  is specific somatic growth rate of body length,  $L_{fin}$  (mm) is linear size of an animal at the day preceding the hatching of the first clutch which below will be called the size of females at the first reproduction,  $L_0$  (mm) is linear size of an animal at the beginning of the experiment,  $t$  is the time period (days) (Lampert, Trubetskova, 1996).

The linear size of cladocerans continues to increase throughout their life cycle, although the somatic growth rate of body length slows down with the size, and the maximum somatic growth

Table 1. The effect of food concentration provided to maternal and offspring generations on the proportion (% of the total) of *Moina brachiata* females that produced resting eggs. N – the total number of tested females

Food concentration in offspring generation, 1000 cells/ml	Food concentration in maternal generation, 1000 cells/ml			
	100	200	300	400
100	93% (N=55)	73% (N=59)	46% (N=80)	65% (N=54)
200	36% (N=59)	33% (N=55)	19% (N=59)	11% (N=55)
300	20% (N=59)	3% (N=60)	10% (N=60)	2% (N=54)
400	3% (N=59)	2% (N=60)	2% (N=59)	0% (N=55)

rates of body length of females are observed in the first days after birth (Manuilova, 1964). That is why in experiments the specific somatic growth rate of body length of juvenile females was calculated for the period of 3 days: from the start of the experiment (animals of 0.5–1 day age) to the day preceding the hatching of the first progeny (animals of 3.5–4 days age).

#### *Experimental studies of maternal effect*

Equally sized juvenile females (0.6–0.7 mm) were selected from the first clutch hatched under the conditions described above and were placed individually in 20 ml culture medium, with food concentration 100, 200, 400 or 800 thousand cells/ml. Then, equally sized juvenile females (0.6–0.7 mm) were selected from the first clutch of these females and were placed individually (15–20 females per treatment) in the similar food conditions. Three replicates were performed for each of the 16 treatments (i.e., 4 maternal food concentrations x 4 experimental food concentrations x 3 replicates x 15–20 females per replicate). The involved cultures were performed in successive batches, each batch consisting in one maternal food concentration and the range of experimental food concentration. Detailed data on the number

of females tested and trophic conditions for the maternal and experimental generations are given in Table 1. Experiments were continued until the hatching of the first parthenogenetic progeny or formation of resting eggs. The number of females that produced resting eggs was counted. During experiments the medium was changed and algae were added daily to maintain the food concentration.

#### *Statistics*

The effect of food concentration on the growth rate of body length, linear size and fecundity of animals was tested by one-way ANOVA. The somatic growth rates of body length and offspring number under different food concentrations were compared using the Fisher LSD test of planned comparisons. The effect of food concentration on the number of females that produced resting eggs was analysed by the chi-square contingency table analysis (chi-square test). The numbers of females produced resting eggs under different food concentrations were compared using the Fisher's exact test performed on 2\*2 contingency table. The effect of food concentration in maternal and experimental generations on the number of females that produced resting eggs was estimated using the Generalized Linear Model assuming a binomial distribution. All statistical calculations,

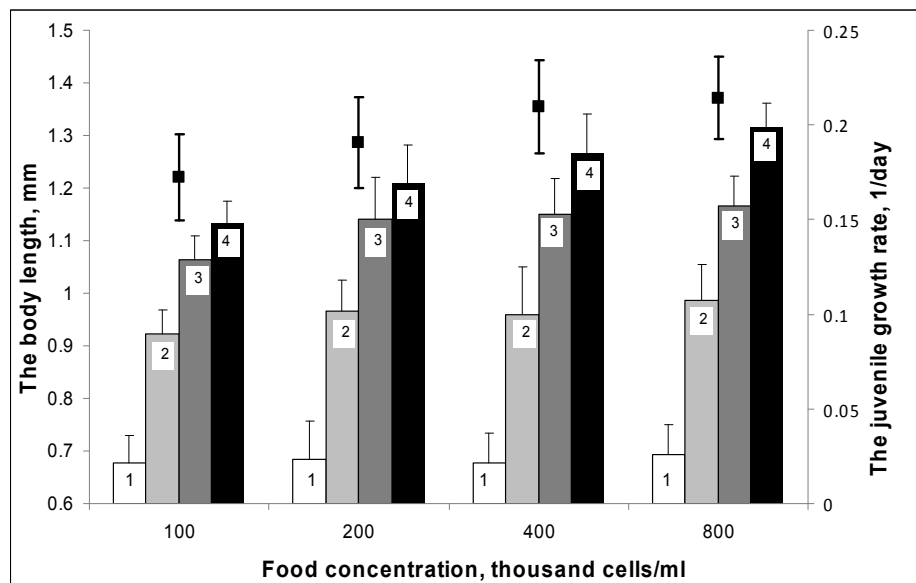


Fig. 1. Daily length (vertical bars) and juvenile somatic growth rate of body length (black dots) of *Moina brachiata* females at different food concentrations. The numbers in the vertical bars correspond to the day of the experiment. Significance of differences between juvenile somatic growth rates of body length at different food concentrations was calculated using post-hoc Fisher LSD test of planned comparisons:  $P_{100-200} < 0.05$ ;  $P_{100-400} < 0.00001$ ;  $P_{100-800} < 0.00001$ ;  $P_{200-400} < 0.05$ ;  $P_{200-800} < 0.01$ ;  $P_{400-800} > 0.5$

except chi-square test and Fisher's exact test, were carried out using the STATISTICA 6.0 software (StatSoft, Inc.).

## Results

### *The effect of food concentration on growth and reproduction*

Specific somatic growth rate of body length of *M. brachiata* females increased with the food concentration (Fig. 1). The one-way ANOVA showed that this effect was significant ( $P < 0.0001$ ,  $F = 10.05$ ). When the average somatic growth rates of body length of *M. brachiata* females under different food concentrations were compared using the Fisher LSD test of planned comparisons (Post-hoc), significant differences were revealed for all food concentrations, except for somatic growth rates of body length at food concentrations of 400 and 800 thousand cells/ml.

The somatic growth rate of body length of female is the function of lengths at two instants:

at the first reproduction and at the beginning of the experiment. The one-way ANOVA showed that the body length of animals at the beginning of experiments (day 1, Fig. 1) with all food concentrations did not differ significantly ( $P > 0.5$ ,  $F = 0.43$ ). In contrast, the size of females at the first reproduction (day 4, Fig. 1) depended on the food concentration ( $P < 0.000$ ,  $F = 28.76$ ).

An increase in food concentration was accompanied by larger numbers of offspring in the first clutch of parthenogenetic females (Fig. 2). One-way ANOVA showed a significant effect of food concentration ( $P < 0.001$ ,  $F = 8.74$ ) on the fecundity of parthenogenetic females of *M. brachiata*. The comparison of the number of hatched neonates at different food concentrations using the Fisher LSD test of planned comparisons showed significant differences for all food concentrations, except for fecundity at food concentrations of 400 and 800 thousand cells/ml (Fig. 2).

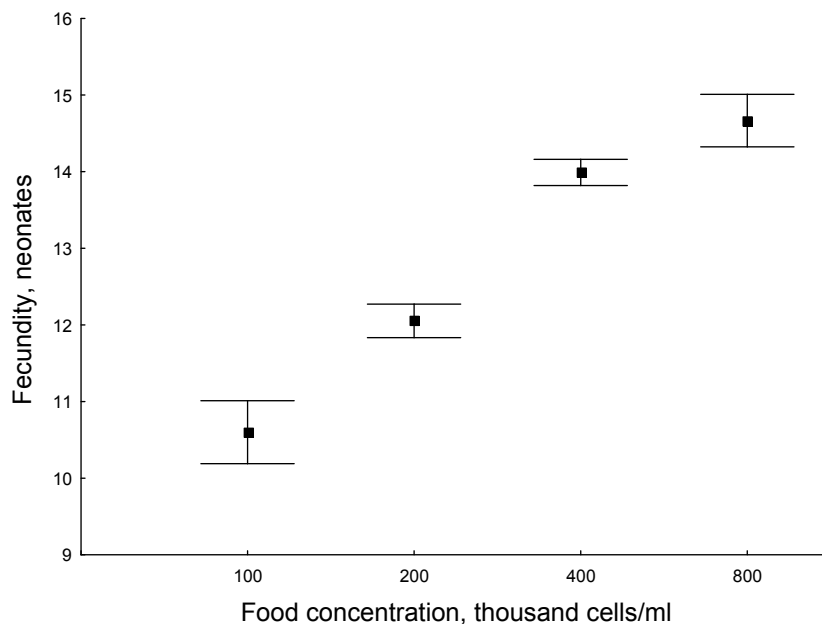


Fig. 2. The effect of different food concentrations on the number of neonates in the first clutch of *M. brachiata* females. Significance of differences was calculated using post-hoc Fisher LSD test of planned comparisons:  $P_{100-200} < 0.05$ ;  $P_{100-400} < 0.001$ ;  $P_{100-800} < 0.001$ ;  $P_{200-400} < 0.05$ ;  $P_{200-800} < 0.05$ ;  $P_{400-800} > 0.5$

The experiment demonstrated the effect of food concentration on the number of *M. brachiata* females that instead of the first parthenogenetic clutch start the formation of resting eggs. The chi-square contingency table analysis showed that this effect was significant ( $P < 0.001$ ,  $X^2 = 20.6$ ). At food concentration of 100 thousand cells/ml, 53% of females initiated formation of resting eggs, while at food concentration of 200 thousand cells/ml, only 13% of females did the same. At food concentrations of 400 and 800 thousand cells/ml, all *M. brachiata* females hatched the first parthenogenetic clutches. Fisher's exact test demonstrated a significant difference between the numbers of females that produced resting eggs at food concentration of 100 thousand cells/ml and 200 thousand cells/ml ( $P_{100-200} = 0.0251$ ), 400 and 800 thousand cells/ml ( $P_{100-400, 800} = 0.0011$ ).

#### Maternal effect

The experiments showed that food concentration at which maternal generation had

been raised affected the reproduction mode of their first progeny (Table 1). The Generalized Linear Model showed that the effect of maternal environment on the production of resting eggs was significant ( $P < 0.005$ ,  $WS = 13.6$ ). When food concentration for the maternal generation was increased, the number of females that were kept at a given food concentration and produced resting eggs tended to decrease.

Another factor responsible for the production of resting eggs was food concentration at which experimental generation was raised. An increase in food concentration in the medium for experimental animals caused a decrease in the number of females that produced resting eggs (Table 1). The significance of this effect has also been proven by the Generalized Linear Model ( $P < 0.000$ ,  $WS = 135.2$ ). It should be noted that the greatest number of the females that produced resting eggs (51 out of 55 tested females) was observed in the experiment with maternal females maintained in the medium with the lowest food

concentration (100 thousand cells/ml) and with the tested animals raised at the lowest food concentration (100 thousand cells/ml). Conversely, the production of resting eggs failed to occur only at the highest food concentrations for maternal females and their offspring (400 thousand cells/ml). The interaction effect between the offspring and the maternal trophic environments on the number of females that produced resting eggs was also significant ( $P < 0.05$ ,  $WS = 17.7$ ).

### Discussion

Experiments with different food concentrations demonstrated that food concentration above 400 thousand cells/ml is favorable for parthenogenetic reproduction of *M. brachiata*. Since there are no literature data on what food concentration induces the production of resting eggs for these species, the results of the experiment define these trophic conditions in *M. brachiata*.

Our study shows that the ability of *M. brachiata* females to produce resting eggs depends not only on the trophic conditions they experienced but also on the trophic conditions under which their mothers were kept. We demonstrated that the number of females that produced resting eggs increased both with a decrease in food concentration used to maintain their mothers and with a decrease in food concentration during the experiment.

The combined effect of maternal and experimental food concentrations on the number of females that produced resting eggs was also significant. In the experiment with the maximum food concentration in the medium for the maternal generation and the minimum food concentration for the offspring generation, more females produced resting eggs than in the experiment with a critical food concentration for the maternal generation and favorable one for its offspring. The significant combined effect

demonstrates that variations in food availability to the offspring generation had a greater effect on the number of the females that produced resting eggs than variations in food availability to the maternal generation. This result can be expected for an r-strategist species. Inhabiting temporary water bodies, *Moina* species faces rapid changes in environmental conditions. Maternal effects should be more important for constant and predictable habitats and factors.

The trophic factor is not the only factor that, when varied in maternal generation, influences the ability of the offspring generation to produce resting eggs. The necessity of considering the conditions under which maternal generation is kept when studying the life cycle of crustaceans, and, in particular, the conditions that induce the production of resting eggs, was discussed in a number of studies. For example, Mikulski and Pijanowska reported (2009) that maternal effect becomes significant for *Daphnia magna* in the presence of a predator (fish): enhanced production of ephippial eggs was observed among the offspring of females affected by this adverse factor. Other studies addressing the significance of maternal effect for *Daphnia* showed that the maternal generation transmits information on food supply (LaMontagne, McCauley, 2001) and photoperiod (Aleksseev, Lampert, 2001) to their offspring, which is exhibited in offspring's production of resting eggs. Another study suggested the adaptive role of maternal effect in the control of the production of resting eggs in cladocerans under the influence of species-specific chemical substances (Zadereev, 2003). The author showed that a maternal generation cultivated in the presence of waste products produces a progeny adapted to this adverse environmental factor. Thus, as reported in the literature, maternal effect is important for determining the conditions inducing the production of resting eggs in cladocerans under

the influence of various adverse environmental factors.

There are also studies that used mathematical modeling to estimate manifestations of maternal effect at the population level. Kazantseva and Alekseev (2007) used a model to verify the significance of maternal effect for the population dynamics of three *Daphnia* generations. Such parameters as temperature, food conditions and photoperiod were varied as factors influencing the characteristics of somatic growth and reproduction. Authors proposed that individual biological potential for growth, reproduction and production of resting eggs depends on the trophic conditions experienced by three maternal generations. Our results, showing that the number of females that produced resting eggs decreased with an increase in food concentration used to maintain their mothers, support this hypothesis. The model proved the significance of maternal effect for seasonal adaptation of crustaceans, as well as the possibility of accumulation of maternal effects in successive generations, which increases population stability under year-to-year variations in environmental parameters. The model also showed that maternal effects combined with population polymorphism serve as a mechanism maintaining the stability of biological systems (Kazantseva, Alekseev, 2007).

In many water bodies, the species under study, *M. brachiata*, coexists with cladoceran *M. macrocopa*, which has similar size and food range (Petrušek, 2002). The mechanisms that are responsible for species coexistence in aquatic ecosystems are unclear. For similar species that have similar food requirements, the outcome of direct competition over a common resource according to the classical Gause principle is elimination of either species (Ciros-Perez et al., 2001). This is not necessarily the case for species which can enter into the diapause. The ability of competing species to go into a resting phase at

different periods can be a powerful mechanism for maintaining species diversity in communities and can eventually lead to coexistence of competitors (Brendonck, De Meester, 2003).

There are studies reported coexistence strategies of several similar species in a common biotope: overlapping generations are seen as the basis of these strategies. The study by Caceres (1998) showed that two species of *Daphnia* (larger *D. pulicaria* and smaller *D. galeata mendotae*) coexist in a lake and dominate alternately in different years and seasons. However, none of the competing species ever replaces the other. Competition and survival are possible due to production of resting eggs that remain viable for a long period of time. A bank of resting eggs in the lake bottom makes possible the existence of overlapping generations, allowing the population to survive in competition. In other words, when environmental conditions are favorable for one population that suppresses the development of its competitor, production of resting eggs provides for restoration of the second population, when more favorable conditions for development are established (Caceres, 1998a). Hairston (1994), who studied diapause in two diaptomid species, *Skistodiaptomus oregonensis* and *Leptodiaptomus minutus*, living in a large Oneida Lake, also suggested that long-term dormancy can ensure the re-establishment of a population through periods of poor recruitment, and can help create conditions for the coexistence of competing species.

The coexistence of two ecologically similar species of *Moina* can also be promoted by a similar effect. In previous laboratory experiments, we determined the favorable trophic conditions for parthenogenetic reproduction of *M. macrocopa* females. We studied the growth of single females of *M. macrocopa* under laboratory conditions that were similar to those used in this study (Zadereev, Gubanov, 1995). Taking into account the similarity of the size and physiological



characteristics of the two *Moina* species, one can assume that their favorable trophic conditions are similar, too. However, food concentration that does not limit the parthenogenetic reproduction of *M. macrocopa* is 100 thousand cells/ml (Zadereev, Gubanov, 1995), while for *M. brachiata*, this value is four times higher (400 thousand cells/ml). Hence, *M. brachiata* females begin to produce resting eggs at a higher food concentration than *M. macrocopa* females do. Based on the results obtained, we propose that coexistence of the two species of cladocerans, *M. macrocopa* and *M. brachiata*, in natural water bodies can be promoted by different threshold values of food supply causing production of resting eggs. The population of *M. brachiata* can react more quickly to the decreasing food concentration in the environment by changing its reproductive mode and forming a bank of resting eggs sooner than *M. macrocopa*.

It is clear that the earlier investment into the egg bank is not a sufficient condition for explaining species coexistence. Let us propose that *M. brachiata* can avoid competition in the water column by producing resting eggs earlier. If the total number of resting eggs produced by *M. macrocopa* is greater than that produced by *M. brachiata*, *M. brachiata* will be less numerous the next growing season. This might lead to the competitive exclusion of *M. brachiata* in the long term. Previously, in model analysis, we demonstrated that the initial population density had very little effect on the result of competition of two species with different reproductive strategies: a species that produces resting eggs and a species that does not produce them (Zadereev, Prokopkin, 2006). We should also remember that the number of resting eggs produced is not the only factor that determines the initial population density during the beginning of the next season. It is well known that only a small fraction of resting eggs produced hatch during

the next season (Caceres, 1998b). Resting eggs of different species can differ in viability, dispersal, vulnerability to predators, hatching success, etc. We can assume that the different threshold value of food supply causing production of resting eggs is a prerequisite for the species coexistence. However, if we want to understand species coexistence, we need to explain why one of these two species has advantages over the other when it is less numerous.

### Conclusion

We determined the food concentration of 400 thousand cells/ml as favorable for the growth and parthenogenetic reproduction of individually cultivated females of *Moina brachiata*. Being favorable for asexual reproduction, this food supply limits neither the specific somatic growth rate of body length, nor the fecundity of females. We detected the effect of food concentration under which the maternal generation was kept on the ability of their progeny to produce resting eggs. The number of females that produced resting eggs tended to decrease with an increase in food concentration provided to their mothers and an increase in food concentration provided to their offspring. We demonstrated that the combined effect of maternal and experimental food concentrations on the number of females that produced resting eggs was also significant; the variations in food availability to the offspring generation had a greater effect on the number of the females that produced resting eggs than variations in food availability to the maternal generation.

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**Действие концентрации пищи  
на ювенильную соматическую скорость роста,  
плодовитость и формирование покоящихся яиц  
у одиночных самок *Moina brachiata*  
(Crustacea: Cladocera)**

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Работа посвящена изучению действия концентрации одноклеточной водоросли *Chlorella vulgaris* на параметры жизненного цикла самок *M. brachiata* (длина тела, удельная ювенильная соматическая скорость роста, количество потомков, количество самок, образующих эфиппальные яйца). Наименьшая концентрация корма, используемая в эксперименте, 100 тысяч клеток/мл, оказывала лимитирующее действие на размер самок в период появления первого потомства, ювенильную соматическую скорость роста и плодовитость; также данная концентрация пищи вызывала образование покоящихся яиц у самок. При увеличении концентрации корма, размер самок в период появления первого потомства, их соматическая скорость роста и плодовитость возрастали, а количество самок, образующих эфиппумы, снижалось. При культивировании с использованием максимальных тестируемых концентраций пищи (400 и 800 тысяч клеток/мл) размер самок в период появления первого потомства, соматическая скорость роста и количество появившихся потомков были наибольшими, при этом ни одна из самок в эксперименте не образовывала покоящихся яиц. Мы также исследовали действие концентрации пищи, при котором содержалось материнское поколение на способность их потомков формировать латентные яйца. Отсутствие эфиппумов наблюдалось только при использовании наибольших концентраций пищи в экспериментах для материнских особей и их потомков (400 тысяч клеток/мл). Таким образом, мы предполагаем, что обеспеченность пищей выше 400 тысяч клеток/мл благоприятна для партеногенетического размножения самок *M. brachiata*. Результаты об уровне пищевой обеспеченности, вызывающей формирование покоящихся яиц у самок *M. brachiata*, получены впервые.

*Ключевые слова:* ракообразные, концентрация пищи, материнский эффект, покоящиеся яйца, сосуществование видов.

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