Estimation of the Possibility of Cladoceran Invasion and Survival under Conditions of Competition in Mesotrophic Lake Glubokoe

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Abstract—A possibility of introducing alien cladoceran species into the pelagial zone of mesotrophic Lake Glubokoe has been estimated. For this purpose, observations have been performed on the cohorts of alien species (*Daphnia magna* and *Simocephalus exspinosus*) and aboriginal species (*Daphnia hyalina* and *Diaphanosoma brachyurum*). The results show that competition is a factor preventing the introduction of weak competitors, such as *D. magna*, but admitting stronger competitors, e.g., *S. exspinosus*. Competition in the lake may influence not only the species structure of the zooplanktonic community, but also its vertical distribution.

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Along with predation, competition plays a great role in the distribution of species and formation of the structure of communities. It is especially acute in the aquatic environment, where food items are uniformly distributed in the warmed upper layers. It was shown (Gilyarov, 1990; Gliwicz, 2003) that food supply has a significant effect on the population dynamics of Cladocera in nature. To survive under conditions of food shortage, crustaceans adapt to conditions of competition in different ways, which is reflected in their life cycle.

At present, many aquatic communities are being restructured due to the invasion of alien species, including zooplankters. For example, the cladoceran *Cercopagis pengoi* from Europe invaded the Great Lakes (Makarewicz, 2001; Laxton et al., 2003), and *Hemimysis* invaded a reservoir in the Netherlands (Ojaveer et al., 2002). Both species inflicted considerable damage to the zooplanktonic communities of these water bodies. In view of such facts, there is a need for predicting the outcome of competition between the alien and aboriginal species. In this field, the hypothesis of "size efficiency" is very popular, according to which large cladocerans are stronger competitors than small cladocerans (Brooks and Dodson, 1965). However, there is an opinion that small species such as *Diaphanosoma* can suppress large species in the course of exploitation competition (Frank, 1952, 1957; Neill, 1975; Lynch, 1978; Romanovsky, 1984).

In this study, we propose a method of laboratory test cultures for predicting the possibility of invasion of mesotrophic Lake Glubokoe (Moscow oblast) by alien cladocerans. Cladocerans are a convenient object for studying the mechanisms of invasion due to a wide overlap of the trophic niches of different species and high rates of biological turnover. In addition, our purpose was to analyze the survival strategies of the test species under conditions of food limitation in the lake, which was revealed in previous studies (Matveev, 1976, 1977, 1983).

MATERIAL AND METHODS

Observations of crustaceans *Daphnia magna, Simocephalus exspinosus, Daphnia hyalina*, and *Diaphanosoma brachyurum* were performed under experimental conditions. The species are listed in order of decreasing body size. *Daphnia magna* and *S. exspinosus* are alien species in relation to the zooplanktonic community of Lake Glubokoe. The former species was taken from a laboratory culture, and the latter species was from shallow ephemeral eutrophic pools near the lake. *Daphnia hyalina* and *D. brachyurum* live in the pelagic zone of the lake. The latter is a dominant species, whereas the former is scarce, and its abundance in the lake has been steadily decreasing in recent years.

The crustaceans were kept in 500-ml glass vessels in a flow-through system. Water flowed in and out of the vessels through silicone tubes at a constant rate, which was adjusted using special clamps so as to replace the entire water volume in each vessel within 12 h. The water was taken from the pelagic zone of Lake Glubokoe, from the epilimnion at a depth of 2 m, twice a day. It was filtered through bolting silk that was permeable to the food for crustaceans but retained zoop-

Population parameters of species used in the experiments

Species	Date of the beginning of experiment	Intrinsic growth rate, r	Size of the third brood, number of eggs per female	Duration of postembrynic development, days
D. magna	Chlorella	0.24	5.0	5
	July 15	−0.02	0.2	30
S. exspinosus	Chlorella	0.27	8.0	5
	July 1	0.14	2.04	6
	July 12	−0.03	0.35	8
	July 19	0.07	0.85	10
	July 31	0.01	0.37	10
	August 12	−0.02	1.45	13
D. brachyurum	July 15	0.04	2.45	5
	July 15	0.05	2.18	5
	July 19	0.04	1.62	5
	July 22	0.04	1.00	5
	July 31	0.04	1.62	5
	August 5	0.04	1.93	5
	August 15	0.04	1.44	5
D. hyalina	July 12	0.01	4.0	8
	July 19	0.01	4.0	8
	July 22	−0.02	4.0	7
	July 26	−0.19	4.0	7
	July 28	0.04	2.5	5
	July 31	−0.2	2.0	7
	August 3	0.02	3.3	5
	August 5	0.01	3.6	5
	August 14	0.05	3.6	5
	August 19	−0.14	1.8	5
	August 22	0.01	4.0	5

lankton. In some experiments, the water was supplemented with chlorella in order to compare the development of zooplanktonic species in the natural lake water and under conditions of improved food supply.

Initially, 25–30 newborn crustaceans produced by females kept in lake water for three to five days were placed in each vessel. Every two days, we recorded the numbers of specimens in cohorts of each species, fecundity of all specimens, their body size, and duration of postembryonic development. The crustaceans were counted and measured in a Bogorov cell under urethane anesthesia and then were returned in the experiment. The cohorts were monitored from July to September. Observations were suspended after the third brood, and then a new series of experiments was started. Experiments with each species were carried out in two to three vessels simultaneously. In the case of D. magna, only one series of experiments with the lake water was performed, as development to maturity in

this species was delayed by more than one month. Other species were tested in several series of experiments (table) in July and August at a temperature of 18–20°C, which was maintained in the laboratory using a heater.

The results of observations on cohorts were used to compile life tables and calculate the intrinsic population growth rate (r) by the equation

$$r = \ln\left\{\sum l(x)m(x)\right\}/T,$$

where $l(x)$ and $m(x)$ are survival and fecundity by ages, respectively, and T is the average generation time. It was assumed that the higher the intrinsic population growth rate, the greater the ability of species to increase its abundance in the lake. A negative growth rate, if observed during the entire observation period, indicated that the species was unable to maintain its abundance in the lake and could be suppressed.
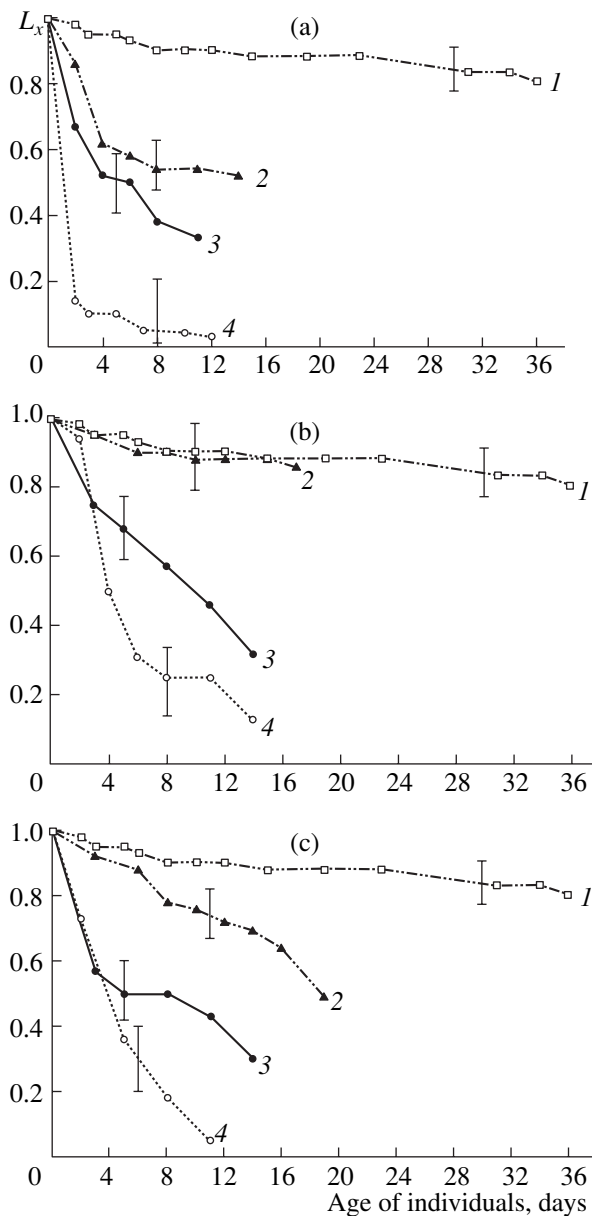
Fig. 1. Curves of survival of species studied in Lake Glubokoe: (*1*) *Daphnia magna*, (*2*) *Simocephalus exspinosus*, (*3*) *Diaphanosoma brachyurum*, (*4*) *Daphnia hyalina* (vertical lines indicate the time of maturation). (a) Series of experiments with cohorts of *S. exspinosus*, D. *brachyurum*, and *D. hyalina* started on July 12; (b) series of experiments with cohorts of *S. exspinosus*, *D. brachyurum*, and *D. hyalina* started on July 19; (c) series of experiments with cohorts of *S. exspinosus*, *D. brachyurum*, and *D. hyalina* started on July 31. One series of experiments with cohorts of *D. magna* was performed from July 15 to late August.

In addition, we jointly cultivated *S. exspinosus* and *D. brachyurum* using the same experimental design. Six mature specimens of each species were placed in a vessel, and the numbers of crustaceans and their fecundity were recorded at four- to five-day intervals. These experiments were performed in two replications. The crustaceans were counted under urethane anesthesia as described above.

RESULTS

The invasive capacity of a population was estimated by the criterion of the average specific growth rate. In the experiments on cohorts in flow-through systems with water from the epilimnion of Lake Glubokoe, the juvenile survival rate of *D. magna* was similar to that in the experiments in which the water was enriched with chlorella, but the duration of development increased from 5 to 30 days (table). The fecundity of mature females decreased from 5 to 0.2 eggs per female. As a consequence, the estimated value of specific growth rate (per day) decreased from +0.24 to –0.02. Hence, it may be concluded that the abundance of *D. magna* culture in the case of its hypothetical introduction into Lake Glubokoe will slowly decrease against the background of very low juvenile mortality. The pressure of predation will markedly accelerate the suppression of *D. magna* in the lake.

Experiments of series 1 performed with the cohorts of *S. exspinosus* according to the same scheme coincided with a two-week period of improved feeding conditions in Lake Glubokoe. This followed from the increased fecundity of *Diaphanosoma brachyurum*, a dominant zooplanktonic filter-feeder, which was observed both in nature and in the cultures. Nevertheless, parameters of the test populations were inferior to those in the environment artificially enriched with food: the duration of development to maturity in *S. exspinosus* increased from five to six days, and fecundity decreased from six to eight eggs per female to only two eggs. The predicted intrinsic growth rates were 0.27 in the experiments with chlorella and 0.14 in the lake (table). Beyond the above two-week period, the intrinsic growth rate in the variant with lake water was lower. The duration of development to maturity increased from 5 to 13 days at very low fecundity, providing evidence for a high sensitivity of this species to food limitation in the lake.

Thus, trophic conditions for both species in the lake proved to be extremely unfavorable. The table shows the values of population parameters in experiments performed on different dates. It would be incorrect to calculate arithmetic means from these data, as food concentration in the lake continuously varied and the values of population parameters changed accordingly.

In all experiments with the cohorts of *D. brachyurum*, juvenile mortality was higher than in species with larger body size (Fig. 1). However, as *D. brachyurum* rapidly reached maturity (within five days), its specific growth rate was always positive, 0.04–0.05, despite low fecundity (1.00–2.45 eggs per female) (table).

The rate of population growth in *D. hyalina* was close to zero or negative in all experiments, but the contributions of survival and fecundity to this value signif-

icantly differed from those in *S. exspinosus* (table). At relatively high values of fecundity and a high growth rate of juveniles, which reached maturity within five to eight days, the latter species was characterized by a very high mortality (Fig. 1).

In the experiments on joint cultivation of *D. brachyurum* and *S. exspinosus* (Fig. 2), both species in both replications successfully coexisted for 40 days. The first decrease of abundance was followed by its increase. No competitive exclusion of either species was observed, and their fecundity was similarly low. Neither species had any obvious advantage, which was confirmed by similar dynamics of their abundance.

DISCUSSION

The results of our study on the influence of trophic conditions on the possibility of introducing new cladoceran species into the natural community of a mesotrophic lake show that, even in the absence of external factors of mortality related to predation, *D. magna* cannot colonize a mesotrophic lake, whereas *S. exspinosus* has a chance to withstand competition with aboriginal species.

The data summarized in the table and Fig. 1 show that the development of large species (*D. magna* and *S. exspinosus*) is significantly retarded if food is limited, but these juveniles are more tolerant to food deficiency than those of small species. In small *D. brachyurum*, the period of development to maturity is significantly shorter, but juveniles are less capable of starvation than juveniles of large species. Evidently, the tendency to reach maturity sooner and produce new progeny entails energy expenditures leading to the high mortality of immature individuals. In large species, conversely, slower growth allows an individual to save the energy necessary for life, but the appearance of new progeny is delayed. However, this is just a hypothesis, because actual energy expenditures in the course of individual growth and their distribution in the organism are not known.

Thus, we can distinguish two different strategies of the maintenance of population size under conditions of food deficiency. Small species increase their abundance more rapidly, reaching maturity within a shorter time. However, their juvenile mortality rate is higher than in large species. The abundance of large species increases more slowly, because the development of juveniles is retarded. However, this occurs against the background of lower juvenile mortality. Juveniles of large cladoceran species are more tolerant to starvation than small species, which agrees with experimental data obtained by other authors (Kreutzer and Lampert, 1999). Thus, both small and large species can survive and maintain their abundance under unfavorable feeding conditions, but in different ways. In the absence of predators in our experiments, we observed the coexistence of small *D. brachyurum* and large *S. exspinosus* in the lake
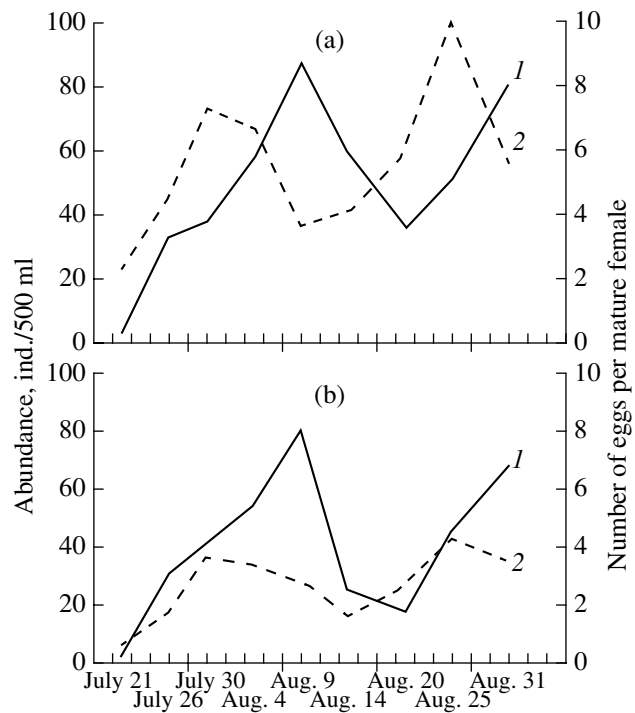

Fig. 2. Population dynamics of (*1*) *S. exspinosus* and (*2*) *D. brachyurum* during their joint cultivation: (a) the first replication, (b) the second replication.

water for 40 days. The pressure of predation by fish would obviously make the situation much less favorable for large species, as fish prefer feeding on large crustaceans, and the ratio would shift toward small species, as is observed in the lake. Other possible causes of changes in abundance in favor of small or large species include fluctuations of feeding conditions due to which, making possible transition of competitive advantage goes from large to small species, or vice versa (Romanovsky and Feniova, 1985); vertical migrations; segregation of species by food spectra; impact of environmental factors resulting in temporary disturbance of ecosystems, and vertical separation of species (Gliwicz, 2003).

For example, a high juvenile mortality in another species, *D. hyalina*, in summer generations (Fig. 1) prevents its successful development in the epilimnion, as follows from its low specific growth rates in the water from the epilimnion and at the temperature corresponding to that in the epilimnion. If feeding conditions in the lake were worse, this species would be viable only in the metalimnion, at 10°C, where expenditures for growth and the related mortality rate are significantly lower than in the epilimnion, where food is scarce and water temperature is high. Sushchenya et al. (1990) showed that when water temperature decreases, the plots of the growth rate of cladocerans as a function of food supply reach a plateau at lower values of food concentration. Therefore, when the food supply is poor, the growth rate of cladocerans may increase as temperature

decreases. In experiments with *Daphnia rosea* (Neill, 1981), most crustaceans kept at low phytoplankton concentrations failed to reach maturity at high summer temperatures and perished, but they successfully completed their development when the temperature was lower, although food concentration remained the same. In Lake Glubokoe, *D. hyalina* live in the metalimnion at lower temperatures during the greater part of the growing season, but they may coexist with other species in the epilimnion in early summer if feeding conditions are favorable (Katunina, 1983). Such separation in space appears to be caused by the impairment of feeding conditions.

Thus, the trophic factor has an effect on not only the species composition but also on the vertical structure of the zooplanktonic community in Lake Glubokoe. The method of cohort test cultures makes it possible to analyze in more detail the intraseasonal variation of trophic conditions in any water body on the basis of comprehensive data on individual growth, survival, and fecundity of species and to reveal critical periods determining the possibility of introduction of new species and the species diversity of aquatic communities.

The test-culture method allows us to predicting the invasion of alien cladoceran species to aquatic communities. It has been shown that *D. magna* cannot settle in Lake Glubokoe because of food deficiency resulting from competition for food between cladoceran species, whereas *S. exspinosus* can withstand competition with aboriginal pelagic species and survive. Small and large species have different strategies for maintaining their abundance when food is in short supply. The development of large species to maturity is retarded, with their juveniles remaining highly tolerant to starvation. Small species reach maturity sooner, but mortality of their juveniles is higher than in large species. Supposedly, the distribution of *D. hyalina* in Lake Glubokoe is limited to the metalimnion due to competition for food.

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