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Effect of food concentration on growth, reproduction and survivorship of *Bosmina longirostris* (Cladocera): an experimental study

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SUMMARY. 1. Body growth, reproduction and survivorship of *Bosmina longirostris* were monitored at four food concentrations (0.05, 0.10, 0.25 and 2.50 mg C l^{-1}) to examine the extent to which food concentration affects these life-history parameters.

2. Food concentration had a significant effect on growth, and most of the reproductive parameters (size and age at maturation, brood size, instar duration and egg development time). More than 60% of animals died before maturation at the lowest food concentration, although most animals survived until maturation at other food concentrations.

3. Change in life-history parameters resulted in a decrease in rate of population growth (r) from 0.310 to 0.020 day^{-1} with decreasing food concentration, showing that this cladoceran is highly food-limited in many lakes.

4. Importance of the effect of food concentration on egg development time was emphasized in relation to analysis of natural populations.

Introduction

Bosmina longirostris (O. F. Müller) is a small, planktonic cladoceran. As it is found commonly in many lakes, being markedly abundant in some, numerous studies have examined various ecological aspects, e.g. feeding mechanism (DeMott, 1982, 1985), population dynamics (Allan, 1977; DeMott & Kerfoot, 1982), productivity (Hanazato & Yasuno, 1985a), adaptive significance of change in morphs (Kerfoot, 1980; Black, 1980) and competitive ability against other cladocerans (Goulden, Henry & Tessier, 1982; Hanazato & Yasuno, 1987). However, only fragmentary information is available on the relationship of environmental factors to growth, reproduction and survivorship (Kerfoot, 1974; Goulden *et al.*, 1982; Hanazato & Yasuno, 1985a,b), although all of these parameters are essential in order to understand not only the nature of population dynamics but also life-history traits (Lynch, 1980).

Recent studies have revealed that freshwater zooplankton frequently meet severe food shortages in natural environments (e.g. Lampert, 1985). Therefore, change in food concentration may be one of the most important factors regulating the population size and influencing the life-history traits of *B. longirostris*. In this study, time sequences of growth, reproduction and survivorship were monitored for *B. longirostris* at different food concentrations, in order to examine the extent to which food concentration affects these life-history parameters. Food concentrations were chosen in order to cover most of the range found in natural environments.

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Methods and Materials

Bosmina longirostris was collected from the mesotrophic Ogochi Reservoir (Lake Okutama), located in the north-western part of Tokyo, Japan. The animals were cultivated in 1-l beakers filled with membrane-filtered (0.2 μm) tap-water at three food concentrations (0.10, 0.25 and 2.50 mg C l^{-1}) in a controlled chamber (20°C, LD=14:10) for at least 1 month before experiments. The water and food were changed every day and the population in each beaker was adjusted to less than 200 individuals in order to minimize the possibility of extreme food depression due to overgrazing.

Mixed algae grown in my laboratory aquarium (45 l) containing tap-water with a small cyprinid fish (*Pseudorasbora parva*) were used for both stock cultures and experiments. A quarter of the water in the aquarium was changed about once a week and a small amount of commercial-base fish food (Tetra flaked staple food) was added several times in a week as nutrient source. The mixed algae were comprised mainly of *Scenedesmus* (<15 μm in coenobia) and, to a minor extent, *Chlorella* and unknown small flagellates. Before being suspended as food, the aquarium water was filtered with 15-μm mesh, and the mixed algae in the filtrate were centrifuged and washed twice with membrane-filtered (0.2 μm) tap-water to minimize bacterial density. Microscopical observation by the epifluorescence technique revealed that the bacterial biomass was very low (<10^5 ml^{-1}) compared with algal biomass in the feeding suspension. *Bosmina longirostris* is known to ingest bacteria inefficiently (DeMott, 1982; Urabe, 1990). Therefore, bacteria in the feeding suspension were negligible in the present study. Algal concentration was quantified by haemacytometer. The algal carbon content and nitrogen/carbon ratio were determined with a CHN corder (Yanagimoto MT-3), yielding a mean of 20 pg C $cell^{-1}$ and 0.158 of N/C ratio. A preliminary experiment had clarified that these mixed algae were more suitable for establishing cultures of *B. longirostris* than any single strain of alga such as *Chlamydomonas* and *Chlorella*, available in the laboratory.

Growth experiments were done using four food levels (0.05, 0.10, 0.25 and 2.50 mg C l^{-1}) with filtered (0.2 μm) tap-water at 20°C and DL=14:10 cycle. Of each growth experiment with the different food treatments, two experiments (0.10 and 2.50 mg C l^{-1}) were done simultaneously in order to reduce the difference in food quality between the treatments. The other two experiments were also done simultaneously following the first two experiments. The animals used were from stock cultures with the same food level as those under the experimental conditions except for 0.05 mg C l^{-1}, for which animals from a stock culture containing 0.10 mg C l^{-1} were used.

For each experiment, twenty to thirty neonates within 12 h of birth were placed individually in 50-ml stoppered bottles. In order to keep the food particles homogeneous in the suspension, the bottles were secured to a grazing wheel which rotated at a speed of 1 rpm. All individuals were transferred every day to clean bottles with fresh feeding suspensions. At each daily transfer, animals were placed in a Sedgewick–Rafter chamber with a drop of water, the carapace length (Kerfoot, 1974) was measured using a microscope and the number of eggs or embryos carried in the brood pouch was recorded. These measurements were made within 3 min to minimize any subsequent effects of handling on individual growth and reproduction (Lynch, Weider & Lampert, 1986). The number of newly born individuals present in the bottles was also recorded, and these were transferred to the stock cultures. Moulting rate was determined from the frequency of appearance of cast skins in the bottles. The growth and reproduction of *B. longirostris* were monitored during the period from birth to 20 days in each experiment. The volume of bottle is so large for *B. longirostris* that change of food concentration in the bottle within a day is negligible: algal concentration after 1 days' feeding in the bottle with the largest individual was less than 8% of that in the bottle without the animal, even at the lowest food concentration (J. Urabe, unpublished).

The following parameters were measured, in addition to carapace length, brood size and number of surviving individuals on each date: carapace length, instar and age at maturation, percentage of reproduction, mean brood size, and LT50. In the present study, maturation was indicated by the first appearance of egg(s) in the brood pouch. The percentage of reproduction was the proportion of experimental animals surviving until maturation. The mean brood size was the mean egg number per adult instar.

The LT50 was the number of days by which 50% of the experimental animals had died. Net reproductive rate (R_0), the mean total of eggs produced per animal (Poolé, 1974) during the period from birth to 20 days, was estimated, and the rate of population increase (r) was computed by solving Lotka's equation.

Differences among food concentrations for each parameter were determined by ANOVA using raw data. The GT-2 method was applied for multiple comparisons (Sokal & Rohlf, 1981).

Results

Bosmina longirostris showed a continuous increase in carapace length from birth to 20 days above a food concentration of 0.10 mg C l^{-1}, although the rate of increase decreased with age (Fig. 1a). However, at the lowest food concentration, 0.05 mg C l^{-1}, no significant increase of carapace length was found after the third instar. Instar duration was significantly affected by food concentration (Table 1). That of the

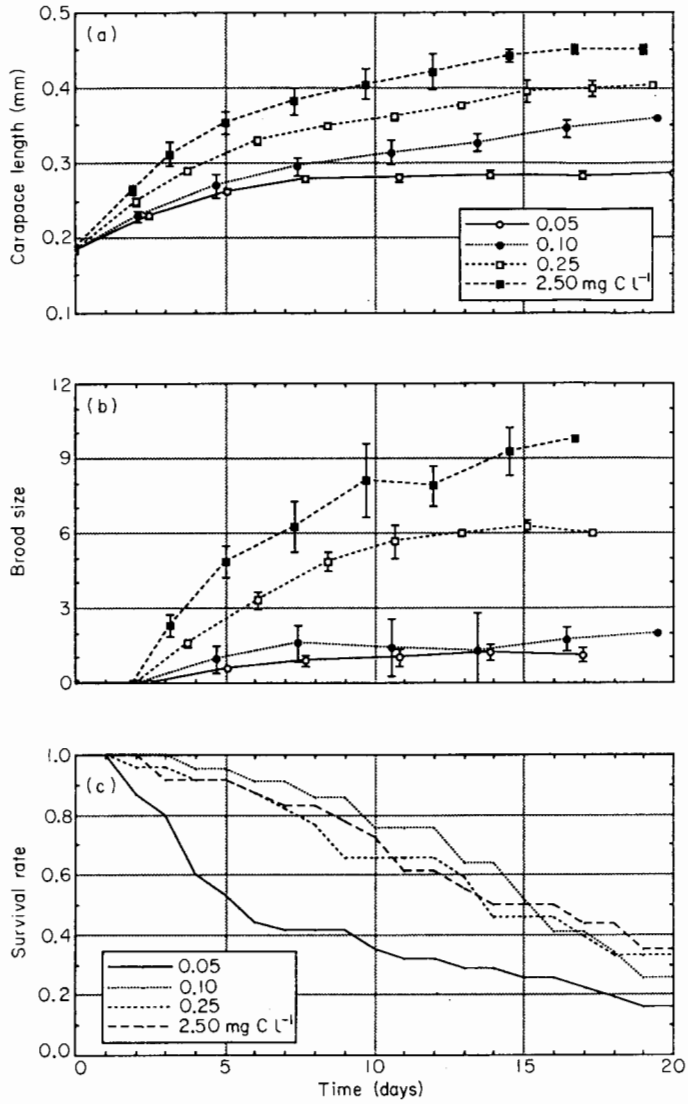

FIG. 1. Time sequence of change in carapace length (a), brood size (b), and survivorship (c) of *Bosmina longirostris* at four food concentrations. Symbols indicate successive instars and are mean ± SD.

TABLE 1. Mean and 1 SE (in parentheses) of instar duration and egg development time (days) for *Bosmina longirostris* at four food concentrations

Exp. no.	1	2	3	4	ANOVA			
Food concentration (mg C l^{-1})	0.050	0.100	0.250	2.500	df	*F*	*P*	Multiple comparison*
First instar	2.48 (0.11)	2.09 (0.06)	2.05 (0.05)	1.92 (0.04)	3, 83	10.435	0.001	1 2 3 4
Other juvenile instars	2.67 (0.09)	2.61 (0.51)	1.69 (0.12)	1.23 (0.09)	3, 84	38.515	0.001	1 2 3 4
Adult instars	3.06 (0.19)	2.91 (0.08)	2.34 (0.08)	2.21 (0.06)	3, 204	23.529	0.001	1 2 3 4
Egg development time	2.67 (0.17)	2.30 (0.09)	2.23 (0.07)	2.06 (0.04)	3, 151	7.431	0.001	1 2 3 4

* Significant differences at 5% level, as determined by the GT2-method, are denoted by different underlining.

first instar at the lowest food concentration was significantly longer than those at higher food concentrations. Between above 0.25 mg C l^{-1} and below 0.10 mg C l^{-1}, a two-fold difference was found in the duration of other juvenile instars, which were mainly second instar. Significant change with food concentration was also detected in the duration of adult instar and egg development time, although the difference between the low and high food concentrations was relatively small.

Size at maturation was significantly larger at the highest food concentration compared with other food concentrations, and the age at maturation decreased with increasing food concentration (Table 2). However, no significant difference was detected in the instar number at maturation among food concentrations, and most individuals matured at the third instar. With increasing food concentration, *B. longirostris* produced more eggs. The brood size increased with age above 0.25 mg C l^{-1} but was relatively constant regardless of the number of the adult instar below 0.10 mg C l^{-1} (Fig. 1b). The maximum mean brood size, eleven, was found in a seventh adult instar at the highest food concentration.

The survival curve showed a considerable difference between the lowest and other food concentrations (Fig. 1c). At the lowest food concentration, more than one-half of all experimental animals died within the first 6 days, and only 36% succeeded in reproducing. After maturation, however, the survival rate was high in this food concentration. On the other hand, the survival rate of juveniles was high above 0.10 mg C l^{-1} and more than 80% of the experimental animals succeeded in reproduction. In these higher food concentrations, the survival curve showed a near linear decline and half of all animals survived until 13 days.

Due to the significant effect of food concentration on most parameters, the net reproductive rate (R_0) and rate of population increase (r) differed markedly among food concentrations. Both R_0 and r decreased with decreasing food concentration and became close to 1 and 0, respectively, at the lowest food concentration (Table 2).

Discussion

Most parameters relating to the body growth and reproduction of *Bosmina longirostris* changed with changing food concentration between 2.50 and 0.05 mg C l^{-1}. The concentration of particulate organic carbon including phytoplankton is known to be less than 2.5 mg C l^{-1} in many lakes and ponds (Aizaki *et al.*, 1981). Therefore, it is not unusual for *B. longirostris* to be food-limited in many lakes.

Previously, *B. longirostris* was thought to increase its body size continually after maturation (Lynch, 1980). Goulden & Henry (1984) suggested that *B. longirostris* tends to cease reproduction when food is scarce. However, because they did not estimate the body growth rate, it was not clear whether *B. longirostris* allocates its net intake more in body growth than in reproduction at a low food concentration. The present study demonstrated that *B. longirostris* ceased to grow after maturation at the lowest food concentration, although it grew continually at a high food concentration. This implies that *B. longirostris* changes its pattern of resource allocation with changing food concentration and invests all of its net intake in reproduction under poor food conditions. Lynch (1980) questioned the adaptive significance of the continuous growth after maturation in *B. longirostris* and thought that the pattern might have evolved because it conferred an advantage against invertebrate predators preying selectively on small zooplankton. The present results suggest that *B. longirostris* may adopt such a resource allocation pattern to reduce its vulnerability to invertebrate predators only in a relatively high-food environment.

The maximum brood size found in the present study was higher than that in previous experimental studies (Kerfoot, 1974; Goulden *et al.*, 1982; Hanazato & Yasuno, 1985a). This implies that the food used here is suitable for *B. longirostris*. With decreasing food concentration, this cladoceran reduced its maturation size and brood size, and increased its maturation time. Similar trends have been shown in various species of *Daphnia* (Hall, 1964; Vijverberg, 1976; Porter & Orcutt, 1980; Taylor, 1985; Urabe, 1988). However, unlike *Daphnia* (Vijverberg, 1976; Porter & Orcutt, 1980; Urabe, 1988), *B. longirostris* did not show any significant difference in the maturation instar among food concentrations, most individuals maturing at the third instar. Kerfoot (1974) also reported that in *B. longirostris* ovulation pro-

TABLE 2. Reproductive and growth parameters for *Bosmina longirostris* at four food concentrations. 1 SE on mean is shown in parenthesis

Exp. no.	1	2	3	4	ANOVA			
Food concentration (mg C l^{-1})	0.050	0.100	0.250	2.500	df	F	P	Multiple comparison*
Carapace length at maturation (mm)	0.274 (0.006)	0.277 (0.003)	0.290 (0.004)	0.311 (0.005)	3, 45	13.64	0.001	1 2 3 4
Instar at maturation	3.33 (0.33)	3.17 (0.09)	3.06 (0.06)	3.00 (0.00)	3, 57	1.79	NS	
Age at maturation (days)	5.83 (0.83)	5.06 (0.34)	3.65 (0.10)	3.14 (0.08)	3, 64	19.33	0.001	1 2 3 4
Mean brood size	1.118 (0.125)	1.392 (0.122)	3.278 (0.294)	5.649 (0.312)	3, 192	70.000	0.001	1 2 3 4
% of reproduction†	36.6	81.0	80.0	87.3				
LT50 (days)†	5.37	15.20	13.69	14.00				
Net reproductive rate (R_0: 20 $days^{-1}$)†	1.313	3.534	9.304	26.854				
Rate of population growth (r: day^{-1})†	0.020	0.109	0.196	0.309				

* Significant differences at 5% level, as determined by the GT2-method, are denoted by different underlining.
† Statistical test was not done because replicate data were not available.
NS, not significant.

ceeds shortly after moulting of the second instar, and that eggs are laid first in the brood chamber at the third instar. Thus, food concentration may have less influence on the instar at which egg production is initiated in *B. longirostris* than in *Daphnia*.

A difference between *B. longirostris* and *Daphnia* was also detected in instar duration. Instar duration of the first juvenile is not affected by food concentration in *Daphnia* (Urabe, 1988), but differed significantly among food concentrations in *B. longirostris*. The extent of the effect on first instar duration seems to depend on the proportion of energy reserve in eggs and the metabolic rate during development of the embryo. In most cladocerans, including *Daphnia* and *Bosmina*, energy for respiration and development of eggs is supplied by parental individuals as yolk, which consists mainly of triacylglycerol (Goulden & Henry, 1984). This reserve material is also used for post-embryonic development (Goulden, Henry & Berrigan, 1987). Goulden *et al.* (1987) showed that although the proportion of yolk in eggs is similar between *Daphnia* and *B. longirostris*, that of residual reserve at birth is significantly smaller in the latter species. The duration of the first instar suggest that *Daphnia* produces eggs with enough yolk to support even the development of the first instar, whereas *B. longirostris* does not. In other words, feeding is essential in order for the first instar of *B. longirostris* to develop to the next. This implies that newborn young *B. longirostris* are more vulnerable to poor food conditions than those of *Daphnia* if the feeding apparatus and digestive system are not well developed immediately after birth. Incomplete development of the feeding system at birth is known in various animals (see review in Goulden *et al.*, 1987).

High vulnerability of juvenile individuals of *B. longirostris* to low food concentration was substantiated by the survival curve. More than 60% of individuals died before maturation, but the death rate decreased thereafter at the lowest food concentration. However, most individuals died after maturation at other food concentrations. A similar survival curve for *B. longirostris* was also obtained by Goulden *et al.* (1982).

The rate of population increase (r) changed with changing food concentration. However, the contribution of life-history parameters in determining r differed among food concentrations. The r is sensitive to changes in maturation time, brood size and survival rate (Allan, 1976). With decreasing food concentration from 2.50 to 0.10 mg C l^{-1}, the brood size decreased and maturation was prolonged, resulting in a decrease in r. However, these two parameters did not significantly change below 0.10 mg C l^{-1}, and thus the further decrease of r with decreasing food concentration was due to the decrease in survival rate. These results suggest that the ability of *B. longirostris* successfully to colonize a given environment under poor food conditions depends on the survival rate, especially that of juvenile instars, rather than the reproduction rate.

In *B. longirostris*, egg development time as well as the instar duration of adults increased with decreasing food concentration. The physiological background factor responsible for this phenomenon is not clear: with decreasing food concentration, *B. longirostris* may change the quality and quantity of yolk in its eggs. However, change of egg development time with food concentration is very important in relation to ecological analysis of a natural population. Analysis based on egg development time (egg ratio method) is known to be a powerful tool for examining the birth and death rates of cladocerans (Edmondson, 1960; Paloheimo, 1974). Many studies have applied this method for examining the population dynamics of cladocerans by assuming that egg development time depends only on water temperature. However, the present findings suggest that the birth rate, and thus the death rate, of *B. longirostris* calculated by the egg ratio method become overestimated under low food conditions if the egg development time of a well fed population is used. The effect of food concentration on egg development time should therefore be considered when applying the egg ratio method to populations of *B. longirostris*.

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