

Effects of Food Quality and Temperature on Life History Traits of *Moina macrocopa* Reared in Laboratory

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Life table experiments were performed in order to examine the effects of food quality on *Moina macrocopa* fed with four kinds of algal foods, *Botryococcus* sp., *Scenedesmus subspicatus*, *Selenastrum capricornutum*, and *Chlorella* sp., at 20°C. The temperature effects on *M. macrocopa* were also assessed, feeding *Chlorella* at 17°C, 20°C, 25°C, and a combination of 28°C (light) and 25°C (dark). The cartilaginous *Botryococcus* cells were inappropriate food for *Moina*. Among the foods tested, *Chlorella* was the food of the best quality in all accounts of life history traits. *Moina* grown on *Chlorella* showed higher net reproductive rate (R_0), longer mean and maximum longevities, earlier mean age at maturity, longer mean carapace length at maturity, larger mean clutch size, and shorter mean time interval between clutch productions than those grown on *Selenastrum* and *Scenedesmus*. An optimal temperature for *Moina* was 20°C. When *Moina* were grown on *Chlorella* at 20°C, they showed the highest r , the highest R_0 , the shortest T , the longest mean longevity, the earliest mean age at maturity, the longest mean carapace length at maturity, and the largest mean clutch size. The results of life table experiments showed that the individual and population growth patterns were much more affected by low temperature (17°C) than by high temperature ($\geq 25^\circ\text{C}$). In the optimal condition, the r value was very high, 5.1 in d^{-1} . In conclusion, the food quality and the temperature are the most important factors to govern the size and continuity of *Moina* population, by which the individual growth rates and reproductivity of members in the population can be controlled to survive in their environment such as small and temporary water bodies in nature.

Cladocerans are a representative group of freshwater zooplankton and the most efficient filter feeders in almost all types of freshwater communities. They play an important role in energy transfers along the food chain and in the seasonal algal community pattern. Thus, cladocerans have been extensively used in a variety of limnological research (Conklin and Provasoli, 1977; Mourelatos and Lacroix, 1990).

Many studies have demonstrated the usefulness of integrating laboratory experiments and field data to analyze trophic interactions between zooplankton and algae (Hall, 1964; Mourelatos and Lacroix, 1990; Brandl and Wittingerova, 1991; Ojala et al., 1995; Arbaciauskas and Gasiunaite, 1996). Through these studies, data on laboratory culture of cladocerans have been accumulated,

and various culture methods for several species have been developed. Nowadays, the laboratory cultures of cladocerans are widely used in various fields of applied biology as well as in limnology. Especially, cladocerans are among the most useful experimental animals in environmental toxicity assessment as test organisms (see Landis and Yu, 1995). However, the previous laboratory experiments have focused mainly on a few daphniid cladocerans, especially on *Daphnia*.

Moinid cladocerans are one of very interesting groups found mainly in temporary pools and saline lakes. They are adapted to survive during frequent dry periods and to populate rapidly in newly formed pools. They have been frequently used as experimental animals in physiological studies as well as in studies of embryology and genetics (Goulden, 1968). However, the life history traits of these animals in laboratory have been poorly understood (Conklin and Provasoli, 1977).

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The present study was carried out to elucidate the optimal culture conditions of *Moina macrocopa*, which is a representative zooplankton in small water bodies, especially found in rice-fields in Korea (Yoon and Kim, 1992), and to examine the effects of food quality and temperature on growth pattern, reproductivity, and fitness by the life table experiments.

Materials and Methods

Experimental animals and foods

The population of *Moina macrocopa* used in this study was obtained from rice-fields near Kwangju, Korea in June, 1997. Four kinds of algal foods, *Botryococcus* sp., *Scenedesmus subspicatus*, *Selenastrum capricornutum*, and *Chlorella* sp., were obtained from the Toxicology Research Center, Korea Institute of Chemical Technology, Korea.

Algal culture and food treatments

Algal cultures were performed in a temperature-controlled room at $25 \pm 1^\circ\text{C}$ under continuous illumination with the light intensity of 6,500-7,000 lux. Single-species sub-cultures of four kinds of algae were maintained axenically on USEPA (U.S. Environmental Protection Agency) algal culture medium (USEPA, 1991).

For preparation of foods for *Moina*, primary algal cultures were performed on USEPA algal culture media. Small inocula from the primary cultures were added to M4 media, which are commonly used for animal cultures (Elenndt and Bias, 1990), and cultured continuously at 25°C . The algae was used singly as food in a constant concentration of approximately 2×10^5 cells/ml.

Animal culture and experimental conditions

Animal cultures and the life table experiments for food quality effects were performed basically on M4 media in a temperature-controlled room at $20 \pm 1^\circ\text{C}$ under a long-day photoperiod (16 h and 8 h alternatively in light and dark conditions) with the light intensity of 6,500-7,000 lux. Based on the *Daphnia* culture conditions described by Hovenkamp (1991), Ojala et al. (1995), and Michels and De Meester (1998), the life table experiments for temperature effects were carried out at $17 \pm 1^\circ\text{C}$, $20 \pm 1^\circ\text{C}$, $25 \pm 1^\circ\text{C}$, and a combination of $28 \pm 1^\circ\text{C}$ (light) and $25 \pm 1^\circ\text{C}$ (dark) [28(L)/25(D)°C].

Uniclonal stock culture of *Moina macrocopa*

Preliminary culture was carried out for their acclimation to the laboratory conditions in rice-field water (filtered through 60 μm paper) supplemented with *Chlorella* sp. for 3 d. For stock culture, a parthenogenetic female from preliminary culture was chosen to establish genetically homogeneous population and was cultured on M4 medium supplemented with *Chlorella* sp. (ap-

proximately 2×10^5 cells/ml) as a food. Culture medium was refreshed every five days with fresh one supplemented with *Chlorella* cells.

Life table experiments

The life table experiments for food quality effects were carried out with *M. macrocopa* and four green algae, which were used as the herbivore and foods, respectively, at 20°C . The experiments for temperature effects were carried out with single kind of algal food at 20°C , 25°C and 28(L)/25(D)°C. All the experiments were performed with a static and renewal method in a temperature-controlled room as described previously (Hall, 1964; Mitchell et al., 1992; Fernando et al., 1996; Michels and De Meester, 1998; Repka et al., 1999).

To begin a life table experiment, an individual *Moina* neonate was removed from a stock culture and grown in a 100 ml test tube under a treatment condition. Thereafter, an offspring from the culture was randomly selected and placed in a fresh test tube for subsequent cohort experiments. The cohort life table experiment was started with the offsprings from the same clutch of this animal. Each of all the *Moina* neonates, less than 6 h old, in a cohort was placed in a fresh test tube under various experimental conditions.

In continuous cultures, *Moina* individuals in each test tube were counted every six hours to quantify survivorship rate, reproduction time, and clutch size. Some individuals (generally 3 in all replicates) were daily collected and the carapace length and the width were measured with a Nikon compound microscope attached to the drawing tube system. In this study, we used the carapace lengths and widths as an indicator of individual growth. All new offsprings were discarded from each culture after count.

The individual culture was placed in a fresh test tube every three days over the whole period of the experiment. There were 4-6 replicate experiments for each treatment. Experiments were begun with 12-38 individuals and continued until death of the last one.

The net reproductive rate (R_0), generation time (T), and intrinsic rate of natural increase (r , population growth per individual) of cohorts were calculated according to the following equation (Pianka, 1983; Fernando et al., 1996):

$$R_0 = \sum l_x m_x, T = \sum l_x m_x x / \sum l_x m_x, \text{ and } r = \ln R_0 / T,$$

where l_x is age-specific survivorship (proportion of individuals to age x), m_x is age-specific fecundity (mean number of offspring produced per surviving individual of age x), and x is age in d. The following life history traits were also quantified: mean longevity (mean period from the birth to the death of an individual); maximum longevity (longevity of the indi-

vidual that lived to the last of a cohort); mean age at maturity (mean age at which an individual produced its first clutch); size (carapace length in mm) at maturity; clutch size (number of offsprings produced at each clutch); time interval between clutch productions (time interval between a brood hatch and the next); survivorship (proportion of cohort surviving) and individual growth (carapace length and width as each a function of age). Values of life history traits were calculated by pooling the total results of 4-6 experiments in each treatment.

Additional abbreviated life table experiments (Vanni and Lampert, 1992; Michels and De Meester, 1998) were conducted for 15 d to examine the low temperature effects at 17°C. The experiments were performed with 2 replicates of total 33 individuals. The results obtained from the cultures at 17°C and 20°C were compared with each other in respect to several life history traits such as mean age at maturity, mean time interval between the first and the second clutch productions, mean clutch size of the first, and survivorship rate to day 15.

Results

Food quality effects on the life history traits of Moina

The life history traits of *Moina macrocopa* were examined with *Botryococcus* sp., *Scenedesmus subspicatus*, *Selenastrum capricornutum*, and *Chlorella* sp. as foods by life table experiments (Table 1). As shown in Table 1, unfortunately, among the four kinds of algae, *Botryococcus* could not be used by *Moina* neonates as a food at all.

When *Moina* were grown on *Scenedesmus*, the intrinsic rate of natural increase (*r*, population growth rate) was below half of those obtained from *Selenastrum* and *Chlorella*. The values of net reproductive rate (*R*₀) and mean longevity on *Scenedesmus* were also much lower than those from the other two algal treatments. However, when *Moina* were fed with *Scenedesmus*, the generation time (*T*) and the maximum longevity were longer than those from the other two treatments. Although the *r* values were the same, *Selenastrum* and *Chlorella* treatments were distinctly different from each other in many life history traits such as *R*₀ and *T*. The cohorts of *Moina* grown on *Chlorella* showed significantly higher values than those on *Selenastrum* in *R*₀, *T*, and mean and maximum longevity (Table 1).

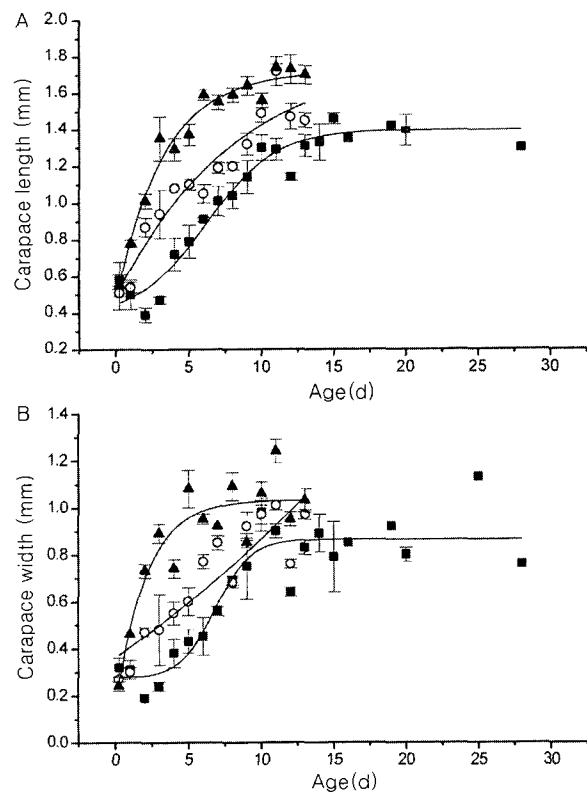


Fig. 1. Growth patterns of *Moina macrocopa* fed with three kinds of algae *Scenedesmus subspicatus* (■), *Selenastrum capricornutum* (○), and *Chlorella* sp. (▲), at 20°C. The growth patterns were determined by measuring the carapace lengths (A) and the widths (B). The algae were fed at a constant concentration of approximately 2 × 10⁵ cells/ml as described in "Materials and Methods".

The individual growth of *Moina* was greatly affected by different algal food sources. As shown in Fig. 1, *Chlorella* was the best food for *Moina* individual growth, as deduced from the carapace length and width. Interestingly, the growth of *Moina* was delayed at early growth stage when they were fed with *Scenedesmus*. All growth curves from three algal treatments showed the logarithmic growth patterns in the carapace length (Fig. 1A). However, the curves in carapace width were somewhat different from each other (Fig. 1B). It seems that these differences may come from the great variability of carapace length depending on individuals carrying eggs or embryos.

The age at maturity was also altered by different

Table 1. Life history traits of *Moina macrocopa* from the life table experiments according to food quality

| Parameter | <i>Botryococcus</i> sp. | <i>Scenedesmus subspicatus</i> | <i>Selenastrum capricornutum</i> | <i>Chlorella</i> sp. |
|---|-------------------------|--------------------------------|----------------------------------|----------------------|
| Intrinsic rate of natural increase (<i>r</i> , d ⁻¹) | - | 0.24 | 0.51 | 0.51 |
| Net reproductive rate (<i>R</i> ₀) | - | 13.49 | 48.67 | 89.23 |
| Mean generation time (<i>T</i> , d) | - | 10.78 | 7.62 | 8.73 |
| Maximum longevity (d) | - | 28.50 | 15.25 | 18.50 |
| Mean longevity (d) | - | 7.25 ± 5.58 | 10.57 ± 2.72 | 14.16 ± 3.26 |
| Mean age at maturity (d) | - | 6.61 ± 1.17 | 4.07 ± 0.36 | 3.91 ± 0.33 |
| Mean carapace length at maturity (mm) | - | 1.16 ± 0.85 | 1.07 ± 0.04 | 1.45 ± 0.04 |
| Mean clutch size | - | 10.96 ± 1.94 | 11.37 ± 4.20 | 12.87 ± 1.49 |
| Mean time interval between clutch productions (h) | - | 58.16 ± 14.21 | 43.67 ± 6.71 | 42.14 ± 3.50 |
| Total number of individuals of experiments at start | - | 69 | 75 | 61 |

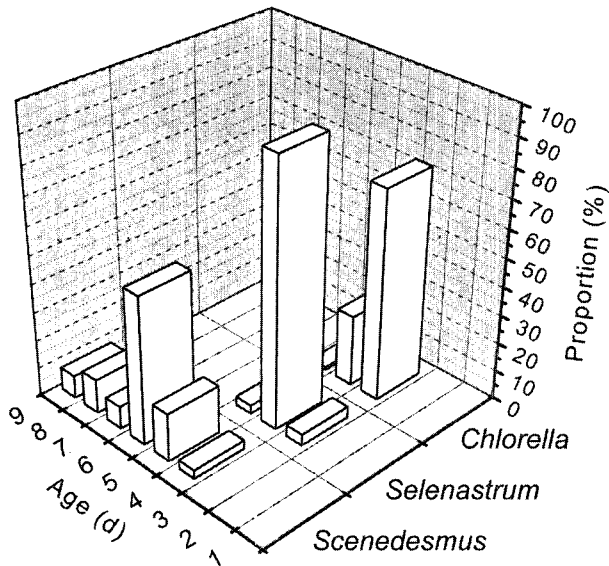


Fig. 2. The food quality effects on the age at maturity of *Moina macrocopa* in day-specific proportion. *Moina* were fed with three kinds of algae, *Scenedesmus subspicatus*, *Selenastrum capricornutum*, and *Chlorella* sp., and cultured at 20°C as described in Fig. 1. The maturity was determined by the first clutch production.

algal treatments (Fig. 2; Table 1). *Moina* matured at much later age when they were grown on *Scenedesmus* than when cultured on *Selenastrum* or *Chlorella*. The age at maturity was delayed more than 1.5 d on the average and more variable to individuals when they were grown on *Scenedesmus* than the other two kinds of algae (Table 1). Individuals grown on *Scenedesmus* produced their first clutches at 3-9 d, while those on *Selenastrum* or *Chlorella* did at 3-5 d. When fed with *Chlorella* and *Selenastrum*, *Moina* produced the first clutches at 3 d (74%) and 4 d (93%), respectively. However, the time point of the first clutch production was delayed to 6 d in 52% individuals fed with *Scenedesmus* (Fig. 2).

The productivity was affected by food quality (Table 1; Fig. 3). When *Moina* were fed with *Chlorella*, *Selenastrum*, and *Scenedesmus*, the mean clutch sizes were 12.87, 11.37, and 10.96, respectively. In addition, the mean time interval between brood hatches (clutch productions) were 42.14 h, 43.67 h, and 58.16 h, respectively (Table 1). As shown in Fig. 3A, there was no general relationship between the clutch size and the order of clutch. Interestingly, the cumulative clutch sizes were larger in *Moina* fed with *Chlorella*, *Scenedesmus*, and *Selenastrum* in decreasing order (Fig. 3B). When *Moina* were fed with *Chlorella* and *Selenastrum*, the intervals between brood hatches were very constant and short (Fig. 3C). However, in case of *Scenedesmus*, the intervals were very unstable and longer. These results indicate that *Chlorella* is the best quality food for *Moina* in these experimental conditions.

The survivorships of *Moina* were examined according to three kinds of algal foods (Fig. 4). When fed with

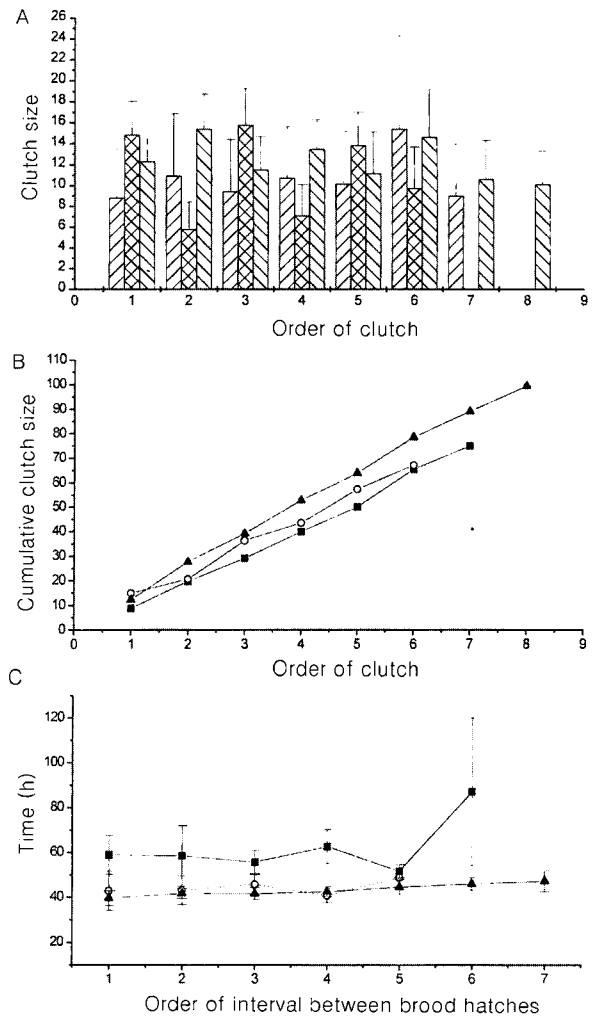


Fig. 3. Mean (A) and cumulative clutch sizes (B), and mean time intervals between clutch productions (C) of *Moina macrocopa* fed with three kinds of algae, *Scenedesmus subspicatus* (□, ■), *Selenastrum capricornutum* (⊗, ⊙), and *Chlorella* sp. (⊞, ▲), and cultured at 20°C as described in Fig. 1.

Chlorella and *Selenastrum*, *Moina* showed 100% survivorship at day 5. However, 40% of *Moina* could not survive at day 5 when they were fed with *Scenedesmus* (Fig. 4). These results suggest that *Scenedesmus* is an inappropriate food for *Moina*, compared to *Chlorella* and *Selenastrum*.

Temperature effects on the life history traits of *Moina* fed with *Chlorella*

The population growth rate (r) and net reproductive rate (R_0) of *Moina* fed with *Chlorella* decreased with increasing temperature from 20°C to 28(L)/25(D)°C. The mean longevity at 20°C was longer than those at two high temperature conditions [25°C and 28(L)/25 (D)°C], however, the generation time (T) and maximum longevity were shorter at 20°C (Table 2).

As shown in Fig. 5, individual growth of *Moina* was

Table 2. Life history traits of *Moina macrocopa* from the life table experiments according to temperature. *Moina* fed with *Chlorella* sp. were cultured at 20°C, 25°C, and a combination of 28°C (light) and 25°C (dark) (28(L)/25(D)°C)

| Parameter | 20°C | 25°C | 28(L)/25(D)°C |
|--|--------------|---------------|---------------|
| Intrinsic rate of natural increase (r , d ⁻¹) | 0.51 | 0.43 | 0.41 |
| Net reproductive rate (R_0) | 89.23 | 64.74 | 40.97 |
| Mean generation time (T , d) | 8.73 | 9.63 | 9.07 |
| Maximum longevity (d) | 18.50 | 20.25 | 20.00 |
| Mean longevity (d) | 14.16 ± 3.26 | 13.36 ± 4.04 | 13.53 ± 4.32 |
| Mean age at maturity (d) | 3.91 ± 0.33 | 4.62 ± 2.06 | 5.86 ± 2.09 |
| Mean carapace length at maturity (mm) | 1.45 ± 0.04 | 1.33 ± 0.02 | 1.28 ± 0.02 |
| Mean clutch size | 12.87 ± 1.49 | 10.37 ± 1.64 | 8.19 ± 2.58 |
| Mean time interval between clutch productions (h) | 42.14 ± 3.50 | 39.84 ± 11.58 | 35.76 ± 13.56 |
| Total number of individuals of experiments at start | 61 | 69 | 62 |

affected by high temperature conditions (>20°C). *Moina* grew slower at high temperature conditions: the growth rates were lower in the range of 25°C and 28(L)/25(D)°C than in that of 20°C and 25°C. Moreover, the individual growth was more delayed in early growth stages at 28(L)/25(D)°C (Fig. 5A).

The age at maturity was also greatly affected by temperature condition (Fig. 6; Table 2). Maturation of *Moina* was greatly delayed by high temperature. The degree of inhibitory effect increased with increasing temperature, but was variable depending on individuals. The standard deviation (SD) values of the mean age at maturity were also much larger at high temperature conditions than at 20°C (Table 2). Individuals grown at above 25°C produced their first clutches in 2-13 d, while it took 3-5 d at 20°C. The proportion of the individuals that began clutch productions after 4 d was 57% at 25°C and 69% at 28(L)/25(D)°C, while a large proportion (74%) of individuals grown at 20°C produced the first clutches in 3 d (Fig. 6). When *Moina* were raised at high temperatures, their maturations delayed to 0.72 d at 25°C and to 1.95 d at 28(L)/25(D)°C, and their carapace lengths were relatively small, compared to those at 20°C (Table 2).

Productivity was affected by temperature as well (Table 2; Fig. 7). When *Moina* were grown at 20°C, 25°C, and 28(L)/25(D)°C, the mean clutch sizes were 12.87, 10.37, and 8.19, respectively. In addition, the mean time interval between brood hatches were 42.14,

39.84, and 35.76 h, respectively (Table 2). As shown in Fig. 7A, there was no general relationship between clutch size and the order of clutch. The cumulative clutch sizes were larger at 20°C than at 25°C, and 28(L)/25(D)°C (Fig. 7B). As shown in Fig. 7C, the intervals between brood hatches were constant when *Moina* were raised at 20°C, but they were relatively unstable at 25°C and 28(L)/25(D)°C. All these results are well matched with the data from food quality effects (Fig. 3).

Effects of temperature on the survivorship of *Moina* were investigated as shown in Fig. 8. Under the high

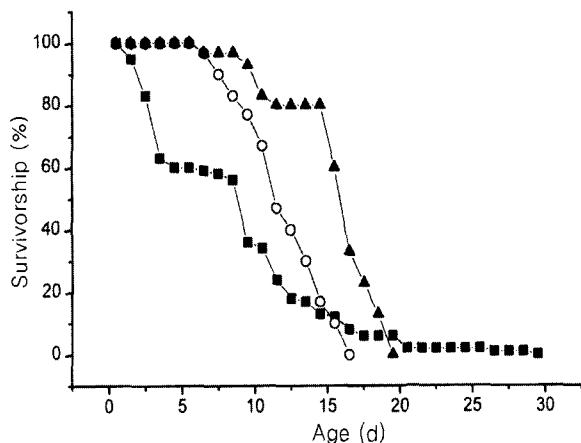


Fig. 4. Survivorship of *Moina macrocopa* fed with three kinds of algae, *Scenedesmus subspicatus* (■), *Selenastrum capricornutum* (○), and *Chlorella* sp. (▲), and cultured at 20°C as described in Fig. 1.

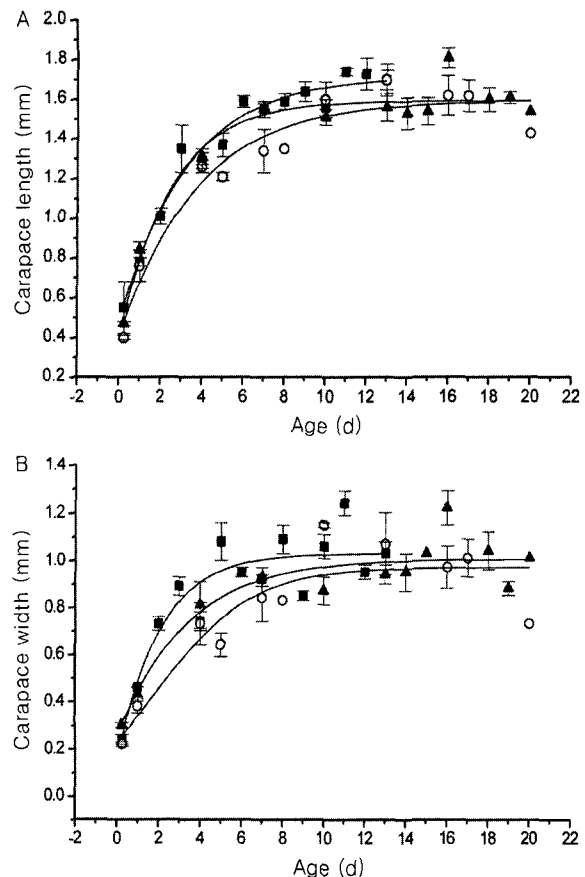


Fig. 5. Growth patterns of *Moina macrocopa* fed with *Chlorella* sp. at 20°C (■), 25°C (○), and a combination of 28°C (light) and 25°C (dark) (28(L)/25(D)°C) (▲). The growth patterns were determined by measuring the carapace lengths (A) and the widths (B). The alga was fed at a constant concentration of approximately 2×10^5 cells/ml as described in Fig. 1.

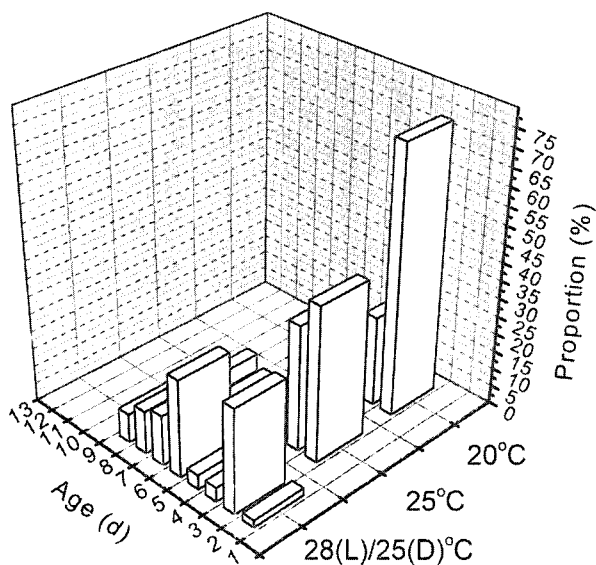


Fig. 6. The temperature effects on the age at maturity of *Moina macrocopa* in day-specific proportion. *Moina* were fed with *Chlorella* sp. and cultured at 20°C, 25°C, and a combination of 28°C (light) and 25°C (dark) (28(L)/25(D)°C). The alga was fed at a constant concentration of approximately 2×10^5 cells/ml as described in Fig. 1. The maturity was determined by the first clutch production.

temperature conditions [25°C and 28(L)/25(D)°C], the rates of survivorship were slightly decreased compared to that of 20°C, suggesting that 20°C is an optimal temperature for *Moina* (Fig. 8).

The rate of survivorship of *Moina* at low temperature (17°C) was maintained at about 72.73% at day 15, which is higher than that at 20°C (Table 3). However, the mean ages at maturity at 17°C and 20°C were 14.31 d and 3.91 d, respectively (Fig. 9). Moreover, the mean time intervals between the first and the second clutch productions at 17°C and 20°C were 177.60 h and 39.66 h, respectively (Table 3). These results suggest that the low temperature (17°C) can reduce the rate of individual growth and reproductivity of *Moina* although it could maintain the rate of survivorship at a relatively higher level than the optimal temperature, 20°C.

Discussion

The results presented above clearly show that food quality and temperature strongly affect the life history traits and fitness of *Moina macrocopa*. This implies that both algal community composition and seasonal change of water temperature are potentially important regulatory factors for natural planktonic herbivore populations.

Food quality strongly affected adults as well as juveniles of *M. macrocopa*. The food quality effect on juveniles was manifested in their mortality when they were raised on *Botryococcus* cells. It has been known that cladoceran juveniles are much more affected by food quality such as cell types than adults. This is owing to the fact that juveniles exhibit incomplete man-

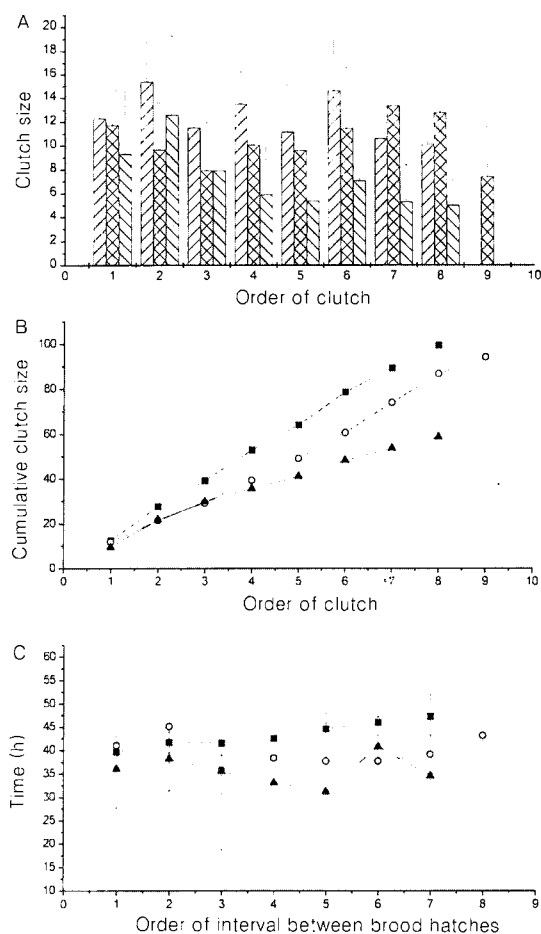


Fig. 7. Mean (A) and cumulative clutch sizes (B), and mean time intervals between clutch productions (C) of *Moina macrocopa* fed with *Chlorella* sp. and cultured at 20°C (hatched), 25°C (cross-hatched), and a combination of 28°C (light) and 25°C (dark) (28(L)/25(D)°C) (diagonal lines).

dible development and have a tendency to pass food through the gut rapidly, reducing the time for sufficient digestion (Vanni and Lampert, 1992). This fact was confirmed by this study that the indigestible cartilaginous *Botryococcus* cells are not an adequate food for juvenile *Moina*. In addition, the delayed maturity age and slower juvenile somatic growth were also observed when *Moina* were grown on *Scenedesmus* or *Selenastrum* (see Table 1).

Food quality also affected *Moina* adults as well. When *Moina* were raised on *Scenedesmus*, it was evident that the mean clutch sizes were relatively small and the longer time was required for producing next clutches, compared to those from *Selenastrum* and *Chlorella*. From these results, it is postulated that the population growth rate (r) can be strongly influenced by food quality through changing both the mean clutch size and the time interval between clutch productions in an adult stage of *Moina*.

These food quality effects are quite different from *Daphnia* adults (DeBiase et al., 1990; Hessen, 1990; Vanni and Lampert, 1992; Rothhaupt and Lampert,

Table 3. Comparison of the life history traits of *Moina macrocopa* grown at 17°C with those at 20°C from the abbreviated life table experiments with *Chlorella* sp.

| Parameter | 17°C | 20°C |
|--|----------------|--------------|
| Mean age at maturity (d) | 14.31 ± 4.42 | 3.91 ± 0.33 |
| Mean time interval between the first clutch and the second productions (h) | 177.60 ± 56.71 | 39.66 ± 3.26 |
| Mean clutch size of the first | 11.72 ± 4.58 | 12.29 ± 2.58 |
| Survivorship rate to day 15 (%) | 72.73 | 60.00 |
| Total number of individuals of experiments at start | 33 | 61 |

1992; Boersma and Vijverberg, 1995). It has been reported that food quality affects *Daphnia* adult traits much less than food quantity. Moreover, *Daphnia* adults are unaffected by food type and can convert various food equally well into eggs (Vanni and Lampert, 1992; Boersma and Vijverberg, 1995). However, the life history traits of *Moina* adults as revealed by the present study were greatly affected by food quality (Table 1; Figs. 1-4). The reason why food quality differently effects to *Moina* compared to *Daphnia* is unclear, but it maybe related to the differentiated habitat preferences. *Moina* prefer small and temporary water bodies such as rice-fields, while *Daphnia* mostly adapt to large and permanent water bodies. In nature, *Daphnia* live together with various kinds of food and predators. Therefore, *Daphnia* are under two opposite major selective pressures of predation in size, that is, small size is preferred by invertebrates and large size by fishes (Hanazato and Dodson, 1992). In this point of view, it is favorable for *Daphnia* to grow continuously throughout adulthood when they attain the size at maturity to reduce mortality inflicted by the invertebrate predators. Larger size is also somewhat preferable in producing larger sized clutch, though it will increase vulnerability to the fish predators (Vanni and Lampert, 1992). In contrast to *Daphnia*, *Moina* usually live on simple food such as algae and have relatively a few predators in nature. Such environment requires them to overcome extreme abiotic conditions such as dry or hot temperature conditions than to avoid being preyed. Thus, the relationship to predators is probably not so important for *Moina*, as compared to *Daphnia*. It seems that the

priority is provided by an intra-specific relationship in determining the population growth for *Moina*. The results presented in this study suggest that *Moina* individuals may adapt to avoid an excessive increase in population by reducing clutch size and by delaying the progress of clutch productions even after maturity when they are faced with inappropriate environmental conditions such as poor food quality.

Temperature was also a critical factor to determine the life history traits of *Moina* in both juvenile and adult stages. It was clearly observed in the delayed maturity age and the slower juvenile somatic growth at high ($\geq 25^\circ\text{C}$) and low (17°C) temperatures, compared to those at 20°C . When *Moina* were raised at high and low temperatures, the mean clutch sizes were relatively small and the longer time was required for producing the next clutches, compared to those at 20°C (Tables 2 and 3; Figs. 5-9). From these results, it is suggested that the population growth rate (r) of *Moina* may be strongly affected by temperature condition through changes in the age at maturity, the juvenile somatic growth rate, the mean clutch size, and the time interval between clutch productions in both juvenile and adult stages. As discussed previously, these results are also well matched with those obtained from food quality experiments (Table 1).

The population increase rate (r , 5.1 in d^{-1}) of *Moina* grown on *Chlorella* or *Selenastrum* at 20°C (Table 1) was more than 1.5 times higher than those of *Daphnia* reported previously (DeBiase et al., 1990; Vanni and Lampert, 1992; Boersma and Vijverberg, 1994). This implies that *Moina* can populate more rapidly than *Daphnia* under a suitable condition.

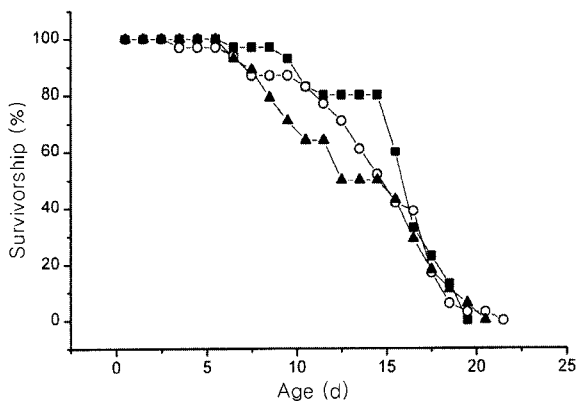


Fig. 8. Survivorship of *Moina macrocopa* fed with *Chlorella* sp. and cultured at 20°C (■), 25°C (○), and a combination of 28°C (light) and 25°C (dark) ($28(\text{L})/25(\text{D})^\circ\text{C}$) (▲).



Fig. 9. Mean age at maturity of *Moina macrocopa* fed with *Chlorella* sp. at 17°C (▨), 20°C (⊠), 25°C (▤), and a combination of 28°C (light) and 25°C (dark) ($28(\text{L})/25(\text{D})^\circ\text{C}$) (▥). The alga was fed at a constant concentration of approximately 2×10^6 cells/ml. The maturity was determined by the first clutch production.

In conclusion, food quality and temperature are the most important factors to govern the size and continuity of *Moina* population. By controlling the individual growth rates and the reproductivities of the members in the population, they can survive in environment such as small and temporary water bodies in nature.

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