Food limitation and seasonal population declines of rotifers

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Summary. *Keratella cochlearis* exhibited consistent seasonal abundance patterns during a four-year study in Little Rock Lake, Wisconsin, U.S.A. In each year, spring population peaks were followed by strong summer reductions. Concomitant with population declines, there were reductions in rotifer egg ratios. *Keratella taurocephala* abundance patterns were similar to those of *K. cochlearis* during 1984 and 1985, but not in 1986 and 1987, when spring peaks and summer declines were not apparent. However, summer declines in the egg ratio of *K. taurocephala* were observed during each year. The reduction in rotifer populations simultaneously with decreased egg ratios suggested that population declines were caused by food limitation. Food-addition experiments conducted in situ in small enclosures indicated that food was limiting for *K. cochlearis* when its populations were declining, but not during other periods of the year. *Keratella taurocephala* did not show a consistent response to food addition.

Key words: Rotifers – *Keratella cochlearis* – *Keratella taurocephala* – Food limitation – Population declines

Drastic declines in zooplankton populations occur commonly in lakes (Comita 1972; Hall 1971; De Bernardi 1974; Petersen 1983). Such declines can often be traced to the effects of predation (Hall 1971; Sprules 1972; Dodson 1974; Threlkeld 1979). However, other mechanisms such as resource limitation and interference competition (Gilbert and Stemberger 1985; Gilbert 1989) may also cause sharp decreases in zooplankton populations, but their general role is not clear. Here we examine the role of resource limitation in the population dynamics of two rotifers, *Keratella cochlearis* and *Keratella taurocephala,* in an oligotrophic lake where population

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parameters had suggested that food limitation led to seasonal declines.

Much of the work on resource limitation in zooplankton population dynamics has been based on cladocerans. For *Daphnia* spp. several instances of population declines have been linked with natural variation in food (Lampert 1978; Goldman et al. 1979; Threlkeld 1979, 1985; Larson et al. 1985; and Lampert et al. 1986). Tessier (1986) provides clear experimental evidence for food limitation in the midsummer declines of *Holopedium gibberum*. Vanni (1987) showed an increase in density of *Bosmina longirostris, Ceriodaphnia lacustris* and *Diaphanosoma birgei* when nutrients were added to enclosures.

Information on the population dynamics of planktonic rotifers is less extensive. Edmondson (1965) correlated the dynamics of three rotifer species with temperature and algal populations and suggested that both parameters have important effects on rotifer populations. Neill (1984) provided experimental evidence that rotifer populations are restricted by competition with cladocerans. Foran and King (1982) concluded that predation by *Chaoborus punctipennis* and low food concentrations were the main factors limiting *Polyarthra vulgaris* in a northern Michigan bog lake. Other investigators (Gilbert and Stemberger 1985; Schneider 1990) have demonstrated that mechanical interference by cladocerans may also depress rotifer abundances. Despite this work, the extent of resource-mediated control of natural rotifer populations remains poorly understood.

Population studies in Little Rock Lake, Wisconsin indicated that two rotifer species, *Keratella cochlearis* and *K. taurocephala,* exhibited a repeated annual pattern of population declines after spring peaks (Frost and Montz 1988). The reduction in rotifer populations occurred simultaneously with a substantial decline in their egg ratios. These patterns led us to hypothesize that the rotifer population declines were caused by resource limitation. Here we report the pattern of *K. cochlearis* and *K. taurocephala* abundances over a continuous four-year study period and the results of experimental tests of food limitation. To evaluate food limitation, we contrasted

rotifer reproduction in enclosures that contained experimentally augmented food with reproduction in control enclosures without food additions.

Study site

Little Rock Lake, is a small oligotrophic lake located in the Northern Highland Lake District of Wisconsin, U.S.A. It is the site of a whole-system manipulation investigating the effects of acid deposition (Watras and Frost 1988). Little Rock's two distinct basins were separated by an impermeable curtain in 1984, and its north basin was acidified beginning in 1985. The work reported here was conducted in the lake's south basin, which was not manipulated chemically. The chemistry of the south basin is typified by low alkalinity (25 μeq/L), low specific conductance (12 μs/cm), near neutral acidity (6.0) and moderate transparency (Secchi depth > 4 m). Its maximum depth is 6.5 m. Brezonik et al. (1986) provide additional details on Little Rock's basic limnology.

Little Rock Lake has a diverse zooplankton assemblage with greater than 40 recorded species, but only a small number of taxa are dominant in the community (Brezonik et al. 1986; Frost and Montz 1988). In the South Basin, *Kellicottia bostoniensis, Keratella cochlearis, Keratella taurocephala* and *Polyarthra* spp. are the most abundant rotifers. *Holopedium gibberum, Daphnia dubia* and *Daphnia parvula* are the most abundant cladocerans. *Diaptomus minutus, Mesocyclops edax* and *Cyclops bicuspidatus thomasi* predominate among the copepods.

Methods

Annual patterns

Zooplankton was collected using a 33–L Schindler-Patalas plankton trap equipped with a 53-μm nitex mesh and preserved in a cold 12%-buffered, sugar-formalin solution (Prepas 1978) to prevent egg loss. Samples were taken at a central station at the deepest portion of the south basin at 0, 4, and 6 m. Collections were made between 10: 00 a.m. and 4: 00 p.m. every 2 weeks during ice free periods and every 5 weeks when the lake was ice covered. Additional samples were collected at weekly intervals during summer of 1984 and 1985. Rotifers were enumerated in subsamples from these samples, and the number of eggs per female was recorded. We report the hypsometrically weighted average number of rotifers per liter in the water column. These values were derived by weighting counts from the 0, 4 and 6 m samples by the volume that each depth stratum occupies relative to the total volume of the lake basin.

Food limitation experiments

To assess food limitation we contrasted the number of eggs per rotifer in enclosures with experimentally increased food availability versus control enclosures with no food addition. We conducted our experiments in 4–L plastic bottles on six dates from June through September in 1986, and on ten dates from April through September during 1987. For each experiment, two zooplankton samples were collected at 4 m at the central station of the south basin of Little Rock Lake using a 31–L Schindler-Patalas Plankton trap equipped with a 53-μm nitex mesh. One sample was preserved immediately

and used to estimate the densities and egg ratios of *Keratella cochlearis* and *K. taurocephala* in the lake at the start of an experiment. The second sample was placed in an insulated container, to avoid drastic changes in temperature, and transported 6 km to the Trout Lake Station for processing. This sample was concentrated and split into 8 subsamples. The subsamples were placed into bottles and diluted with 53-μm filtered lake water to yield lake-level zooplankton densities and food conditions similar to those in the lake. For food-added enclosures, *Chlamydomonas reinhardtii* (Chlorophyceae UTEX 90) was added to yield a final concentration of 10^4 cells/ml (dry mass = 0.54 μg/ml). We included all zooplankton species present in the samples in the enclosures. Therefore the interaction among species inside the enclosures should be similar to those in the lake, except for the effect of the food addition.

The total manipulation time of the zooplankton samples varied from 3 to 4.5 hours from their capture to their return to Little Rock Lake. The number of replicates for both food-added and control treatments was two in the 1986 experiments, except during the August 13 and September 20 experiments when there were three replicates. During 1987, the number of replicates was four, except for the May 5 and July 31 experiments, when there were three.

Chlamydomonas reinhardtii was cultured at 20° C under constant illumination using Guillard's W.C. medium with added vitamins, trace metals, and boron (Guillard 1975). In 1986, the algae were suspended in 100 ml of culture medium when they were added to the enclosures. In 1987, in order to eliminate the possibility that nutrients added along with *Chlamydomonas reinhardtii* could increase the growth of lake phytoplankton, algae were separated from W.C. medium by gentle centrifugation and resuspended in 53-μm filtered lake water prior to addition to the enclosures. We used *Chlamydomonas reinhardtii* in the food-addition experiments for several reasons: 1) *Chlamydomonas* is ingested by *K. cochlearis* (Bogdan et al., 1980) and *K. taurocephala* (Sierszen and Frost 1990); 2) it supported reproduction in *K. cochlearis* (González and Frost, personal observation) and *K. taurocephala* (Sierszen 1990); 3) it is an easily cultured and fast growing alga.

The enclosures were incubated in Little Rock Lake at a depth of 4 m for two or three days depending upon the temperature in the lake. After incubation the contents of each enclosure were concentrated using a 53-μm nylon mesh and preserved. While we did not specifically quantify periphyton growth, we did not observe obvious periphyton growth inside the enclosures. Population densities were determined by counting the numbers of *K. cochlearis* and *K. taurocephala* in a subsample representing 20–25% of the sample. We observed very low proportions of empty loricas in the samples, and these were not included in the density counts. Egg ratios (E) were determined as number of eggs divided by the total number of females (Edmondson 1965). Density of crustaceans in the enclosures was not calculated. However, we feel that we can use information about crustaceans collected at biweekly intervals in the routine monitoring of Little Rock Lake to estimate crustacean abundances in our enclosures. It is also unlikely that the number of crustaceans in the enclosures would increase drastically in a two or three-day incubation period.

For each experiment, we tested for differences in density and egg ratio between the control enclosures at the end of the experiments and the lake sample collected at the beginning of the experiments using a *t*-test (Sokal and Rohlf 1981). We performed such comparisons to test for enclosure effects. The egg ratios were transformed as arcsin $\sqrt{x}$, where x is the egg ratio. Densities in the control enclosures usually paralleled those in the lake. *K. cochlearis* density was significantly higher in the control enclosures that in the lake on only 4 out of 16 dates (19 June 1986, 27 April, 18 May and 22 June 1987; $p < 0.05$). *K. taurocephala* density was significantly higher in the control enclosures than in the lake on 12 June 1986 ($p = 0.02$). Egg ratios in the enclosures also paralleled those in the lake. While egg ratios tended to be higher in the control enclosures than in the lake, significant differences were observed in only one experiment for *K. cochlearis* (22 June 1987; $p = 0.005$), and in two experiments for *K. taurocephala,* (19 May 1987; $p = 0.02$ and 22 September 1987; $p = 0.03$). The higher density and egg ratios in the control enclosures

may be an effect of the incubation. Egg ratios were also compared between control and food-addition treatments using a *t*-test. A significant increase ($\alpha \leq 0.05$) in the egg ratio with the addition of food was interpreted as evidence of food limitation.

Results

Annual patterns

Keratella cochlearis abundance showed a similar seasonal pattern during each year in the 1984–1987 study period. This rotifer typically reached annual maximum abundances in May or June and then declined during the summer. Some year to year variability was apparent in the density of *K. cochlearis*. Years when density was high in spring and low in winter (1984 and 1986) alternated with years when density was low in spring and high in winter (1985 and 1987). The highest spring density was observed in 1986, while the lowest was observed in 1987. After the midsummer decline, *K. cochlearis* populations remained low during fall, except in 1986, when numbers increased during early fall (Fig. 1a). *Keratella taurocephala* showed a pattern similar to that of *K. cochlearis* during 1984 and 1985. High abundances occurred in the spring followed by population declines during the summer. Abundance patterns were different in 1986 and 1987, when neither spring peaks nor summer declines were evident (Fig. 2a).

Egg ratios for *K. cochlearis* showed annual patterns similar to those exhibited in abundance. Maximum egg ratios usually occurred during April and May and were followed by low values during June and July, with higher values later in the year (Fig. 1b). In general, egg ratios of *K. cochlearis* tended to be lower than 0.1 during June and July. Egg ratios for *K. taurocephala* also usually exhibited a spring peak followed by a decline in summer. The one exception occurred in 1984, when no spring peak was evident and maximum values were observed in December. In general, *K. taurocephala* egg ratios were higher than *K. cochlearis* egg ratios during June and July (Fig. 2b).

Food limitation experiments

The response of *Keratella cochlearis* to food addition varied within a year but the annual pattern of response was similar in 1986 and 1987. In 1986, food-addition experiments were initiated in June during a period when *K. cochlearis* populations were declining (Fig. 3a and c). Overall, egg ratios were greater in food-addition treatments but significant differences between treatments occurred predominantly during the period of maximum population decline (June 12 $p = 0.004$, June 19 $p = 0.01$ and July 2 $p = 0.006$). These significant effects were associated with periods when control egg ratio values were lower than 0.1. In contrast, when control egg ratios were greater than 0.2, no food-addition effects were evident (Fig. 3a). During late summer, after population declines occurred, *K. cochlearis* egg ratio increased with food
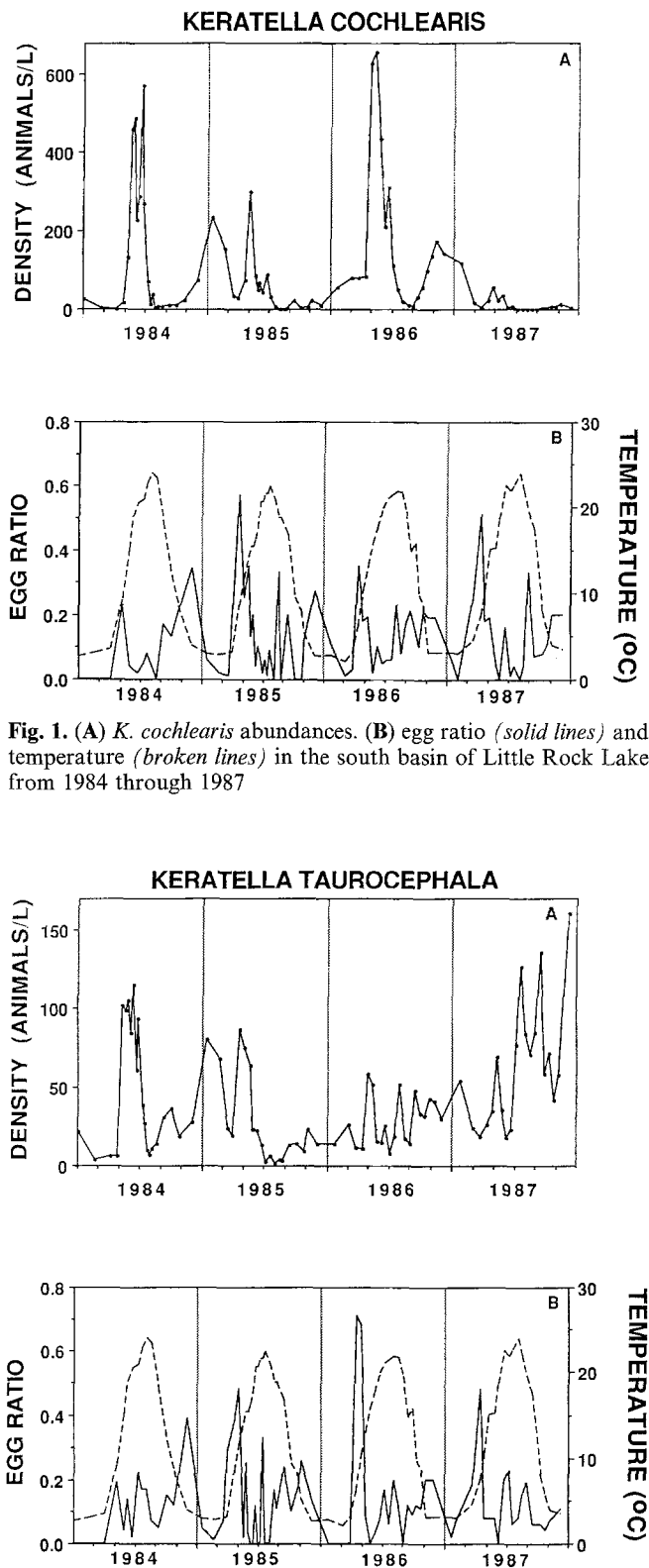

Fig. 1. (**A**) *K. cochlearis* abundances. (**B**) egg ratio *(solid lines)* and temperature *(broken lines)* in the south basin of Little Rock Lake from 1984 through 1987

Fig. 2. (**A**) *K. taurocephala* abundances. (**B**) egg ratio *(solid lines)* and temperature *(broken lines)* in the south basin of Little Rock Lake from 1984 through 1987

addition. However, due to high variability among replicates, probably associated with low population densities, significant differences between treatments were not detected (August 13 $p = 0.08$). In early fall, population
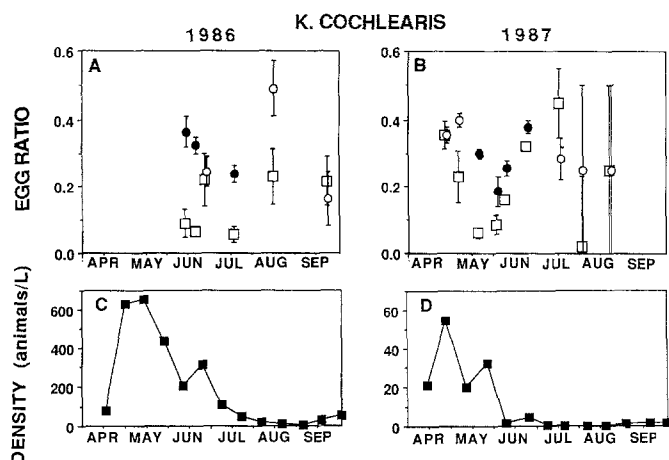
Fig. 3A–D. Egg ratios for *K. cochlearis* grown for 2–3 days in control *(squares)* and food-addition enclosures *(circles)*, placed in the south basin of Little Rock Lake during (A) summer and early fall of 1986 and (B) spring, summer and early fall of 1987. Solid symbols indicate significant differences ($p < 0.05$) between controls and food-addition enclosures by t-test and open symbols indicate no significant differences between controls and food-addition enclosures. Error bars indicate 1 S.E. Lake density of *K. cochlearis* (C) during spring, summer and early fall of 1986; (D) spring, summer and early fall of 1987
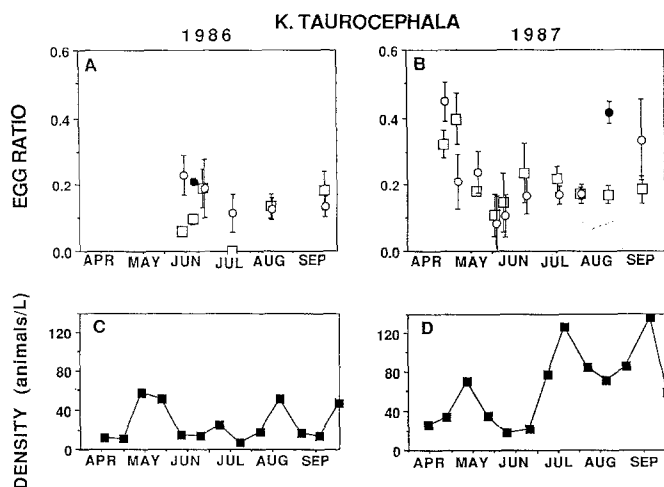

Fig. 4A–D. Egg ratios for *K. taurocephala* grown for 2–3 days in control *(squares)* and food-addition enclosures *(circles)*, placed in the south basin of Little Rock Lake during (A) summer and early fall of 1986 and (B) spring, summer and early fall of 1987. Solid symbols indicate significant differences ($p < 0.05$) between controls and food-addition enclosures by t-test and open symbols indicate no significant differences between controls and food-addition enclosures. Error bars indicate 1 S.E. Lake density of *K. taurocephala* (C) during spring, summer and early fall of 1986; (D) spring, summer and early fall of 1987

densities were also low and no response to food addition was observed (September 20 $p = 0.54$).

During 1987, we conducted our first food-addition experiment prior to the period of population decline, and no food-addition effect was detected (April 27 $p = 0.98$, May 5 $p = 0.12$). Subsequently, in a pattern that matched our 1986 experiments, egg ratios were significantly higher in the food-added enclosures while populations were

declining (May 19 $p = 0.0001$, June 1 $p = 0.009$, June 8 $p = 0.008$, June 22 $p = 0.04$; Fig. 3b and d). The association between significant food-addition effects and egg-ratio values in the control enclosures was less consistent in 1987. Egg ratios were higher than 0.2 in one out of the four dates where food addition had a significant effect. Similarly to 1986, after the population decline occurred during summer and early fall, the variability among replicates was very high, probably associated with low population densities, and no evidence of food limitation was observed (July 15 $p = 0.23$, July 31 $p = 0.79$, August 20 = 0.9; Fig. 3b).

Keratella taurocephala exhibited no obvious patterns in its response to food additions. In 1986 egg ratios increased in early June and July experiments, but significant differences were detected in only one experiment (June 12 $p = 0.08$, June 19 $p = 0.03$ and July 2 $p = 0.11$; Fig. 4a). In 1987 significant increases in egg ratios occurred only in one of ten experiments in 1987 (August 20 $p = 0.001$; Fig. 4b). There were no obvious relationships between population declines and the effects of food additions. Food-addition effects were associated with low control egg ratios in 1986 but not in 1987.

Discussion

The results of our food limitation experiments in 1986 and in 1987 support the hypothesis that summer declines of *K. cochlearis* in Little Rock Lake are caused by food limitation. In both years, this rotifer showed strong responses to food additions during the periods of population decline and low egg ratios, and little response during other times of the year. The consistently significant response of *K. cochlearis* to food additions when egg ratios were low suggests that an egg ratio < 0.2 may be useful as a general indicator of food limitation for this rotifer under field conditions. Not all periods of low *K. cochlearis* densities are associated with food limitation. In late summer and early fall low *K. cochlearis* densities occurred while egg ratios were high and there was no indication of food limitation. This suggest that death rates rather than birth rates were controlling population fluctuations during this period. Substantial changes in crustacean abundance occurred during late summer and early spring in Little Rock Lake (see below).

In contrast with the situation for *K. cochlearis*, our experiments provided little support for the food limitation hypothesis for *K. taurocephala*. However, two factors make it difficult to link our test with the general role of food limitation in the population dynamics of *K. taurocephala*. First, when we conducted our food-addition experiments in 1986 and 1987, *K. taurocephala* did not exhibit the strong summer population declines that it had in 1984 and 1985 and which occurred consistently for *K. cochlearis*. Food limitation may not have occurred during the periods when we tested for it. Second, although work previous to this study had shown that *K. taurocephala* could reproduce when *Chlamydomonas* was used as a food source (Sierszen 1990), subsequent experiments indicated that *K. taurocephala* egg

ratios were higher using *Cryptomonas* as a food source than *Chlamydomonas* (González and Frost, in preparation). Therefore, additions of different algal foods might have elicited stronger responses.

Our experimental design was intended to examine food limitation under conditions occurring in Little Rock Lake. As such, interaction among rotifers and crustaceans occurred inside the enclosures. Rotifers could be affected by exploitative and interference competition with cladocerans and predation by copepods. However, interactions in the enclosures should be similar to those in the lake since we placed the zooplankton in the enclosures at approximately the same density as that in the lake. Likewise, although we did not count crustaceans directly in our samples, we think it is reasonable to assume that the densities of crustaceans in the enclosures could not change drastically in a 2–3 day incubation period. On the other hand, based on our information on crustacean abundance in the lake, interactions could vary with seasonal changes in rotifer and crustacean abundance. Such interactions could provide an alternative explanation to the seasonality observed in the responses of *K. cochlearis* to food addition. But they could also mask food limitation effects during periods when crustacean abundances are high.

The seasonality observed in the responses of *K. cochlearis* to food addition indicated that other factors must also contribute significantly to the population dynamics of rotifers in Little Rock Lake, particularly in summer when food limitation was not detected. Predators that may have had an impact on *Keratella* population dynamics showed seasonal changes in abundances in Little Rock Lake. Some of these predators showed an increase in abundance during late summer and early spring, when food limitation was not detected. The rotifer predator *Mesocyclops edax* (Stemberger and Gilbert, 1984; Williamson, 1984) showed seasonal changes in abundances in Little Rock Lake. *Mesocyclops* density was 1–2 ind/L from April to late June, while maximum abundance was observed during late July and early August (8 ind/L). The predatory rotifer *Asplanchna* (Gilbert and Williamson 1978) showed an increase in abundance during early fall in Little Rock Lake. Other potential predators of rotifers, *Diacyclops thomasi* and *Tropocyclops prasinus* (Stemberger 1985, 1986) showed no drastic seasonal changes in abundance during the period of our study. Their densities in the lake were 0–2 ind/L during the time period of our study. Similarly, the body size range and abundance patterns of *Daphnia* in Little Rock Lake suggest that interference competition did not have a substantial impact in the rotifer population until late summer. Mechanical interference by *Daphnia* could depress rotifer abundance (Gilbert and Stemberger 1985) and influence egg ratio by stripping eggs off ovigerous individuals (Burns and Gilbert 1986b). But the effect on rotifers by interference competition depends of the size and density of *Daphnia*. Burns and Gilbert (1986a) showed that when daphnids are larger than 2 mm and present at densities $\geq$ 1–5 ind/L they could have a major impact on the population dynamics of the rotifer. The dominant species in Little Rock Lake are smaller than

2 mm, *Daphnia dubia* (mean size = 0.73 mm) and *D. parvula* (mean size = 0.66 mm). In addition, during the periods in which we observed a response to food addition the total *Daphnia* density was $\leq$ 2 ind/L. However the impact of interference by *Daphnia* on rotifers could be important during late July and August when maximum *Daphnia* density (5 ind/L) was observed.

Our test of food limitation could have been confounded if differential interactions among rotifers and crustaceans occurred between controls and food-added enclosures. The addition of food could decrease the clearance rates of crustaceans in the enclosures causing a reduction in interference competition. If interference were reduced by food additions, increased egg ratios could have occurred yielding a false indication of food limitation. Some reduction in cladoceran clearance rates could have occurred in our enclosures. The food concentration used in the food-added enclosures (0.54 mg/L dry weight) corresponds to the incipient limiting concentration (ILC) for *Daphnia* with a body size between 1.75–2.7 mm (Porter et al. 1982; Muck and Lampert 1984). Since the ILC decreases with decreasing body size (McMachon 1965; Downing and Peters 1980), this food concentration should be higher than the ILC for the smaller *Daphnia* species present in Little Rock Lake, *Daphnia dubia* and *D. parvula*. Burns and Gilbert (1986b) showed that when algae concentration was above the ILC of *Daphnia,* rotifers were killed at a lower rate than when algae were below or near the ILC. However, as discussed above, overall levels of interference competition in Little Rock Lake would have been low. Moreover, there was no evidence for food limitation during the periods when a reduction in interference competition was most likely to be important (i.e. late summer, when *Daphnia* populations were at their peak). Similarly, copepod predation rates on rotifers could decrease if an increase in omnivory by predatory copepods occurred with increasing algal food concentration. However current studies of omnivory on *Mesocyclops edax* suggest that the predation rates of this copepods are not affected by an increase in algal food availability (R. Adrian, personal communication).

In summary, although interactions between rotifers and crustaceans occurred in our enclosures, our evidence of food limitation during early summer seems unlikely to have been affected by these interactions due to the low crustacean abundance. Our measurement of food limitation is conservative, however, since such interactions could mask our evidence of food limitation during late summer when crustacean abundance was high.

Differences in the design of the food-limitation experiments between 1986 and 1987 had the potential to confound year-to-year comparisons. In 1986, algae were added while suspended in an aliquot of the medium in which they had been grown. Thus, nutrients, which could have fostered the growth of natural phytoplankton, were added along with algae. In 1987, algae were concentrated and then resuspended in filtered lake water prior to their addition to the experimental chambers. In this case, no additional dissolved nutrients were introduced. Despite these differences, however, there were no obvious

changes in rotifer responses to food additions between 1986 and 1987.

Our data on seasonal abundance patterns do indicate that year-to-year variability in rotifer populations is not simply related to food availability. Higher egg ratios were observed in years with low population numbers for both *Keratella* species (1985 and 1987). Likewise the *K. taurocephala* increase in 1987 was not linked with higher egg ratios.

What factors lead to the occurrence of food limitation during early summer for *K. cochlearis?* There is no obvious association between total chlorophyll in the lake and the incidence of food limitation (T.M. Frost, unpublished data). Community clearence rate by the herbivorous zooplankton in Little Rock Lake's south basin routinely exceeded 50% of the water column per day during spring, when values were often at their annual maximum (Sierszen and Frost 1990). Rotifers were the dominant group during the period of high grazing although the cladoceran *Holopedium gibberum* was responsible for 20 to 32% of total grazing during this period (Sierszen and Frost, 1990). These patterns suggest that high community grazing rates may have influenced the composition of the phytoplankton community and generated the conditions that led to food limitation. Other seasonal patterns are also likely to have influenced the phytoplankton and zooplankton communities.

Our evidence for food limitation for *K. cochlearis* may be somewhat surprising considering results from previous laboratory experiments. *Keratella cochlearis* has shown low threshold food levels under laboratory conditions, and it is considered a species adapted to low-food conditions (Stemberger and Gilbert 1985). Comparisons of *K. cochlearis* growth rates estimated from our data and those from laboratory experiments indicate that growth rates under field conditions were lower than in the laboratory. We calculated birth rates for *K. cochlearis* using our egg ratio information and published values of development time (Baker 1983). Assuming only natural mortality of 0.1 day^{-1}, we calculated growth rates using the equation described by Edmondson (1977). In the control enclosures the average growth rate of *K. cochlearis* during the period when food limitation was detected were -0.03 in 1986 and 0.05 day^{-1} in 1987. These values are substantially lower than the maximal value 0.28 day^{-1} reported for laboratory conditions (Stemberger and Gilbert, 1985). When the egg ratio was 0.2, which is the egg ratio value we suggest as an indicator of food limitation, growth rate values are 0.02 day^{-1} at 15° C and 0.07 day^{-1} at 19° C. When egg ratios were ≤ 0.1 these calculations suggest growth rates for *K. cochlearis* that are 0 or negative.

With the addition of food, *K. cochlearis* growth rate values increased (overall average $= 0.14$ day^{-1}), but they were also lower than 0.28 day^{-1}, except on 19 August 1986 when our growth rate estimate was 0.34. This discrepancy could be attributed to the use of different algae as a food source, a higher threshold food level due to different food quality under field conditions, higher mortality rates due to the presence of predators in our enclosures and the higher variability associated with experi-

ments under field conditions. Future studies that will compare *K. cochlearis* growth rates with those of other rotifers under field food conditions could provide valuable information.

Although alternative mechanisms may be important at times, in this study we show clear evidence that resource limitation can play an important role in rotifer population dynamics. Also the differences observed between *K. cochlearis* and *K. taurocephala* suggest that the occurrence and severity of food limitation in the field may vary substantially even among closely related species.

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