

## Competition between *Keratella cochlearis* and *Daphnia ambigua*: effects of temporal patterns of food supply

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**SUMMARY.** 1. Population growth rates and relative competitive abilities of the rotifer *Keratella cochlearis* f. *tecta* and the small-bodied cladoceran *Daphnia ambigua* were studied under different schedules of food addition but equal total food quantity (per 4-day interval). The initial population growth rate of *Keratella* was significantly affected by the feeding schedule and by the presence of competitors, while that of *Daphnia* was affected by neither factor. Population densities of both species tended to increase as the frequency of food addition increased.

2. *Daphnia* suppressed and excluded *Keratella* from mixed-species cultures when food was provided intermittently at a high concentration, but it failed to exclude the rotifer when food was provided in a near-continuous supply at low concentration. *Keratella* had only a minor suppressive effect on *Daphnia* in all mixed-species treatments.

3. Starvation experiments indicate that *Daphnia* is able to withstand food shortages for significantly longer periods of time than *Keratella*. These and other results indicate that the outcome of interspecific competition between these species may be influenced by the frequency and concentration at which food is supplied. *Daphnia ambigua* is competitively superior to *K. cochlearis* when food is concentrated or 'pulsed', but much less so when ambient food levels are chronically low. Patterns of food availability may have important effects in determining the relative abundance of rotifers and small cladocerans in natural zooplankton communities.

### Introduction

The extent to which temporal patterns of resource variability and environmental heterogeneity affect the growth of populations, and exploitative interactions between species, is poorly understood (Price, 1984; Wiens, 1984).

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Hutchinson (1961) argued that the relative competitive abilities of species in a community were labile, a consequence of changing environmental conditions. Specifically, he suggested that the high diversity typical of many limnetic phytoplankton assemblages was fostered, in part, by the inability of any one species to experience competitive dominance for a sufficiently long period as to cause the exclusion of other species. Condition-dependent competitive

outcomes have been demonstrated with both freshwater (Grover, 1988) and marine (Turpin & Harrison, 1979) phytoplankton taxa.

The consequences of temporal variability in food supply to zooplankton population growth and interspecific exploitative competition are less well known (for review see DeMott, 1989). It is clear that phytoplankton food may vary in quality and quantity over both spatial and temporal scales, and may limit zooplankton growth at times (Fee, 1976; Mullin & Brooks, 1976; Kerfoot *et al.*, 1985; Lampert *et al.*, 1986; Sommer *et al.*, 1986). However, comparative studies exploring responses by zooplankton to variation in patterns of food supply are rare. Dagg (1977) determined that the starvation times and reproductive output of the marine copepods *Acartia tonsa* Dana and *Centropages typicus* Krøyer varied under different food supply regimes, and reasoned that the species appeared adapted to different scales of food patchiness. Similarly, Lampert & Muck (1985) found that while *Daphnia* had higher rates of production and food uptake than *Eudiaptomus* at high food concentrations, the copepod was better able to buffer variability in food concentration and survive when food was scarce.

The only study that provides data relating interspecific competitive abilities of zooplankton to temporal patterns of food supply was not designed with this explicit purpose, and is confounded by varying total food concentration across treatments (Goulden, Henry & Tessier 1982). Consequently it is difficult to assess whether species responded to variation in the total quantity of food provided or to the temporal manner in which it was supplied. In this study we vary the frequency at which food is added to cultures of the rotifer *Keratella cochlearis* f. *tecta* (Gosse) and the cladoceran *Daphnia ambigua* Scourfield while keeping the total amount delivered over successive 4-day periods constant (Fig. 1). The experiments were designed to test the hypothesis that *Keratella* is favoured over *Daphnia* when food is available in a near-continuous supply at low concentrations, while *Daphnia* dominates when more concentrated food is supplied intermittently. This hypothesis is based on physiological attributes of the species: *K. cochlearis* f. *tecta* has a lower threshold food level (the food concentration at which the population growth rate equals zero) than *D. ambigua* (Stemberger &

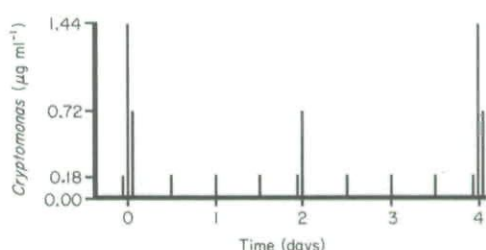


FIG. 1. Temporal patterns of food addition to zooplankton cultures in 0.5-, 2- and 4-day food addition treatments. Bar height depicts cell concentration and food addition schedule. Food addition patterns were identical for each successive 4-day interval.

Gilbert, 1985; Kirk & Gilbert, 1990), but large zooplankton species have greater starvation tolerance than small species (Threlkeld, 1976; Goulden, Henry & Berrigan, 1987). *Daphnia ambigua* is capable of competing with *K. cochlearis* through the exploitation of common resources, but it does not mechanically interfere with the rotifer (Gilbert & MacIsaac, 1989; MacIsaac & Gilbert, 1991).

## Materials and Methods

**Food addition protocols.** Laboratory populations of *K. cochlearis* f. *tecta* and *D. ambigua* were maintained in renewed batch cultures (Stemberger, 1981) for at least one generation on *Cryptomonas* sp. at  $0.18 \mu\text{g dry weight ml}^{-1}$  ( $2 \times 10^3$  cells  $\text{ml}^{-1} \text{ day}^{-1}$ ). Populations were exposed to three food supply treatments; each treatment received  $1.44 \mu\text{g dry weight Cryptomonas sp. ml}^{-1}$  ( $1.6 \times 10^4$  cells  $\text{ml}^{-1}$ ) during each 4-day interval. Treatments consisted of successive additions of one pulse of  $1.44 \mu\text{g ml}^{-1}$  every four days, pulses of  $0.72 \mu\text{g ml}^{-1}$  every two days, or pulses of  $0.18 \mu\text{g ml}^{-1}$  every 0.5 days for the duration of the experiment (Fig. 1). Experimental food levels were selected on the basis of the 0.5-day treatment; Stemberger & Gilbert (1985) and Kirk & Gilbert (1990) estimated the threshold food levels for *K. cochlearis* f. *tecta* and *D. ambigua* fed *Cryptomonas* to be  $0.06 \mu\text{g ml}^{-1}$  and  $0.15 \mu\text{g ml}^{-1}$ , respectively. Consequently, all treatments received food at concentrations above the estimated threshold levels of both species.



Competition trials were initiated by placing 200 mixed-age *Keratella* individuals and three juvenile *Daphnia* individuals either alone or together into covered, 100-ml glass beakers. Initial animal densities were selected to provide approximately equal biomasses of each species. Each beaker contained 100 ml of suspension composed of 95% (v/v) glass-fibre-filtered Post Pond water (Lyme, New Hampshire), 5% (v/v) MBL algal growth medium, and *Cryptomonas* (MacIsaac & Gilbert, 1989). All treatments were run in triplicate in controlled-environment chambers at 20°C under dim light (~400 lx; L:D 15:9).

Zooplankton populations were transferred to fresh medium every 4 days, and usually were enumerated prior to transfer. Rotifer population densities were estimated by three subsamples (0.5–10 ml) with replacement when subsample variability was low, or by four subsamples when this variability was high (i.e. coefficient of variation >~15%). Suspected outlier subsample estimates were evaluated with Dixon's test and removed when appropriate ( $\alpha=0.05$ ; Dunn & Clark, 1974). Only subsamples estimates were tested as outliers, not samples. This procedure was justified by the need to quantify rotifer populations as accurately and precisely as possible when these populations were too large to count in total. *Daphnia* populations were counted in total.

Populations were transferred by gently reverse-filtering 90 ml of culture suspension through 25  $\mu$ m Nitex mesh and pouring the remaining 10-ml fraction into a new beaker containing the appropriate combination of pond water, MBL medium and food. Food concentrations were adjusted to account for dilution by the 10-ml fraction containing the zooplankton. The total volume of MBL medium added to cultures was equal for all treatments.

Estimates of the rates of population increase ( $r$ ) were calculated for each species in each treatment using population growth data from day 4 to day 12 and the formula:

$$r = (\ln N_t - \ln N_0) / t$$

where  $N_t$  and  $N_0$  are population densities at times  $t$  and 0, and  $t$  is time in days. Differences in the estimates of  $r$  for *Keratella* and *Daphnia* populations in control and mixed-species cultures at each food level were analysed with two-way analysis of variance tests. Differences in

overall population growth trajectories of populations in control and mixed-species cultures exposed to different food addition schedules were analysed using analyses of variance with repeated measures (SAS Institute, 1985). Analyses were restricted to the first 32 days of the experiment for *Daphnia* populations because *Keratella* went extinct in some mixed-species cultures and because one *Daphnia* control culture was spilled and prematurely terminated. All data (44 days) were included in analyses of *Daphnia* effects on *Keratella*. Population data for both species were transformed [ $\log_{10}(x+1)$ ] prior to analysis to stabilize variance.

**Zooplankton starvation.** Starvation experiments were conducted using *D. ambigua* and *K. cochlearis* individuals acclimated for at least 3 weeks to 0.36  $\mu$ g ml<sup>-1</sup> *Cryptomonas* sp. Thirty adult *Keratella* were placed individually into 1.8-ml wells of a covered, tissue-culture plate (Falcon brand). Each well contained 1 ml of culture medium with or without supplemental food (0.18  $\mu$ g *Cryptomonas* ml<sup>-1</sup>). The medium was composed of 90% (v/v) glass-fibre-filtered Post Pond water and 10% (v/v) MBL solution. Twenty-four mixed-age (size) *Daphnia* were placed individually into covered, 100-ml beakers containing 50 ml of culture suspension either with or without supplemental food (as above). All individuals were transferred to fresh medium every 2 days. Survivorship was assessed every 12 h for the first 7 days, but less regularly thereafter. Progeny produced during the experiment were removed from test containers when first noticed (<1 day). All vessels were maintained under the same conditions used for the competition experiment.

Differences in survivorship patterns between starved populations of *Keratella* and *Daphnia* were analysed using a nonparametric log rank test (LIFETEST procedure, SAS Institute, 1985). This method is appropriate for data sets with right-censored observations (i.e. some individuals still alive when the experiment is terminated), such as the one described herein.

## Results

Populations of both *Keratella* and *Daphnia* experienced rapid initial growth under all food treatments (Figs 2 & 3). However, differences in initial population growth rates between

species were evident. The initial population growth rate ( $r$ ) of *Keratella* was significantly affected by the presence of competing *Daphnia* and by the frequency of food addition (two-way ANOVA,  $P < 0.05$ ; Table 1). *Keratella*'s popu-

lation growth rates were always lower in mixed-species cultures and in intermittent food addition treatments. These patterns of initial population growth contrast with those of *Daphnia*, whose population growth rate was unaffected by both competitor presence and by the frequency of food addition (two-way ANOVA,  $P > 0.05$ ; Table 1).

Long-term growth patterns of *Keratella* popu-

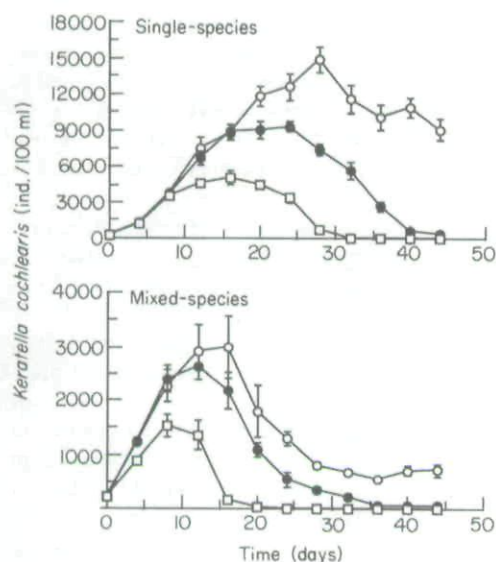


FIG. 2. Population density (mean  $\pm$  1 SE;  $n=3$ ) of *Keratella cochlearis* in control and mixed-species cultures under different temporal schedules of food addition. *Cryptomonas* addition schedule:  $\circ$  0.5 days ( $0.18 \mu\text{g ml}^{-1}$ );  $\bullet$  2 days ( $0.72 \mu\text{g ml}^{-1}$ );  $\square$  4 days ( $1.44 \mu\text{g ml}^{-1}$ ).

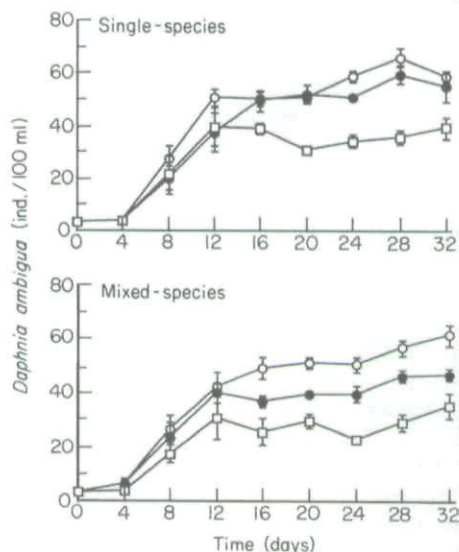


FIG. 3. As per Fig. 2, except for *Daphnia ambigua* in control and mixed-species cultures.

TABLE 1. Mean ( $\pm$  1 SE) rate of population increase  $r$  ( $\text{day}^{-1}$ ) of *Keratella cochlearis* f. *tecta* and *Daphnia ambigua* in control and mixed-species cultures between days 4 and 12 of the experiment (see Figs 2 and 3). The effects of competitors and food addition schedules on population size were assessed for each species using two-way ANOVA. Significance levels for  $F$ -values: NS ( $P > 0.10$ ), \* ( $P < 0.05$ ), \*\* ( $P < 0.0001$ ). All means are based on three replicate populations

Food addition treatment (days)	Species	Control populations $r \pm$ (SE)	Mixed populations $r \pm$ (SE)	ANOVA effects $F$ value (df)		
				Competitor	Food	Competitor $\times$ food
<i>K. cochlearis</i>	0.5	0.22 (0.02)	0.10 (0.02)	69.6** (1,12)	4.5* (2,12)	0.1 <sup>NS</sup> (2,12)
	2.0	0.20 (0.01)	0.09 (0.00)			
	4.0	0.17 (0.02)	0.05 (0.02)			
<i>D. ambigua</i>	0.5	0.34 (0.03)	0.24 (0.02)	2.4 <sup>NS</sup> (1,12)	0.1 <sup>NS</sup> (2,12)	0.5 <sup>NS</sup> (1,12)
	2.0	0.29 (0.06)	0.26 (0.05)			
	4.0	0.30 (0.05)	0.26 (0.01)			



lations complement the short-term patterns. *Keratella* was significantly affected by the presence of *Daphnia*, by food addition schedules, and by an interaction between these factors (Table 2; Fig. 2a). The addition of food in a nearly-continuous fashion favoured coexistence of *Keratella* and *Daphnia*. Both control and mixed-species cultures of *Keratella* achieved higher population densities in treatments receiving food every 0.5 days; progressively lower population maxima were achieved in the 2- and 4-day food addition treatments (Fig. 2a,b). The presence of *Daphnia* caused both sharply reduced *Keratella* population densities and an earlier onset of population decline in all mixed-species cultures relative to control populations (Table 2; Fig. 2a). *Keratella* population growth

also varied through time in different *Daphnia* (time  $\times$  *Daphnia*) and food (time  $\times$  food) treatments. *Keratella* mixed-species populations persisted in abundance only in the 0.5-day food treatment (Fig. 2b). The decline of control *Keratella* populations in 2-day food addition treatments was unexpected, as we routinely maintain laboratory cultures of this rotifer by adding supplemental food every two days (though generally at a higher concentration).

*Daphnia* population growth was most strongly affected by the feeding schedule (Table 3; Fig. 3a,b). As with *Keratella*, animals in the 0.5-day food addition treatment achieved and maintained the highest population densities. *Keratella* had no overall direct effect on *Daphnia* population growth (*Keratella*;  $P > 0.10$ ); in

TABLE 2. Analysis of variance with repeated measures demonstrating the effects of *Daphnia ambigua* and food addition schedules on the growth of *Keratella cochlearis* populations from day 0 until day 44. Data were transformed as  $\log_{10}(x+1)$  prior to analysis. All MS and *F* values are rounded to two significant digits. Tests of main effects (*Daphnia* and food) and their interaction utilize the replicate (*Daphnia*  $\times$  food) term as the error term in the construction of *F*-tests; the other effects use the residual error term and Huynh-Feldt probability corrections

Factor	DF	Type III MS	<i>F</i>	Significance ( <i>P</i> <)
<i>Daphnia</i>	1,6	7.19	178.40	0.001
Food	2,6	6.10	151.36	0.001
<i>Daphnia</i> $\times$ food	2,6	0.22	5.58	0.05
Replicate ( <i>Daphnia</i> $\times$ food)	6,138	0.04	1.27	>0.10
Time	11,138	6.85	216.23	0.001
Time $\times$ <i>Daphnia</i>	11,138	1.90	60.02	0.001
Time $\times$ food	22,138	2.78	87.71	0.001
Time $\times$ <i>Daphnia</i> $\times$ food	22,138	0.53	16.87	0.001
Residual	138	0.03		

TABLE 3. Analysis of variance with repeated measures demonstrating the effects of *Keratella cochlearis* and food addition schedules on the growth of *Daphnia ambigua* populations from day 0 until day 32. Data were transformed as  $\log_{10}(x+1)$  prior to analysis. Models were constructed as per Table 2

Factor	DF	Type III MS	<i>F</i>	Significance ( <i>P</i> <)
<i>Keratella</i>	1,6	<0.01	<0.01	>0.10
Food	2,6	0.09	9.04	0.05
<i>Keratella</i> $\times$ food	2,6	0.03	2.66	>0.10
Replicate ( <i>Keratella</i> $\times$ food)	6,102	0.01	0.84	>0.10
Time	8,102	3.27	273.56	0.001
Time $\times$ <i>Keratella</i>	8,102	0.02	1.65	>0.10
Time $\times$ food	16,102	0.01	1.34	>0.10
Time $\times$ <i>Keratella</i> $\times$ food	16,102	<0.01	0.35	>0.10
Residual	102	<0.01		

addition, the growth trajectories of *Daphnia* populations in mixed-species cultures did not differ significantly from those in control cultures (time  $\times$  *Keratella*;  $P > 0.10$ ). Differences between control and mixed-species populations were most pronounced after day 12 in the 2- and 4-day food treatments. Most populations were likely food-limited on and after this date as visual inspections revealed that food was very sparse. Neonate mortality was also high in all 4-day food treatment cultures on day 16. *Daphnia* populations in mixed-species cultures tended to be only slightly suppressed by *Keratella*. *Keratella* population declines in mixed-species cultures appeared to elicit small, time-lagged increases in *Daphnia* populations. These responses were most evident in the 0.5- and 2.0-day food treatments (Figs 2b, 3b).

*Keratella* had a significantly ( $\chi^2 = 38.2$ ,  $df = 1$ ,  $P < 0.0001$ ) shorter time to starvation than *Daphnia* (Fig. 4). On day 5, less than 38% of starved rotifers were alive as opposed to 83% of starved *Daphnia*. However, even well-fed *Keratella* experienced much higher mortality than *Daphnia*, demonstrating that even under favourable conditions the rotifer does not live

as long as the cladoceran. Surprisingly, there were no clear differences in adult and juvenile *Daphnia* survival patterns.

## Discussion

Natural phytoplankton communities often exhibit striking temporal and spatial patterns of patchiness in species composition and abundance (Fee, 1976; Mullin & Brooks, 1976; Sommer *et al.*, 1986). While the effects of nutrient supply rates on phytoplankton competition have been well studied (Tilman, 1977, 1982; Turpin & Harrison, 1979; Holm & Armstrong, 1981; Robinson & Sandgren, 1983; Sommer, 1983, 1984, 1985; Gaedeker & Sommer, 1986; Grover, 1988), the impact of phytoplankton patchiness on competitive interactions between zooplankton has received scant attention. The results of this laboratory study indicate that patterns of food supply can influence zooplankton population growth rates and the dynamics of exploitative competition between *Keratella* and *Daphnia*. These findings are consistent with expectations based on physiological responses by the species to temporal variation in the concentration of food (see below), and they concur with Bengtsson's (1987) assertion that environmental factors, such as temperature and food concentration and food type, may affect the competitive abilities of zooplankton. While our study attempts to simulate natural temporal variation in food supply, spatial variability in algal density could also influence the dynamics of exploitation competition between zooplankton.

Taylor & Williams (1975) and Tilman (1977) developed a resource-based mechanistic model for predicting the outcome of exploitative competition among species utilizing an essential, limiting resource in continuous-flow experiments. The model predicts that, given a spatially and temporally homogeneous environment, the species able to maintain positive population growth at the lowest resource concentration will exclude those with greater requirements. It has received experimental support in studies with bacteria (Hansen & Hubbell, 1980), phytoplankton (Tilman, 1977; Holm & Armstrong, 1981; Sommer, 1983) and rotifers (Rothhaupt, 1988). The model appears, however, to be sensitive to violations of the steady-state assumption. A number of studies

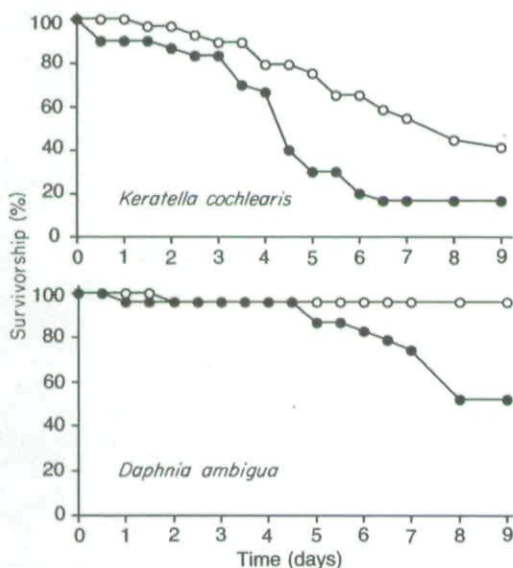


FIG. 4. Survivorship of *Keratella cochlearis* and *Daphnia ambigua* in fed (○) and starved (●) cultures. Initial cohorts consisted of 30 *Keratella* and 24 *Daphnia* of mixed ages in each treatment. Individual cultures were transferred to fresh medium every 2 days. *Cryptomonas* ( $0.18 \mu\text{g ml}^{-1}$ ) was added to food-supplemented cultures.



have demonstrated that coexistence of competing species is promoted by temporal variation in resource supply rates. For example, discontinuous nutrient supply protocols fostered the coexistence of species in natural and contrived algal communities (Turpin & Harrison, 1979; Robinson & Sandgren, 1983; Sommer, 1984, 1985; Gaedeke & Sommer, 1986; Grover, 1988). In addition, Holm & Armstrong (1981) proposed that the persistence of small populations of *Microcystis aeruginosa* Kütz with competitively-dominant *Asterionella formosa* Hass may have resulted from, among other factors, the pulsed nature of their semi-continuous experimental methods.

According to the resource-based competition model and Stemberger & Gilbert's (1985) and Kirk & Gilbert's (1990) estimates of the threshold food levels of *K. cochlearis* f. *tecta* and *D. ambigua*, the former species should have excluded that latter from culture in each food addition treatment. We selected the food concentration for the 0.5-day treatment to exceed only minimally, in individual pulses, the threshold food concentration of *Daphnia*. We expected that grazing by the mixed-species assemblage would result in an ambient food level depressed below the threshold level of *Daphnia*, but not of *Keratella*, and consequently result in the exclusion of *Daphnia*. While we observed increased competitive ability of the rotifer and protracted periods of coexistence of the species as the concentration of individual food pulses was lowered toward the threshold food level of the daphnid, we did not observe the expected exclusion of *Daphnia* from any mixed-species cultures. The most plausible explanation for the departure of our results from theoretical expectations relates to our use of batch culture methods, in violation of the resource-based competition model's assumption of steady state conditions (Tilman, 1982). Fluctuations in food concentration associated with batch culture methods (cf. Fig. 1, Tillmann & Lampert, 1984) tend to favour *Daphnia* over *Keratella*, by virtue of *Daphnia*'s greater ability to store energy when food is abundant and resist starvation when it is not (Fig. 4). The basis for *Daphnia*'s superiority over *Keratella* under fluctuating food concentrations is not clear, though it likely stems from differential responses by the species to 'glut' and 'starve' conditions; McCauley *et al.* (1990) determined that extended starvation

periods need not result in irrevocable reproductive impairment in *Daphnia*. While a similar pattern may hold for *Keratella*, the maximum permissible starvation interval would necessarily be truncated relative to that for *Daphnia*. Indeed, the poor performance of *Keratella* in 2- and 4-day control treatments (Fig. 2a,b), while surprising, emphasizes the sensitivity of small species to variation in food supply.

As an alternate explanation for the departure of our results from theory, the threshold food concentration estimates for *Keratella* and *Daphnia* assumed a constant food concentration (Kirk & Gilbert, 1990), and, as a result, may not be directly applicable under the non-steady-state conditions of the present study.

Under chronic low-food conditions, *Daphnia* had a greatly reduced competitive advantage over *Keratella*, in partial conformity with theoretical predictions. The persistence of populations of *Daphnia* in the 0.5-day mixed-species treatment may have resulted from the supplementation of the algal diet by unmeasured food sources, including detritus and bacteria. The extended survival of *Daphnia* under starved conditions in glass-fibre-filtered water (Fig. 4) may also have resulted from the growth and subsequent consumption by *Daphnia* of bacteria (W. R. DeMott, pers. comm.).

We have observed three different outcomes in competition trials between *Keratella cochlearis* f. *tecta* and *D. ambigua*. In a previous study, *Keratella* excluded *Daphnia* from mixed-species cultures when *Cryptomonas* was provided at a rate of  $0.18 \mu\text{g ml}^{-1} 2 \text{ day}^{-1}$ , while the species coexisted when *Cryptomonas* was delivered at a rate of  $0.32 \mu\text{g ml}^{-1} 2 \text{ day}^{-1}$  (MacIsaac & Gilbert, 1989). Both of these rates are considerably lower than the food concentrations used in the present study ( $0.72 \mu\text{g ml}^{-1} 2 \text{ day}^{-1}$  and  $1.44 \mu\text{g ml}^{-1} 4 \text{ day}^{-1}$ ) which resulted in the exclusion or near-exclusion of *Keratella* by *Daphnia*. It seems reasonable, therefore, to conclude that the outcome of competition between these taxa is dependent upon the rate of food supply as well as its rate of depletion. More generally, these experiments demonstrate that investigators ought to consider carefully the selection of initial conditions when designing exploitation competition experiments.

A number of studies have demonstrated that zooplankton competitive outcomes can depend

upon the quantity of food supplied (see review, DeMott, 1989). In general, cladoceran body size is by itself a poor predictor of competitive ability, but when combined with considerations of food concentration, clear patterns emerge (Romanovsky & Feniova, 1985; Bengtsson, 1987). Bengtsson (1987) noted that *Daphnia magna* Straus dominated over smaller *D. pulex* Leydig and *D. longispina* (O.F.M.) under high food conditions, but was suppressed by them under low food concentrations. Similarly, Goulden *et al.* (1982) observed a competitive hierarchy with dominance positively associated with body size (*D. magna* > *D. galeata mendotae* Birge > *Bosmina longirostris* (O. F. Müller) under high food conditions, but they noted that the latter relationship was reversed under lower food levels. Also, *D. pulex* dominated over smaller *Ceriodaphnia reticulata* (Jurine) when food was abundant but was excluded by it when food was sparse (Romanovsky & Feniova, 1985). Finally, the production by *D. magna* exceeded that by the smaller species *D. pulicaria* Forbes and *D. longispina* at high food concentrations, while the reverse was true when populations were food limited (Tilman & Lampert, 1984). Consequently, there may be a tradeoff between survival ability under chronically low food conditions and reproductive potential under higher food conditions as predicted by Tilman's (1977) resource-based competition model and Goulden, Hornig & Wilson's (1978)  $r_{\max}$  hypothesis, respectively. A comparable model has also been proposed for rotifers (Stemberger & Gilbert, 1985).

#### Zooplankton community composition

To colonize new habitats successfully zooplankton must tolerate ambient physical, chemical and food (energetic) conditions. Threshold food concentration and starvation resistance are two factors potentially crucial in determining the persistence of zooplankton in new habitats, especially under oligotrophic and ultra-oligotrophic conditions where food limitation may be common and severe. Some rotifer and copepod species appear to be particularly successful under these conditions, though for different reasons. Small-bodied rotifers have very low threshold food levels which would be exceeded by ambient food levels in even very oligotrophic waters (Stemberger & Gilbert,

1985). On the other hand, some copepod species (e.g. Calanoida) appear well adapted to low-food environments by virtue of their low incipient limiting concentration (Muck & Lampert, 1984) low threshold food concentration (Frost, 1985), ability to tolerate fluctuating food supply (Dagg, 1977; Lampert & Muck 1985), and by the production of resting eggs during unfavourable periods. Consistent with these observations, Hobbie (1973) found that the zooplankton fauna of very oligotrophic arctic lakes consisted of rotifer taxa only, while more productive habitats also supported calanoid copepods, cyclopoid copepods, and finally cladocerans. Similarly, McLaren (1964) observed that *Cyclops scutifer* Sars and *Keratella hiemalis* Carlin accounted for almost all of the zooplankton biomass in an ultra-oligotrophic arctic lake. Finally, food depletion by rotifers and copepods may have resulted in the extinction of cladocerans from ultra-oligotrophic lakes in the Tatra Mountains of Poland, though predation by introduced fish may confound this hypothesis (Gliwicz, 1985). While these studies implicate species-specific responses to the rate of food supply as an important determinant of zooplankton community composition, the generality of this relationship remains to be determined.

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