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Competition between rotifers and cladocerans of different body sizes

Hugh J. MacIsaac and John J. Gilbert
Department of Biological Sciences Dartmouth College Hanover, NH 03755, USA

Summary. We conducted laboratory experiments to test the hypothesis that rotifers could coexist with small (<1.2 mm) but not large (>1.2 mm) cladocerans. *Keratella cochlearis* was excluded in <8 days by the large cladocerans *Daphnia pulex* and *D. magna*, probably through both interference and exploitative competition. On the other hand, *K. cochlearis* persisted for 8 weeks with two small cladocerans (*Bosmina longirostris* and *Ceriodaphnia dubia*) and excluded a third small cladoceran (*D. ambigua*). Similarly, *Synchaeta oblonga* coexisted with *B. longirostris* for >7 weeks, and *K. testudo* coexisted with *D. ambigua* for >4 weeks. Coexistence of small cladocerans and rotifers was always accompanied by suppression of one or both populations, probably primarily if not exclusively by exploitative competition for limiting food resources. These results indicate that the competitive dominance of cladocerans over rotifers decreases markedly with cladoceran body size and that factors other than body size may determine the competitive outcome between rotifers and small cladocerans. Our study provides a mechanistic explanation for a commonly observed pattern in natural zooplankton communities: planktonic rotifers often are abundant when only small cladocerans occur but typically are rare when large cladocerans are present.

Key words: Body size – Competition – Rotifera – Cladocera – Zooplankton

Rotifers and cladocerans are major constituents of most freshwater zooplankton communities. Determinants of the relative abundance of these and other zooplankton groups affect the size-structure of plankton communities. Size-selective predation by planktivorous fish on large zooplankton species is one of the best understood community determinants to date. Zooplankton communities regulated by planktivorous fish are often dominated by rotifers and small-bodied cladocerans, presumably due to a release of these species from competition with the larger forms that are preferred as prey by the fish (Brooks and Dodson 1965; Hall et al. 1976).

Our understanding of the nature of the interactions among the zooplankton is much less complete. Brooks and Dodson (1965) suggested that large (1.3–3.0 mm) zooplankton species dominate over small (0.2–1.3 mm) ones in the absence of fish predation because they feed more 'efficiently'. Most tests of the 'size-efficiency' hypothesis (Brooks and Dodson 1965; Hall et al. 1976) have been limited to members of cladoceran taxa (Sprules 1972; Lynch 1979; Goulden and Hornig 1980; Goulden et al. 1982; DeMott and Kerfoot 1982; DeMott 1983; Romanovsky and Feniova 1985). Only recently have intensive studies been directed at elucidating the nature of competitive relationships between rotifers and cladocerans (Gilbert 1988).

Rotifers and cladocerans are organisms particularly well suited to tests regarding the outcome of competition between different-sized taxa, since they usually have similar food niches but body sizes that may differ by several orders of magnitude. Field studies have demonstrated that rotifer populations often vary inversely in abundance with the density of large species of *Daphnia* (Andersson et al. 1978; Lynch 1979; Shapiro et al. 1982; Ruttner-Kolisko and Malicky 1988; see review in Gilbert 1988). For example, Neill (1984, 1985) found that *D. rosea*, a cladoceran ~2 mm in body length, dominated the zooplankton community biomass of Gwendoline Lake, British Columbia whenever *Chaoborus trivittatus* populations and their resultant predation impact were low. However, rotifers and small cladocerans dominated when predation on *Daphnia* was intense and *Chaoborus* was abundant. Neill (1985) suggested that the rotifers and *Daphnia* from his study lake were competing almost exclusively through exploitation for limiting food resources, although other workers (Gilbert and Stemberger 1985; Burns and Gilbert 1986) have established that large *Daphnia* (>1.2 mm body length) may also kill rotifers by mechanical interference.

Very little is known regarding the strength and occurrence of exploitative competition between rotifers and small cladocerans. These two groups may co-dominate in lakes and ponds in nature, especially when large cladoceran populations are sparse (Hrbáček 1962; Lynch 1979; Pace and Orcutt 1981; Shapiro et al. 1982; Kerfoot and DeMott 1985; Yan and Geiling 1985). Small cladocerans have lower clearance rates (Porter et al. 1983), a much lower potential for interference with rotifers (Burns and Gilbert 1986) and shorter starvation times (Threlkeld 1976; Tessier et al. 1983) than large species. These differences may be sufficient to preclude interference competition between the groups and permit prolonged coexistence when shared food resources are in limiting supply.

In the current study, we utilize laboratory experiments to assess the ability of three rotifer species (*Keratella cochlearis* f. *tecta*, ~90 µm; *Keratella testudo*, ~115 µm; *Synchaeta oblonga* ~190 µm) to coexist with cladocerans of small (*Bosmina longirostris*, ~400 µm), intermediate (*Ceriodaphnia dubia*, ~890 µm; *Daphnia ambigua*, ~1200 µm)

Offprint requests to: H.J. MacIsaac

and large (*Daphnia pulex*, ~2500 µm; *Daphnia magna*, ~3000 µm) body size (length excluding tail spine).

Materials and methods

Experiments with K. cochlearis

All species of cladocerans and *K. cochlearis* were cloned and maintained on *Cryptomonas* sp. in glass-fiber-filtered lake water (Post Pond, NH) using methods described elsewhere (Stemberger 1981; Gilbert and Stemberger 1985). Experiments were conducted in covered, 100-ml glass beakers containing 100 ml of a suspension of 0.18 µg dry weight·ml^{-1} *Cryptomonas* sp. (2×10^3 cells·ml^{-1}) in a 9:1 (v/v) mixture of lake water and *Cryptomonas* growth medium. The beakers were kept in a constant environment chamber at 20° C under dim light (~400 lx; L:D 15:9). Initial conditions were 100 *K. cochlearis* in the single- and mixed-species cultures and 1 adolescent (*D. pulex* or *D. magna*), 2 adolescent (*D. ambigua*), 1 adult (*C. dubia*), or 3 adult (*B. longirostris*) cladocerans in the single- and mixed-species cultures. The initial biomass of each species in the mixed-species cultures was similar. Individuals were acclimated to the experimental conditions for at least 4 days prior to the start of each experiment. Cultures of all treatments were run in triplicate. Experiments with *D. pulex* and *D. magna* were conducted immediately prior to those with the other cladocerans.

Cultures were replenished with 0.18 µg dry weight·ml^{-1} *Cryptomonas* sp. every 2 days. Populations were enumerated and transferred to fresh media every 4 days for 56 days or until one species was excluded by the other. Populations were counted in total when densities were low (<200 animals) or by 3 subsample estimates when densities were higher. A preliminary analysis revealed that subsampling had no influence on the final population estimate when corrected for the fraction of the total volume sampled ($P=0.22$, Mann-Whitney U-test). Cultures were transferred to new media by reverse filtration of 90 ml of the culture through 30 µm Nitex mesh with a gentle vacuum to prevent the loss of animals. The remaining 10 ml fraction was then poured into a new beaker containing 90 ml of a suspension of 0.20 µg dry weight·ml^{-1} *Cryptomonas* to yield a final concentration of 0.18 µg dry weight·ml^{-1} *Cryptomonas* (2.0×10^3 cells·ml^{-1}). The 'old' beaker was rinsed with a portion of the new suspension to ensure the transfer of all individuals. *Cryptomonas* densities were examined in 'old' beakers by visual inspection prior to the transfer of animals to fresh media.

Population growth trajectories of both rotifers and cladocerans in single- and mixed-species cultures were analyzed using log-transformed population data and univariate Analysis of Variance with repeated-measures (SAS Institute 1985; Gurevitch and Chester 1986). Overall differences in population means between treatments were assessed using Student-Newmann-Keuls (SNK) tests (SAS Institute 1985).

Experiments with S. oblonga and K. testudo

The methods for these experiments were similar to those employed for the *K. cochlearis* experiments but differed in several respects. The experiments were conducted in covered, 50-ml beakers containing 40 ml of a suspension of 0.90 µg·ml^{-1} *Cryptomonas* (10^4 cells·ml^{-1}) in the 9:1 (v/v) mixture of lake water and growth medium. Initial conditions were 15 *S. oblonga* and 5 gravid *B. longirostris* in single- and mixed-species cultures or 10 *K. testudo* and 2 gravid *D. ambigua* in single- and mixed-species cultures. All populations were counted in total and pipetted (along with the loose eggs of *S. oblonga*) into fresh *Cryptomonas* suspensions every 2 days. Statistical analyses were similar to those used for the *K. cochlearis* experiments.

Results

Daphnia pulex and *D. magna* had dramatic and rapid effects on *K. cochlearis* (Fig. 1). All *K. cochlearis* populations in the mixed-species cultures went to extinction within 8 days. Although visible inspections indicated that food was largely depleted in the mixed-species cultures by day 4, *K. cochlearis* can persist for up to 4 days under starvation conditions with low mortality (~30%; MacIsaac unpubl.); thus it is unlikely that exploitative competition alone was responsible for the rapid decline of the rotifers during the initial 4-day period. Rather, the large daphnids probably were imposing high mortality rates through mechanical interference (mutilation and ingestion) on the *K. cochlearis* (see Burns and Gilbert 1986).

K. cochlearis persisted in mixed-species cultures with other, small cladocerans for extended periods of time, though always at suppressed densities (Fig. 1). *C. dubia* significantly (Table 1) suppressed the overall population growth of *K. cochlearis* and nearly excluded it in each of the replicate cultures. *K. cochlearis* population growth was significantly reduced by *B. longirostris* (Table 1), though the suppression was much less pronounced than with any of the larger cladocerans, especially for the first 16 days (Figure 1). Replicate *K. cochlearis* populations in mixed-species culture with *B. longirostris* began to diverge from one another after day 44; two populations were stable or in decline while the third was increasing to near control levels when the experiment was terminated. Overall, however, the mean *K. cochlearis* population size was significantly ($P<0.05$; SNK test) lower in mixed- than single-species cultures. *B. longirostris* also significantly ($P<0.05$, SNK test; Table 1) suppressed the growth of *S. oblonga* populations (Fig. 2A); however, as with *K. cochlearis*, all *S. oblonga* populations persisted for the duration of the experiment. In both single- and mixed-species cultures, *S. oblonga* populations were decreasing rapidly and close to extinction

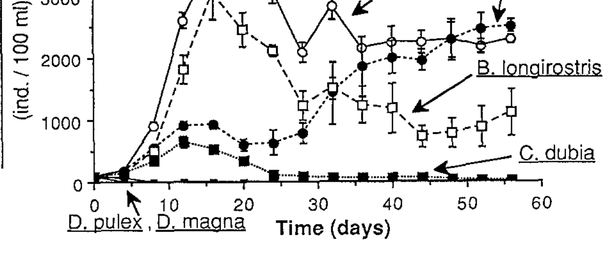

Fig. 1. Effect of five cladocerans on growth of *Keratella cochlearis* populations. Values presented are means of three replicates ± 1 SE

Table 1. Results of repeated-measures ANOVA describing cladoceran effects on *Keratella cochlearis*, *Synchaeta oblonga* and *Keratella testudo* population growth. F values are shown. Significance tests are based on type III models (partial sums of squares). ns – $P > 0.05$; * – $P < 0.01$; ** – $P < 0.001$; *** – $P < 0.0001$

Rotifer	Cladoceran competitor	Effect			
		Cladoceran	Replicate	Time	Cladoceran* time
Keratella cochlearis	*Ceriodaphnia dubia*	953***	11***	17***	19***
	Daphnia ambigua	149***	4*	115***	14***
	Bosmina longirostris	147***	9***	113***	3**
Synchaeta oblonga	*Bosmina longirostris*	38***	4*	44***	4***
Keratella testudo	*Daphnia ambigua*	$<1^{ns}$	3^{ns}	8*	12**

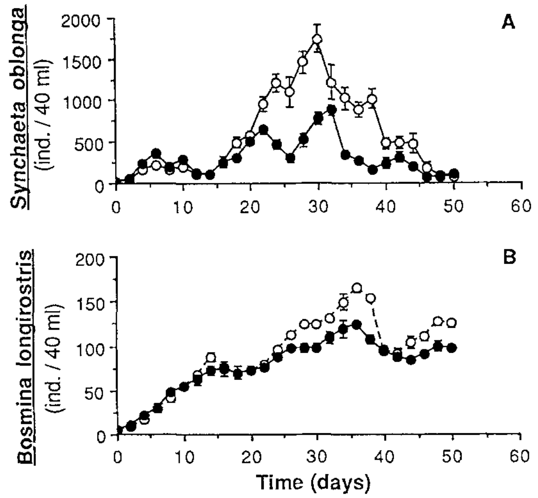

Fig. 2A, B. Dynamics of (**A**) *Synchaeta oblonga*, and (**B**) *Bosmina longirostris* in single- (open circles) and mixed-species (closed circles) cultures. Values as per Fig. 1

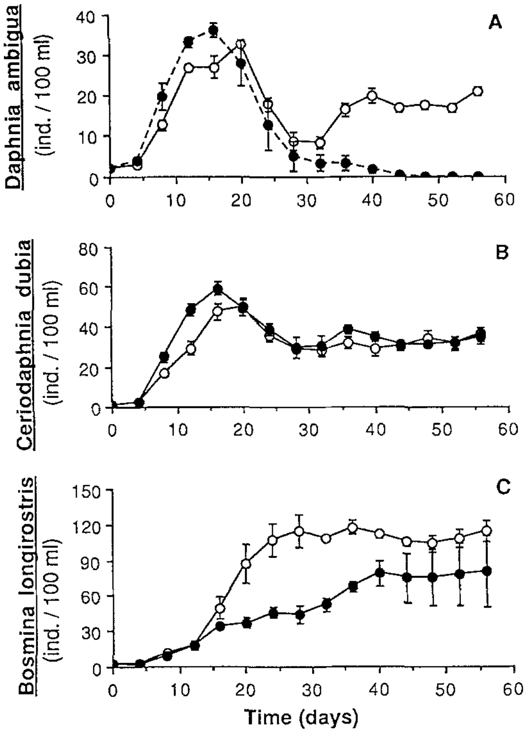

Fig. 3A–C. Dynamics of (**A**) *Daphnia ambigua*, (**B**) *Ceriodaphnia dubia*, and (**C**) *Bosmina longirostris* in single- and mixed-species cultures with *Keratella cochlearis*. Values as per Fig. 1; Symbols as per Fig. 2

when the experiment was terminated. This unexpected decline was associated with the use of a new batch of filtered-lake water on day 36.

Keratella cochlearis population densities in mixed-species cultures with *D. ambigua* were much lower than those in single-species control cultures for the first 28 days (Table 1). After that time, however, the rotifers approached control levels (Fig. 1) while *D. ambigua* went extinct. The decline of the *D. ambigua* in both single- and mixed-species cultures began after day 16 (Fig. 3A), concomitant with a decrease in the amount of food remaining in the vessels. Both juvenile and adult *D. ambigua* individuals died off during this period of intense food limitation. The rapid decline of *D. ambigua* populations in the single-species cultures was followed by a recovery to a lower, more stable maximum density. By contrast, the populations in mixed-species cultures continued to decline as *K. cochlearis* populations increased. Thus, *K. cochlearis* had a significant effect on the overall dynamics of *D. ambigua* population growth (Table 2).

Keratella testudo coexisted with, but was significantly suppressed by, *D. ambigua* (Fig. 4A; Table 1). Control populations of *K. testudo* declined after day 22, coincident with the use of new filtered-lake water. *D. ambigua* populations were not affected by the presence of *K. testudo* (Fig. 4B; Table 2).

Neither *D. pulex* nor *D. magna* were affected by the presence of *K. cochlearis* during the brief interval during which the species coexisted ($P > 0.10$; *t*-tests). *C. dubia* populations in mixed- and single-species cultures tracked one another very closely, though the former were inexplicably slightly higher for the first 16 days (Fig. 3B; Table 2). As a result, overall mean population size was significantly ($P < 0.05$, SNK test) higher in the mixed-species cultures. By contrast, *B. longirostris* populations were significantly ($P < 0.001$; Table 2) lower in cultures with *K. cochlearis* than in control, single-species cultures (Fig. 3c). In addition, replicate mixed-species cultures began to diverge on about day 35; two replicates increased to control levels while the third, in a beaker with a large and growing population of *K. cochlearis*, was declining rapidly. *B. longirostris* populations were also significantly ($P < 0.01$; Table 2) lower in mixed-species cultures with *S. oblonga* than in single-species cultures (Fig. 2B), though all populations persisted until the experiment was terminated.

Table 2. Results of repeated-measures ANOVA describing *Keratella cochlearis*, *Synchaeta oblonga* and *Keratella testudo* effects on the population growth of cladocerans. See Table 1 for details of tests. ns – $P>0.05$; * – $P<0.05$; ** – $P<0.01$; *** $P<0.0001$

Rotifer	Affected cladoceran	Effect			
		Rotifer	Replicate	Time	Rotifer* time
Keratella cochlearis	*Daphnia ambigua*	98***	7**	8***	9***
	Ceriodaphnia dubia	7*	3*	252***	2^{ns}
	Bosmina longirostris	11**	1^{ns}	16***	1^{ns}
Synchaeta oblonga	*Bosmina longirostris*	14**	3*	190***	2**
Keratella testudo	*Daphnia ambigua*	$<1^{ns}$	$<1^{ns}$	16***	$<1^{ns}$

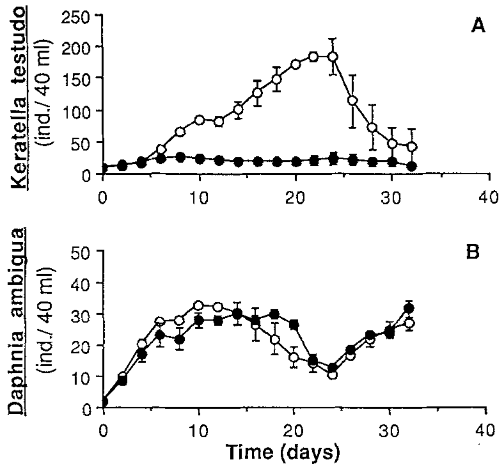

Fig. 4A, B. Dynamics of (**A**) *Keratella testudo* and (**B**) *Daphnia ambigua* in single- and mixed-species cultures. Values as per Fig. 1; Symbols as per Fig. 2

Discussion

The results of this study show that rotifers are able to coexist for long periods of time in laboratory cultures with small (<1.2 mm) cladocerans, but not with larger (>1.2 mm) ones. These results are consistent with patterns observed in numerous experimental and descriptive field studies (see review in Gilbert 1988). Coexistence of small cladocerans and rotifers commonly occurs when large cladocerans are sparse or absent. This condition is realized most often in nature when planktivorous fish selectively remove large cladocerans, permitting greater exploitation of available phytoplankton food resources by smaller, less-susceptible species. As examples, Shapiro et al. (1982) documented large increases in both rotifer and small cladoceran populations in Loch Losa, Minnesota, USA following the elimination of the superior competitor *D. pulex* by planktivorous fish, while Neill (1985) observed a similar pattern when populations of the dominant herbivore *D. rosea* in Gwendoline Lake, British Columbia, Canada were experimentally depleted.

We observed prolonged coexistence of both *K. cochlearis* and *S. oblonga* with the smallest cladoceran, *B. longirostris*, despite using food levels which ensured exploitative competition between the species. Furthermore, the densities of competitors in some cultures were much higher than those encountered in nature. Accordingly, it is not surprising that planktonic rotifers can occur in abundance along with *B. longirostris* in natural communities. Experimental manipulations of zooplankton predators in Pleasant Pond, Minnesota, USA, revealed a competitive release of both *B. longirostris* and the rotifers *K. cochlearis*, *Brachionus* spp., *Monostyla* sp. and *Lecane* when the superior competitors *Ceriodaphnia reticulata* and *D. pulex* were eliminated (Lynch 1979). Similarly, Yan and Geiling (1985) found that the planktonic zooplankton biomass of a fishless, acid lake located near Sudbury, Ontario, Canada was dominated almost exclusively by *Keratella*, *Synchaeta* and *B. longirostris*. Taken together these studies suggest that both rotifers and small cladocerans like *Bosmina* may benefit from the reduction or elimination of larger-bodied cladocerans through selective predation by planktivorous fish or lake acidification. The coexistence of these taxa may occur because differences in their exploitative abilities are insufficient to cause competitive exclusion of some species, because predation by invertebrates may prevent populations of either group from expanding to the point where exploitative competition occurs, or both.

Daphnia can suppress rotifers by both exploitative and interference competition. The extent to which each of these mechanisms contributes to the suppression of rotifers in natural communities is poorly understood. Vanni (1986) suggested that the suppression of rotifer populations following the introduction of *D. pulex* into enclosures in Larimore Pond, Illinois, USA, resulted primarily from exploitative competition. However, laboratory studies have revealed that large species of *Daphnia* may inflict high rates of lethal mechanical interference on small rotifers (Gilbert and Stemberger 1985; Burns and Gilbert 1986), and that suppression of *K. cochlearis* by interference exceeds that from exploitation for *D. pulex* (MacIsaac, unpubl.). In addition, mechanical interference may increase when *Daphnia* are starved (Burns and Gilbert 1986). Consequently, rotifers may be increasingly suppressed by large cladocerans in natural communities when the supply of food resources is depleted, as mortality due to interference is augmented by lower birth rates and higher death rates associated with exploitative competition.

Most experiments investigating mechanical interference by cladocerans on *K. cochlearis* have used adult rotifers. These studies indicated that interference was limited to cladocerans with body sizes >1.2 mm. However, small cladocerans may be able to interfere with young rotifers that are smaller in body size and have more delicate integuments. For example, newborn *K. cochlearis* individuals are more susceptible than adults to interference by both *D. galeata mendotae* (Gilbert and Stemberger 1985) and *C. dubia* (Gilbert and MacIsaac 1989). The near-extinction of *K. cochlearis* populations by *C. dubia* in the present study suggests that the rotifers may have been subject to size (age) – specific interference (Fig. 1). Recruitment of *K. cochlearis* in mixed-species cultures with *C. dubia* was 33% lower than in corresponding single-species cultures by day 4 of the experiment, even though each *C. dubia* population was represented by only one ovigerous adult at the time and visual inspection revealed that food was abundant. The 'bottleneck' limiting rotifer recruitment would become increasingly severe as the number of adult *C. dubia* increased. The rotifer population would decline since fewer juveniles would survive to the adult stage and as the number of existing adults declined due to normal scenescence. Hence, cladoceran species smaller than 1.2 mm may be able to suppress *K. cochlearis* by interfering with the recruitment of juveniles as well as by exploitative competition. We observed lower initial growth rates of *K. cochlearis* in mixed-species cultures with *D. ambigua* and *B. longirostris* than in corresponding single-species cultures, but the suppression was not as marked as with *D. magna*, *D. pulex* and *C. dubia* (Fig. 1).

Daphnia ambigua populations appeared to oscillate in both single- and mixed-species cultures in the experiments with *K. cochlearis* and *K. testudo*. Slobodkin (1954) and Goulden and Hornig (1980) determined that oscillations in cladoceran populations occur as a consequence of time lags between the acquisition and expenditure of energy (food). *Daphnia* store energy as triacylglycerols when population densities are low and food is abundant (Goulden and Hornig 1980). Adult females survive and may continue to reproduce by utilizing their lipid reserves even after the food supply has been depleted. Thus, species with substantial energy storage capabilities have an inherent tendency to overshoot the carrying capacity of their environment.

The differential response of *D. ambigua* following the initial population oscillations in mixed-species cultures with *K. cochlearis* and *K. testudo* is noteworthy (Figs. 3a, 4b). While the populations in mixed-species cultures with *K. testudo* rebounded and closely tracked control populations, those in mixed-species cultures with *K. cochlearis* went extinct. A number of possibilities may account for this difference – different rotifer species, different initial competitor densities, or different food concentrations. Because the difference in body size between *K. testudo* and *K. cochlearis* is small relative to that between the rotifers and *D. ambigua*, it is unlikely that the use of different rotifer species was responsible for the result. Moreover, while prolonged coexistence of *K. cochlearis* and *D. ambigua* is characteristic of competition between these species, *K. cochlearis* is not always competitively dominant; another experiment revealed that *D. ambigua* suppressed *K. cochlearis* more severely than the converse (Fig. 5). Thus, the performance of *K. testudo* does not differ radically from that of *K. cochlearis* when in competition with *D. ambigua*.

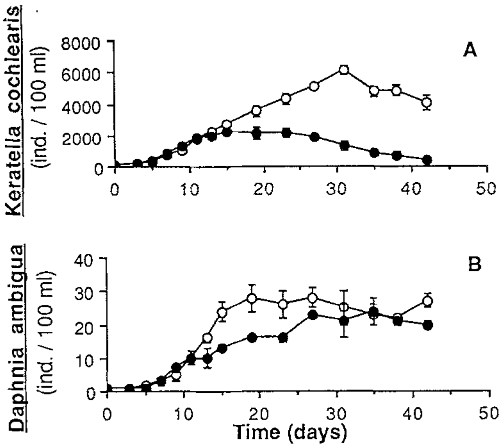

Fig. 5A, B. Dynamics of (**A**) *Keratella cochlearis* and (**B**) *Daphnia ambigua* in single- and mixed-species cultures. Experimental conditions were identical to the *K. cochlearis* experiments described in the methods section, except that animals were acclimated at 0.36 μg·ml^{-1} *Cryptomonas* sp. while the experiment was conducted at 0.32 μg·ml^{-1} provided every 2 d. Initial densities: 100 *K. cochlearis*, 1 gravid *D. ambigua*. Values as per Fig. 1; Symbols as per Fig. 2

Most investigators attempt to balance initial competitor population densities, biomasses or filtration rates in order to assess the outcome of interspecific competition. Balancing initial competitor densities probably is more critical for organisms competing through exploitative than interference competition, since organisms capable of interference need not be present at high densities to have demonstrable effects on susceptible species (Burns and Gilbert 1986). However, studies comparing relative exploitative ability at different density (biomass) ratios provide conflicting results. Matveev (1985) suggested that the initial frequencies of two bosminid species was important in determining which species achieved long-term competitive dominance, while Smith and Cooper (1982) found that the outcome of competition between *D. pulex* and *Ceriodaphnia* was insensitive to initial species ratios. *D. pulex* excluded the large rotifer, *Brachionus calyciflorus*, from culture via exploitative competition, regardless of initial species density ratios (Gilbert 1985).

Our results with rotifers and small cladocerans are consistent with resource-based competition theory. Theory predicts that when a shared, essential resource is available in limited supply, the species with the lowest resource requirement will exclude all others (see Tilman 1982). The theory has been supported by experiments with the rotifers *B. calyciflorus* and *B. rubens* (Rothhaupt 1988). Life-table experiments have estimated the threshold food levels (i.e., the food level at which the population growth rate [r_m] equals zero) of *K. cochlearis* f. *tecta*, *K. testudo* and *D. ambigua* at 0.06, $\leq$0.40 and 0.16 μg dry weight·ml^{-1}, respectively (Stemberger and Gilbert 1985; Stemberger 1988; Kirk 1988, respectively). Consequently, under conditions of long-term and severe food limitation, *K. cochlearis* should exclude *D. ambigua* by depleting food to a point below the threshold level of *D. ambigua* but above its own. Conversely, *D. ambigua* should exclude *K. testudo* by the same mechanism. Our results presented here support these predictions, although as demonstrated in Fig. 5, *K. cochlearis* and *D. ambigua* may coexist and experience mutual suppression. Actually, the competitive abilities of these species seem to depend on the temporal availability and concentration of food. *K. cochlearis* excluded *D. ambigua* when food was provided at 0.18 μg·ml^{-1} every two days (Fig. 3a) but was unable to do so when food was provided at 0.32 μg·ml^{-1} every two days (Fig. 5B). In addition, *D. ambigua* excludes *K. cochlearis* when food is concentrated but highly pulsed in availability but not when the same total quantity of food is delivered in a more dilute and continuous fashion (MacIsaac and Gilbert, unpublished work). Temporal variability in food availability would tend to favour cladocerans over rotifers because of their greater capacity to store energy and withstand brief periods of starvation.

Food concentration may be critical in affecting competition among other zooplankton taxa. In general, large species appear to be favoured when food is abundant, while small species dominate when food is sparse. As evidence, Tessier and Goulden (1987) determined that the weight-specific growth rates of *D. magna* and *D. pulex* were greater than that of *C. reticulata* when food was plentiful, but lower when food was limited. Romanovsky and Feniova (1985) described a competitive reversal between *D. pulex* and *C. reticulata* mediated by food levels, with *D. pulex* winning at high but not low levels. Similarly, *D. magna* dominated in mixed-species cultures with *D. pulex* and *D. longispina* when food was abundant, but was suppressed by them under low food conditions (Bengtsson 1987). Tillmann and Lampert (1984) obtained similar results with *D. magna* and the smaller species *D. pulicaria* and *D. longispina*. Finally, Goulden et al. (1982) observed that under high food conditions, *D. magna* dominated in cultures with *D. galeata mendotae*, while *D. galeata mendotae* in turn dominated over *B. longirostris*. However, the latter result was reversed under low food conditions. Thus, there is strong evidence that the competitive performance of rotifers and cladocerans is sensitive to both cladoceran body size and food concentration.

Lastly, caution must be applied in interpreting the results of competition experiments with species capable of induced morphological changes. While we began all our *Keratella cochlearis* experiments using individuals lacking a posterior spine (f. *tecta*), there was a higher incidence of spined morphs (f. *typica*) in mixed- than single-species cultures when the experiments were terminated. While spines would likely render the rotifers less vulnerable to mechanical interference by the cladocerans (Stemberger and Gilbert 1984), they might also affect energy uptake and utilization by the rotifers (Stemberger 1988).

In conclusion, our experiments clearly show that there is a fundamental difference in the ability of rotifers to coexist with large and small cladocerans. The ability of at least three rotifer species to coexist with, suppress, and in one case even outcompete, small cladocerans is of considerable significance regarding our understanding of zooplankton community structure. Although rotifers are much smaller than even small cladocerans, they can be expected to cooccur with them in situations where large cladocerans are rare or absent.

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References

Andersson G, Berggren H, Cronberg G, Gelin C (1978) Effects of planktivorous and benthivorous fish on organisms and water chemistry in eutrophic lakes. Hydrobiologia 59:9–15

Bengtsson J (1987) Competitive dominance among Cladocera: are single factors enough? Hydrobiologia 145:245–250

Brooks JL, Dodson SI (1965) Predation, body size, and composition of plankton. Science 150:28–35

Burns CW, Gilbert JJ (1986) Effects of daphnid size and density on interference between *Daphnia* and *Keratella cochlearis*. Limnol Oceanogr 31:848–858

DeMott WR (1983) Seasonal succession in a natural *Daphnia* assemblage. Ecol Monogr 53:321–340

DeMott WR, Kerfoot WC (1982) Competition among cladocerans: nature of the interaction between *Bosmina* and *Daphnia*. Ecology 63:1949–1966

Gilbert JJ (1985) Competition between rotifers and *Daphnia*. Ecology 66:1943–1950

Gilbert JJ (1988) Suppression of rotifer populations by *Daphnia*: a review of the evidence, the mechanisms, and the effects on zooplankton community structure. Limnol Oceanogr 33:1286–1303

Gilbert JJ, MacIsaac HJ (1989) The susceptibility of *Keratella cochlearis* to interference from small cladocerans. Freshwater Biol (in press)

Gilbert JJ, Stemberger RS (1985) Control of *Keratella* populations by interference competition from *Daphnia*. Limnol Oceanogr 30:180–188

Goulden CE, Hornig LL (1980) Population oscillations and energy reserves in planktonic Cladocera and their consequences to competition. Proc Nat Acad Sci (USA) 77:1716–1720

Goulden CE, Henry LL, Tessier AJ (1982) Body size, energy reserves, and competitive ability in three species of Cladocera. Ecology 63:1780–1789

Gurevitch J, Chester ST Jr (1986) Analysis of repeated measures experiments. Ecology 67:251–255

Hall DJ, Threlkeld ST, Burns CW, Crowley PH (1976) The size-efficiency hypothesis and the structure of zooplankton communities. Ann Rev Ecol Syst 7:177–208

Hrbáček J (1962) Species composition and the amount of zooplankton in relation to fish stock. Rozpravy Ceskoslovenske Akademie Ved Rada Matematickych a Prirodnick Ved 72:3–116

Kerfoot WC, DeMott WR (1985) Interactions among cladocerans: food limitation and exploitative competition. Arch Hydrobiol 21:431–451

Kirk KL (1988) The effect of suspended sediments on planktonic rotifers and cladocerans. Doctoral thesis, Dartmouth College, Hanover, New Hampshire, USA

Lynch M (1979) Predation, competition, and zooplankton community structure: an experimental study. Limnol Oceanogr 24:253–272

Matveev V (1985) Competition and population time lags in *Bosmina* (Cladocera, Crustacea). Int Rev Ges Hydrobiol 70:491–508

Neill WE (1984) Regulation of rotifer densities by crustacean zooplankton in an oligotrophic montane lake in British Columbia. Oecologia 61:175–181

Neill WE (1985) The effects of herbivore competition upon the dynamics of *Chaoborus* predation. Arch Hydrobiol 21:483–491

Pace ML, Orcutt JD Jr (1981) The relative importance of protozoans, rotifers, and crustaceans in a freshwater zooplankton community. Limnol Oceanogr 26:822–830

Porter KG, Feig YS, Vetter EF (1983) Morphology, flow regimes, and filtering rates of *Daphnia*, *Ceriodaphnia*, and *Bosmina* fed natural bacteria. Oecologia 58:156–163

Romanovsky YE, Feniova IY (1985) Competition among Cladocera: effect of different levels of food supply. Oikos 44:243–252

Rothhaup KO (1988) Mechanistic resource competition theory applied to laboratory experiments with zooplankton. Nature 333:660–662

Ruttner-Kolisko A, Malicky G (1988) Succession and abundance of rotifers in Lunzer Untersee as determined by biological interactions and abiotic events. Verh Internat Verein Limnol 23:510–515

SAS (Statistical Analysis System) Institute (1985) User's Guide: Statistics Ed. 5 Cary, North Carolina, USA

Shapiro J, Forsberg B, Lamarra V, Lindmark G, Lynch M, Smeltzer E, Zoto G (1982) Experiments and experiences in biomanipulation. US Environmental Protection Agency EPA-600/3-82-096

Slobodkin LB (1954) Population dynamics in *Daphnia obtusa* Kurz. Ecol Monogr 24:69–88

Smith DW, Cooper SD (1982) Competition among Cladocera. Ecology 63:1004–1015

Sprules WG (1972) Effects of size-selective predation and food composition on high altitude zooplankton communities. Ecology 53:375–386

Stemberger RS (1981) A general approach to the culture of planktonic rotifers. Can J Fish Aquat Sci 38:721–724

Stemberger RS (1988) Reproductive costs and hydrodynamic benefits of chemically induced defenses in *Keratella testudo*. Limnol Oceanogr 33:593–606

Stemberger RS, Gilbert JJ (1984) Spine development in the rotifer *Keratella cochlearis*: induction by cyclopoid copepods. Freshwater Biol 14:639–647

Stemberger RS, Gilbert JJ (1985) Body size, food concentration, and population growth in planktonic rotifers. Ecology 66:1151–1159

Tessier AJ, Goulden CE (1987) Cladoceran juvenile growth. Limnol Oceanogr 32:680–686

Tessier AJ, Henry LL, Goulden CE, Durand MW (1983) Starvation in *Daphnia*: energy reserves and resource allocation. Limnol Oceanogr 28:667–676

Threlkeld ST (1976) Starvation and the size structure of zooplankton communities. Freshwater Biol 6:489–496

Tillmann U, Lampert W (1984) Competitive ability of differently sized *Daphnia* species: an experimental test. J Freshwater Ecol 2:311–323

Tilman D (1982) Resource competition and community structure. Princeton University Press, Princeton, New Jersey

Vanni M (1986) Competition in zooplankton communities: suppression of small species by *Daphnia pulex*. Limnol Oceanogr 31:1039–1056

Yan ND, Geiling W (1985) Elevated planktonic rotifer biomass in acidified metal-contaminated lakes near Sudbury, Ontario. Hydrobiologia 120:199–205

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