Freshwater Biology (1989) **22,** 333–339

The susceptiblity of *Keratella cochlearis* to interference from small cladocerans

JOHN J. GILBERT and HUGH J. MACISAAC* Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire, U.S.A.

SUMMARY. 1. Even at high population densities (300–2000 ind. l^{-1}), only one of five small cladoceran species (adult body length <1 mm) significantly suppressed population growth of the rotifer *Keratella cochlearis* through interference (encounter) competition. At 500 ind. l^{-1}, adults of *D. ambigua* (0.96 mm body length) imposed an instantaneous per capita death rate of 0.21 day^{-1} on this rotifer. These short-term experiments may have underestimated cladoceran interference because newborn rotifers were rarely present.

2. Newborn rotifers (<12 h old) were much more susceptible than adult rotifers (> 24 h old) to interference from *Ceriodaphnia dubia.* All of the small cladoceran species tested were very much less likely than large *Daphnia* (body lengths >1.2 mm) to interfere with *K. cochlearis,* but perhaps at high population densities they could suppress population growth of susceptible rotifer species by damaging, and possibly eating, relatively small and soft-bodied newborn individuals.

3. *K. cochlearis* of the *tecta* form, without a posterior spine, produced offspring of the *typica* form, with a posterior spine, in the presence of *C. dubia*. This developmental response is stimulated by at least several, and possibly all, cladocerans and probably reduces the susceptibility of the rotifer to cladoceran interference.

Introduction

Low population densities of large species of *Daphnia* O. F. Müller can impose high mortality rates on *Keratella cochlearis* (Gosse) and some other small, or soft-bodied rotifers through mechanical interference (encounter) competition (Gilbert & Stemberger, 1985; Burns & Gilbert, 1986a, b; Gilbert, 1988a, b, 1989a). In this interaction, rotifers are swept into *Daphnia*'s branchial chamber with the feeding current; although most of these rotifers are rejected by the postabdomen, some are damaged in transit and some may be ingested.

The ability of *Daphnia* to interfere with *K. cochlearis* decreases with the size of the *Daphnia* and becomes negligible, at least in short-term experiments, at body lengths less than 1.2 mm (head to base of tail spine) (Burns & Gilbert, 1986a). This size relationship occurs both within a given species and among different species of *Daphnia*. The mechanistic basis for the relationship is that *Daphnia*'s tendency to retain captured rotifers in its branchial chamber, and to transport them to its mouth and eat them, decreases with its body size (Burns & Gilbert, 1986b). *Daphnia* smaller than 1.2 mm draws

Correspondence: Dr John J. Gilbert, Department of Biological Sciences, Dartmouth College, Hanover, NH 03755, U.S.A.

rotifers into its branchial chamber but rejects them very rapidly and apparently unharmed.

The primary purpose of the present study is to determine the extent to which a 1.2 mm size threshold for interference might apply to cladocerans other than *Daphnia*. Specifically, we test the hypothesis that cladocerans with body lengths less than 1.2 mm from various genera will not interfere with *K. cochlearis*. Additional experiments with one of these cladoceran species examines whether this hypothesis holds even under conditions when *K. cochlearis* should be maximally vulnerable – when it is young (relatively small and soft-bodied) and when the cladocerans have no algal food and hence should be more likely to eat captured rotifers (Gilbert & Stemberger, 1985; Burns & Gilbert, 1986b). Finally, some observations from these experiments are used to assess whether *K. cochlearis* produces a posterior spine in the presence of cladocerans.

Material and Methods

The rotifer *Keratella cochlearis* f. *tecta* (Gosse) and the cladocerans *Bosmina longirostris* (O. F. Müller), *Ceriodaphnia dubia* Richard, *Holopedium gibberum* Zaddach, *Diaphanosoma brachyurum* (Liéven) and *Daphnia ambigua* (Scourfield) were cultured on a species of *Cryptomonas* Ehrenberg ($\approx 9\times10^{-5}\,\mu$g cell^{-1}) in glass-fibre-filtered lake water as described elsewhere (Gilbert, 1985, 1988a). Cultures of all species contained exclusively females and, except for *H. gibberum*, were clones. Adult body lengths of the cladoceran species are reported in Table 1. The body length of *K. cochlearis*, without spines, was about 80 μm. All cultures were maintained, and all experiments were conducted, at 20°C in a photocycle (LD 16:8, ~300 lux).

The ability of each cladoceran species to interfere mechanically with *K. cochlearis* was determined from population growth rates (r) of the *Keratella* with and without cladocerans. Death rates imposed on the *Keratella* by the cladocerans (d_c) were calculated from the differences between these two population growth rates (Gilbert, 1988a). Experiments were conducted in 50 ml beakers containing 40 or 50 ml of a *Cryptomonas* suspension (2.5 or 5×10^4 cells ml^{-1}) in lake water with about 10% (v/v) fresh

TABLE 1. Abilities of five species of small cladocerans to interfere with the rotifer *Keratella cochlearis* f. *tecta*. The mortality rate imposed on *K. cochlearis* by a cladoceran species (d_c) is the population growth rate (r) of the rotifer without cladocerans minus that with cladocerans. Experimental conditions: 20°C, 40 ml (50 ml in experiments 5 and 6), 5×10^4 cells ml^{-1} *Cryptomonas* sp. (2.5×10^4 cells ml^{-1} in experiments 7 and 8), initially twenty non-ovigerous *Keratella*, 20–28.5 h incubation, LD 16:8, ~300 lux, three replicates per treatment. All values of sizes and rates are means ±1 SD. Significance of difference between mean r-values with and without cladocerans (Student's t-test) denoted by NS ($P>0.05$) or * ($P<0.05$).

Experiment	Cladoceran			*Keratella* r day^{-1}		*Keratella* d_c day^{-1}
	Species	Size (mm)	Initial number per beaker	Without cladocerans	With cladocerans	
1	*Bosmina longirostris*	0.43±0.06	20	0.03±0.05	0.01±0.02NS	0.02±0.07
2		0.44±0.03	40	0.04±0.04	0.04±0.07NS	0.00±0.04
3	*Ceriodaphnia dubia*	0.70±0.06	15	0.21±0.14	0.21±0.04NS	0.00±0.10
4		0.69±0.04	15	0.34±0.09	0.31±0.12NS	0.03±0.20
5	*Holopedium gibberum*	0.76±0.03	10	0.00±0.00	−0.05±0.05NS	0.05±0.05
6		0.66±0.04	10	0.05±0.06	0.03±0.05NS	0.03±0.02
7	*Diaphanosoma brachyurum*	0.83±0.07	6	0.20±0.17	0.17±0.16NS	0.03±0.06
8		0.80±0.14	30	0.08±0.08	0.04±0.04NS	0.04±0.07
9	*Daphnia ambigua*	0.96±0.16	20	0.00±0.00	−0.21±0.11*	0.21±0.11

algal growth medium – Woods Hold MBL medium (Nichols, 1973) as modified by Stemberger (1981). *Cryptomonas* cells were enumerated either with an electronic particle counter (Particle Data, Inc.) or with a haemacytometer. All *Keratella* populations were initiated with twenty non-ovigerous, although rarely juvenile (<12 h old), individuals of the *tecta* form. Cladoceran densities ranged from six to forty individuals per beaker (150–1000 ind. l^{-1}). Incubation periods were about 1 day, but varied among experiments from 20 to 28.5 h. In all experiments the treatments with and without cladocerans were replicated three times. At the end of the population-growth-rate experiments with *Ceriodaphnia*, non-ovigerous *Keratella* (mostly individuals born towards the end of the incubation period) were preserved in 10% formalin and measured for body and posterior spine lengths. These measurements were made with a compound microscope and were accurate to the nearest 2.5 μm.

Three experiments testing the effects of food availability and *Keratella* size (age) on the survivorship of *Keratella* with and without *Ceriodaphnia* were conducted within a 13 day period in 50 ml beakers with 40 ml of a suspension of *Cryptomonas* in 9:1 (v/v) lake water and algal growth medium. The design of the experiments and the number of replicates in the different treatments are given in Table 2. Prior to the experiments, the *Ceriodaphnia* was acclimated for 1 day on a *Cryptomonas* suspension containing 1.15×10^4 cells ml^{-1}. In the experiments, this same concentration of *Cryptomonas* cells was used in all cultures in treatments with food, while no *Cryptomonas* cells were present in the cultures in treatments without food. Each culture in the treatments with *Ceriodaphnia* contained thirteen, usually gravid, adults of this cladoceran (325 ind. l^{-1}). All cultures were inoculated with either fifty adult or fifty juvenile *K. cochlearis* f. *tecta*. Juveniles were <12 h old and starved since birth; adults were non-ovigerous individuals >24 h old and starved for 24 h. Incubation periods of the experiments were 24 h. Visual inspection showed that *Cryptomonas* cells were still abundant at the end of the experiments in those cultures where they were initially present. Total lengths of the *Ceriodaphnia* and *Keratella* were measured using live and preserved (10% formalin) individuals, respectively, with a stereomicroscope to the nearest 9.3 μm.

K. cochlearis survival during the 24 h period in the different treatments was analysed using the procedure CATMOD of the Statistical Analysis System (SAS Institute, 1985). This procedure generates an analysis of variance table by performing a weighted-least-squares analysis on categorical, dependent-variable responses and estimating the significance of design effects by using a Wald statistic and the chi-square distribution. Survival data for the different experiments were pooled prior to statistical analysis. Treatments with more than three replicates (Table 2) were run on more than one date; the variability between such replicates was always low, indicating that test conditions were similar across test dates.

Results

The effects of five species of small cladocerans on the population growth rate of *K. cochlearis*

TABLE 2. Design and treatment replication of experiments testing effects of *Ceriodaphnia dubia*, rotifer size (age), and presence (P) or absence (A) of food on the survivorship of *Keratella cochlearis* f. *tecta* over a 24-h period

	Treatment							
	Ceriodaphnia present				*Cerodaphnia* absent			
Keratella cochlearis:	Adult		Juvenile		Adult		Juvenile	
Food:	P	A	P	A	P	A	P	A
	Number of experimental replicates							
Experiment								
1		2		3		3		3
2	3	3						
3	3		3	3	3		3	

TABLE 3. Effect of presence of *Ceriodaphnia* on the development of a posterior spine in *Keratella cochlearis* f. *tecta*. The *Keratella* examined were non-ovigerous individuals removed at the end of the 1-day (24–27.5 h) incubations – mostly offspring produced during the experiment, but probably also some of the initial females. Details of experiments are in Table 1.

Experiment (Table 1)	*Keratella*				
	Without *Ceriodaphnia*		With *Ceriodaphnia*		
	Body length (μm) [$\bar{x}\pm1$ SD (N)]	Proportion with posterior spine	Body length (μm) [$\bar{x}\pm1$ SD (N)]	Proportion with posterior spine	Posterior spine length (μm) [$\bar{x}\pm1$ SD (N)]
3	81.3±3.7 (18)	0	80.1±4.6 (16)	0.75	14.9±9.4 (16)
4	80.7±4.3 (21)	0	80.9±4.2 (20)	0.85	14.8±7.6 (20)

are shown in Table 1. Although all of the cladoceran species were present at high population densities (150–1000 ind. l^{-1}), only the largest species (*D. ambigua*) significantly suppressed the *Keratella. Cryptomonas* densities were not determined at the end of the incubation periods, but visual inspection at such times showed that this algal food resource was still abundant in treatments with and without cladocerans in all experiments.

The presence of cladocerans induced most of the few offspring of *K. cochlearis* produced during these experiments to develop a posterior spine not possessed by their mothers. This effect was documented in experiments 3 and 4 with *C. dubia* (Table 3). Thus, some cladoceran factor can cause a transformation of the *tecta* form of *K. cochlearis* to the *typica* form in one generation. The presence of some (15–25%) *tecta* individuals among the non-ovigerous *Keratella* at the end of the incubation periods in the cultures with *Ceriodaphnia* indicates that these rotifers either were offspring not responding to the *Ceriodaphnia* factor or belonged to the initial cohort of *tecta* individuals.

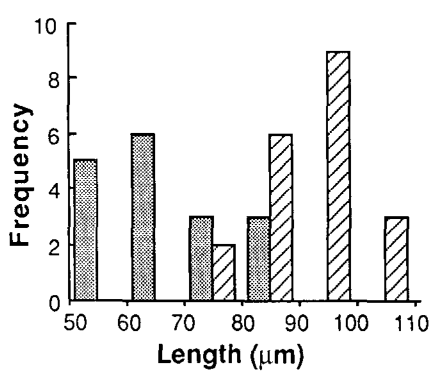

FIG. 1. Frequency distributions of lorica lengths (including anterior spines) of juvenile (<12-h-old) (stipples) and adult (>24-h-old) (diagonals) *Keratella cochlearis* f. *tecta*.

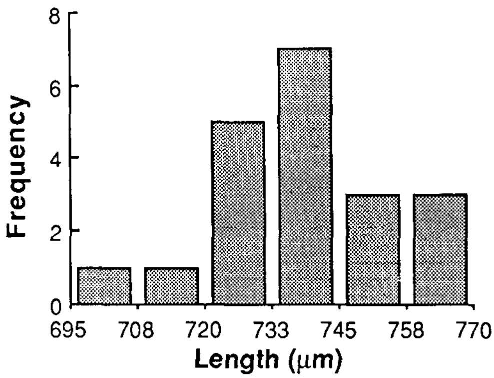

FIG. 2. Frequency distributions of body lengths of adult *Ceriodaphnia dubia*.

The results of experiments on the effects of food availability and rotifer size on the susceptibility of *K. cochlearis* to interference from *C. dubia*, at a population density of 325 adults l^{-1}, are shown in Figs. 1–3 and Table 4. Size frequency distributions of the juvenile and adult

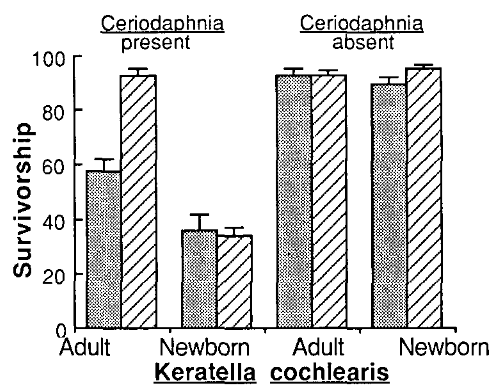

FIG. 3. Mean survivorship (+1 SE) over a 24-h period of newborn (<12-h-old) and adult (>24-h-old) *Keratella cochlearis* f. *tecta* as affected by *Ceriodaphnia dubia* and presence (stipples) or absence (diagonals) of food.

TABLE 4. Analysis of variance table depicting the effects of adult *Ceriodaphnia dubia*, rotifer size, and food presence on the survivorship of *Keratella cochlearis* f. *tecta*

Effect	df	Chi-square	Significance (P)
Ceriodaphnia	1	139	<0.0001
Size	1	30	<0.0001
Food	1	16	<0.0001
Ceriodaphnia × size	1	34	<0.0001
Ceriodaphnia × food	1	3	0.0672
Size × food	1	4	0.0348
Ceriodaphnia × size × food	1	19	<0.0001
Intercept	1	264	<0.0001

Keratella at the start of the experiments (Fig. 1) were significantly different (P=0.014, Kolmogorov-Smirnov two-sample test). The mean total length (including anterior spines) of the juveniles (68 μm) was significantly smaller than that of the adults (91 μm) (P <0.001, Student's t-test). The mean length of the adult *Ceriodaphnia* (Fig. 2) was 0.737 mm. *Keratella* survivorship in the different treatments is shown in Fig. 3, and the statistical analysis is presented in Table 4. The juveniles of *Keratella* were much more susceptible than the adults to interference from *C. dubia*. This age or size effect occurred whether or not *Cryptomonas* food was present. *Keratella* mortality from *Ceriodaphnia* interference did not increase in the absence of food. The survivorship of juvenile *Keratella* with *Ceriodaphnia* was similarly low in the presence and absence of food, and that of adult *Keratella* was actually significantly higher without food (Table 4). This latter, unexpected result occurred in all replicates of two different experiments where adult *Keratella* were tested with *Ceriodaphnia* in the presence and absence of *Cryptomonas*. In the statistical analysis, this result increases the importance of the presence of *Ceriodaphnia* and food, increases the importance of the *Ceriodaphnia* × size × food interaction, and reduces the importance of size and the *Ceriodaphnia* × size interaction.

Discussion

The results of the population growth experiments generally confirmed the hypothesis that cladocerans with body lengths less than 1.2 mm will not interfere mechanically with *K. cochlearis* (Table 1). The one exception in these experiments was *D. ambigua*. This cladoceran had a mean adult body length of 0.96 mm and, at a population density of 500 ind. l^{-1}, caused a mortality rate of 0.21 day^{-1} on a *K. cochlearis* population. Of course, such a high density of *Daphnia* would rarely, if ever, occur in nature; thus, it seems reasonable to suggest that much lower, natural densities of this small daphnid probably would not have appreciable, direct effects on populations of *K. cochlearis*. Most interestingly, another study indicated that adults of the very small cladoceran, *Scapholeberis kingi* Sars, which had body lengths of 0.4–0.6 mm, strongly interfered with the rotifer *Synchaeta oblonga* (Ehrenberg) (Gilbert, 1989b). Accordingly, there may be some exceptions to the rule that cladoceran species with adult body lengths less than 1.2 mm cannot interfere with rotifers.

Another, more general exception to this rule is that small cladocerans may interfere with very young but not older rotifers. The experiments on the effect of *Ceriodaphnia* on the survivorship of different-aged *K. cochlearis* showed this to be the case. Newborn rotifers (<12 h old) were much more likely to be killed by *Ceriodaphnia* than adult rotifers (>24 h old), whether or not food resources were present (Fig. 3, Table 4). This observation is consistent with results from an earlier study (Gilbert & Stemberger, 1985) showing that newborn individuals of *K. cochlearis* are more susceptible to *Daphnia* interference than adults. This finding was based on direct observations of rotifers swept into and rejected from the branchial chamber of *D. galeata* Sars *mendotae* Birge. The greater vulnerability of newborn rotifers almost certainly is due to their smaller size and softer integument.

The experiments on the effects of *Ceriodaphnia* on the survival of *K. cochlearis* showed that the presence or absence of food affected the survival of adult but not newborn rotifers (Fig. 3). The effect on adult rotifers was contrary to expectations. For some unknown reason adults were more vulnerable when food was present. Burns & Gilbert (1986b) found that *K. cochlearis* was more likely to be damaged or eaten by *D. pulex* Leydig when algal food resources were absent; and so we had hypothesized that the same would be true with *Ceriodaphnia*. The failure of the absence of food to further decrease the survivorship of the newborn rotifers was also surprising.

Ceriodaphnia's ability to interfere with newborn *K. cochlearis* certainly could increase its ability to suppress competitively this rotifer species. In our survivorship experiments, slightly more than 60% of the newborn *K. cochlearis* were killed within 1 day by *C. dubia* at a population density of 325 adults l^{-1} (Fig. 3). Strong suppression of *K. cochlearis* by *Ceriodaphnia* has, in fact, been indicated in experimental ponds with *C. reticulata* (Jurine) (Hall, Cooper & Werner, 1970) and demonstrated in laboratory competition experiments with *C. dubia* (MacIsaac & Gilbert, 1989). In general, susceptibility of newborn rotifers to small cladocerans could cause a bottleneck for rotifer population growth.

Our short-term experiments on the effect of *C. dubia* and other cladoceran species on the population growth rate of *K. cochlearis* probably underestimated the abilities of these cladocerans to interfere with *K. cochlearis*, because newborn rotifers were not included in the initial populations and generally were not often produced during the experiment. In experiments 3, 4 and 7 there was considerable *K. cochlearis* reproduction: *r*-values ≥ 0.2 day^{-1} (Table 1), but these newborn rotifers were produced towards the end of the incubation period and thus would have had very limited exposure to the cladocerans.

While *D. ambigua* and *C. dubia* in the present study showed some ability to interfere with *K. cochlearis*, it is clear that large *Daphnia* (body lengths >1.2 mm) are much more likely to interfere with this rotifer than small cladocerans (body lengths <1.2 mm) are. For example, interference from *Daphnia* with a body length of 2.5 mm and at a density of 5 ind. l^{-1} imposed a mortality rate (*d*) of about 0.46 day^{-1} on a population of *K. cochlearis* (Burns & Gilbert, 1986a), while that from *D. ambigua* with a body length of 0.96 mm and at a density two orders of magnitude greater (500 ind. l^{-1}) caused a much lower mortality rate (0.21 day^{-1}). This fundamental difference between the abilities of large and small cladocerans to interfere with rotifers must contribute to the fact that rotifers in natural communities generally are rare when large *Daphnia* are present but often abundant when only small cladocerans occur (Gilbert, 1988b).

Another potentially important explanation for the ability of rotifers to coexist with small cladocerans is that rotifers are able to compete quite effectively with them for shared food resources, despite their relatively much smaller body size. Competition experiments have demonstrated mutual suppression, long-term (up to 7 weeks) coexistence, and even occasional exclusion of cladocerans by rotifers (MacIsaac & Gilbert, 1989).

It should be noted that *K. cochlearis* is one of the most susceptible rotifer species to interference from large *Daphnia* so far tested (Gilbert, 1988a). Therefore, it seems reasonable to conclude that species less susceptible to *Daphnia* interference than *K. cochlearis* should also be less susceptible to interference from smaller cladocerans. Accordingly, it follows that if small cladocerans are generally unlikely to interfere with *K. cochlearis*, then they are even more unlikely to interfere with less susceptible rotifer species. The only rotifers likely to be directly affected by interference from small cladocerans are those that have soft integuments and body sizes similar to, or smaller than, that of *K. cochlearis*.

The experiments on the population growth rates of *K. cochlearis* with and without *C. dubia* showed that the *tecta* form of this rotifer, with no posterior spine, produced offspring of the *typica* form, with a posterior spine, in the presence of *C. dubia* (Table 3). A posterior spine in *K. cochlearis* probably is induced by most, if not all, other cladocerans. Long-term competition experiments with this rotifer and either *B. longirostris* or *D. ambigua* showed that the rotifers in mixed-species cultures were much more likely to have posterior spines than those in single-species cultures (MacIsaac & Gilbert, 1989). Induction of a posterior spine in *K. cochlearis* also is stimulated by the rotifer *Asplanchna* (Gosse) and by cyclopoid copepods (Stemberger & Gilbert, 1984). Similarly, induction of two posterior spines in *K. testudo* (Ehrenberg) is caused by these same taxa – *Asplanchna,* calanoid as well as cyclopoid copepods, and *Daphnia* (Stemberger & Gilbert, 1987). In all these cases that have been investigated, the posterior spines in both *K. cochlearis* and *K. testudo* are induced through the release of a chemical factor into the environment (Gilbert & Stemberger, 1984; Stemberger & Gilbert, 1984, 1987).

The production of one or two posterior spines in *Keratella* in response to *Asplanchna,* copepods, and cladocerans reduces the mortality rate imposed on the *Keratella* by the inducing organisms. Spined morphs are less likely than unspined ones to be eaten by *Asplanchna* and copepods, and to be damanged or eaten by *Daphnia* (Gilbert & Stemberger, 1984; Stemberger & Gilbert, 1984, 1987; Gilbert, 1988a). Accordingly, it seems likely that the production of a posterior spine by *K. cochlearis* in response to the *Ceriodaphnia* in the present study should decrease the susceptibility of neonates to mechanical interference from this cladoceran. The reason why one or two posterior spines can protect *Keratella* from interference was revealed by observing encounters between *K. testudo* morphs and *D. pulex* (Stemberger & Gilbert, 1987). When captured in *Daphnia*'s branchial chamber, the morph with two posterior spines was rejected more quickly and was less likely to be transported along the food groove to the mouth than the morph without posterior spines. *Keratella*'s developmental response to cladocerans must be particularly important in reducing intense interference from large *Daphnia,* but it is probably also important in reducing the susceptibility of the most vulnerable, young individuals to the much less intense interference from smaller cladocerans.

Acknowledgments

This study was supported by National Science Foundation (U.S.A.) research grants BSR-8415024 and BSR-8717074 to J.J.G., by a Natural Sciences and Engineering Research Council of Canada postgraduate scholarship to H.J.M., and by Dartmouth College Cramer funds to H.J.M. We thank Larry Wasserman for statistical advice, Maxine Bean for laboratory assistance, and William DeMott and an anonymous reviewer for improving the manuscript.

References

Burns C.W. & Gilbert J.J. (1986a) Effects of daphnid size and density on interference between *Daphnia* and *Keratella cochlearis. Limnology and Oceanography,* **31,** 848–858.

Burns C.W. & Gilbert J.J. (1986b) Direct observations of the mechanisms of interference between *Daphnia* and *Keratella cochlearis. Limnology and Oceanography,* **31,** 859–866.

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

Gilbert J.J. (1988a) Susceptibilities of ten rotifer species to interference from *Daphnia pulex. Ecology,* **69,** 1826–1838.

Gilbert J.J. (1988b) Suppression of rotifer populations by *Daphnia*: a review of the evidence, the mechanisms, and the effects on zooplankton community structure. *Limnology and Oceanography,* **33,** 1288–1305.

Gilbert J.J. (1989a) The effect of *Daphnia* interference on a natural rotifer and ciliate community: short-term bottle experiments. *Limnology and Oceanography,* **34,** 606–617.

Gilbert J.J. (1989b) Competitive interactions between the rotifer *Synchaeta oblonga* and the cladoceran *Scapholeberis kingi* Sars. *Hydrobiologia* (in press).

Gilbert J.J. & Stemberger R.S. (1984) *Asplanchna*-induced polymorphism in the rotifer *Keratella slacki. Limnology and Oceanography,* **29,** 1309–1316.

Gilbert J.J. & Stemberger R.S. (1985) Control of *Keratella* populations by interference competition from *Daphnia. Limnology and Oceanography,* **30,** 180–188.

Hall D.J., Cooper W.E. & Werner E.E. (1970) An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnology and Oceanography,* **15,** 839–928.

MacIsaac H.J. & Gilbert J.J. (1989) Competition between rotifers and cladocerans of different body sizes. *Oecologia (Berlin)* (in press).

Nichols H.W. (1973) Growth media – freshwater. *Handbook of Phycological Methods* (Ed. J. R. Stein), pp. 7–24. Cambridge University Press.

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

Stemberger R.S. (1981) A general approach to the culture of planktonic rotifers. *Canadian Journal of Fisheries and Aquatic Sciences,* **38,** 721–724.

Stemberger R.S. & Gilbert J.J. (1984) Spine development in the rotifer *Keratella cochlearis*: induction by cyclopoid copepods and *Asplanchna. Freshwater Biology,* **14,** 639–647.

Stemberger R.S. & Gilbert J.J. (1987) Multiple-species induction of morphological defences in the rotifer *Keratella testudo. Ecology,* **68,** 370–378.

(Manuscript accepted 6 April 1989)

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.