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

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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
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* Richar, *Hoplodinium gibberum* Zaddach, *Diaphanosoma brachyurum* (Liéven) and *Daphnia ambigua* (Scourfield) were cultured on a species of *Cryptomonas* Ehrenberg (=9×10^5 µg 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 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 (r_i - r_c). Initial population densities were 2000 cells ml^{-1} and 10% (v/v) fresh. Values are means ±1 SD. Significance of difference between means was determined by *t* test. Asterisks denote *P < 0.05*.

<table>
<thead>
<tr>
<th>Cladoceran</th>
<th>Initial</th>
<th>Without cladocerans</th>
<th>With cladocerans</th>
<th>K. cochlearis</th>
<th>d_c, day^{-1}</th>
</tr>
</thead>
<tbody>
<tr>
<td>B. longirostris</td>
<td>4.0 ± 0.0</td>
<td>4.3 ± 0.0</td>
<td>0.3 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>C. dubia</td>
<td>3.7 ± 0.0</td>
<td>3.7 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>H. gibberum</td>
<td>4.0 ± 0.0</td>
<td>4.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>D. ambigua</td>
<td>4.0 ± 0.0</td>
<td>4.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.0 ± 0.0</td>
<td>0.00 ± 0.00</td>
</tr>
</tbody>
</table>
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 1.15×10⁴ 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 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.

<table>
<thead>
<tr>
<th>Experiment (Table 1)</th>
<th>Keratella Without Ceriodaphnia</th>
<th>Keratella With Ceriodaphnia</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Body length (µm) [±1 SD (N)]</td>
<td>Proportion with posterior spine</td>
</tr>
<tr>
<td>3</td>
<td>81.3±3.7 (18)</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>80.7±4.3 (21)</td>
<td>0</td>
</tr>
</tbody>
</table>

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.

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

![Graph](https://via.placeholder.com/150)

**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.

![Graph](https://via.placeholder.com/150)

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

![Graph](https://via.placeholder.com/150)

**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.
Keratella cochlearis 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 \(\mu m\)) was significantly smaller than that of the adults (91 \(\mu m\)) \((P<0.001\), 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 x size x food interaction, and reduces the importance of size and the Ceriodaphnia x 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. 1\(^{-1}\), 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

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**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**

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>Chi-square</th>
<th>Significance (P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ceriodaphnia</td>
<td>1</td>
<td>139</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Size</td>
<td>1</td>
<td>30</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Food</td>
<td>1</td>
<td>16</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Ceriodaphnia x size</td>
<td>1</td>
<td>34</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Ceriodaphnia x food</td>
<td>1</td>
<td>3</td>
<td>0.0672</td>
</tr>
<tr>
<td>Size x food</td>
<td>1</td>
<td>4</td>
<td>0.0348</td>
</tr>
<tr>
<td>Ceriodaphnia x size x food</td>
<td>1</td>
<td>19</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Intercept</td>
<td>1</td>
<td>264</td>
<td>&lt;0.0001</td>
</tr>
</tbody>
</table>
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 dadocerans 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 cyclopoaods (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_ (Stem-
berger & 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 damaged 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.

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References


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