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Rotifers as predators on small ciliates

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Abstract

Clearance rates of *Synchaeta pectinata*, *Brachionus calyciflorus* and *Asplanchna girodi* on *Tetrahymena pyriformis* (46 μm in length) at a density of 10 cells ml^{-1}, in the presence of algal food, were 2.5 to 6.1 ml rot.$^{-1}$ day^{-1}. Clearance rates of these rotifers were, respectively, about 2, 3, and 13 times lower on *Strobilidium gyrans* (58 μm in length) than on *T. pyriformis*, indicating that the saltations of *S. gyrans* are an effective escape response. Clearance rates of *S. pectinata* were considerably lower on *Colpidium striatum* (81 μm) than on *S. gyrans*, suggesting that *S. pectinata* may not be able to ingest ciliates of this size. *S. pectinata* had a clearance rate of 19 ml rot.$^{-1}$ day^{-1} on *S. gyrans* at a density of 1.2 cells ml^{-1}, in the absence of edible algal food. Rotifers may prey extensively on ciliates in natural plankton communities, ingesting 25 to 50 individuals in the 45–60 μm size range day^{-1}.

Introduction

Ciliated protozoa are often important components of freshwater plankton communities. Their numerical abundance ranges up to ~250 ind ml^{-1}, depending on ecosystem trophic state, season, and depth in the water column (Sorokin & Paveljeva, 1972; Pace & Orcutt, 1981; Beaver & Crisman, 1982, 1989; Pace, 1982; Gates, 1984; Lewis, 1985; Taylor & Heynen, 1987; Beaver *et al.*, 1988; Finlay *et al.* 1988; Carlough & Meyer, 1989; Müller, 1989; Weisse *et al.*, 1990). Ciliate biomass concentrations generally range from ~2 to 600 but may reach 1700 mg dry weight m^{-3} (Sorokin & Paveljeva, 1972; Hecky & Kling, 1981; Beaver & Crisman, 1982; Gates, 1984; Beaver *et al.*, 1988; Weisse *et al.*, 1990).

Ciliate biomass often represents a substantial fraction of total zooplankton biomass – up to ~90% in Lake Erken (Nauwerck, 1963); probably ~25% at some depths in Lake Dalnee (Sorokin & Paveljeva, 1972); ~30% in mid-July in Øvre Heimdalsvatn (Larsson, 1978); ~10–50% in Lake Ogelthorpe (Pace & Orcutt, 1981); 7–47% in Cayuga Lake (Hunt & Chein, 1983); and 5–22% in some south-central Ontario lakes (Gates, 1984; Gates & Lewg, 1984). Ciliates are even more important components of the zooplankton on a productivity basis. During the spring bloom in Lake Constance, ciliates accounted for ~38% of total zooplankton biomass but ~67% of total zooplankton production (Weisse *et al.*, 1990).

The fate of ciliate production in freshwater plankton communities is very poorly understood. However, much of it probably is ingested by cladocerans, copepods, and some rotifers. Cladocerans remove ciliates from laboratory cultures and natural plankton communities (McMahon & Rigler, 1965; Tezuka, 1974; Porter *et al.*, 1979; Archbold & Berger, 1985; Gilbert, 1989; Wickham & Gilbert, 1991 in press; Jack & Gilbert, in press) and can utilize them as food (Tezuka, 1974; DeBiase *et al.*, 1990; Wickham & Gilbert, unpublished). Cyclopoid copepods eat ciliates (Sorokin & Paveljeva, 1972; Porter *et al.*, 1979; Archbold & Berger, 1985), and calanoid copepods probably do so as well, although freshwater species have not been tested. Marine calanoids prey extensively on ciliates (Gifford & Dagg, 1988; Tiselius, 1989; Wiadnyana & Rassoulzadegan, 1989; Jonsson & Tiselius, 1990; Stoecker & Capuzzo, 1990).

A rotifer generally known to prey on ciliates is *Asplanchna*. Several species have been cultured on the large ciliate *Paramecium* (Gilbert, 1968, 1975; Maly, 1969, 1975; Robertson & Salt, 1981; Stemberger & Gilbert, 1984; Gilbert & Confer, 1986), and stomach contents of individuals from natural communities often include tintinnids and other loricate ciliates (Nauwerck, 1963; Pejler, 1957; Ejsmont-Karabin, 1974; Ghilarov, 1977; Guiset, 1977; Salt *et al.*, 1978; Stenson, 1984; Garreau *et al.*, 1988), sometimes at frequencies indicating high preference (Ejsmont-Karabin, 1974). Feeding rates of *Asplanchna* have been measured on *Paramecium*. Some ingestion rates of *A. brightwelli* on *P. aurelia* were ~100 ind^{-1} day^{-1}, giving clearance rates of 10 to 17 ml ind^{-1} day^{-1} (Maly, 1969). Comparable clearance rates were found for *A. girodi* on a similar if not identical species of *Paramecium*, *P. tetraurelia*, and on another large species, *Bursaridium difficile* (Jack & Gilbert, unpublished).

The rotifer *Synchaeta* probably also preys on ciliates. It eats large flagellates (Gilbert & Bogdan, 1984), and two marine species have been shown to ingest ciliates (Arndt *et al.*, 1990).

The purpose of this study is to determine the abilities of *A. girodi* de Guerne, *Brachionus calyciflorus* Pallas and *Synchaeta pectinata* Ehrenberg to feed on several small ciliates, especially the aloricate oligotrich *Strobilidium gyrans* Stokes. Such oligotrichs, most notably the genera *Strobilidium* and *Strombidium*, are common and often the most abundant ciliates in freshwater plankton communities (Sorokin & Paveljeva, 1972; Hecky & Kling, 1981; Pace & Orcutt, 1981; Pace, 1982; Hunt & Chein, 1983; Taylor & Heynen, 1987; Barbieri & Orlandi, 1989; Müller, 1989; Weisse *et al.*, 1990; Taylor & Johannsson, 1991; Wickham & Gilbert, 1991). *Strobilidium* and some other aloricate oligotrichs have a pronounced flight response to disturbance (Tamar, 1979), which might decrease their susceptibilities to predators. The effectiveness of the escape response of *S. gyrans* is examined by comparing the abilities of the rotifers to feed on *S. gyrans* and the similarly-sized, hymenostome ciliate, *Tetrahymena pyriformis* (Ehrenberg).

Materials and methods

Asplanchna girodi, *Brachionus calyciflorus*, and *Synchaeta pectinata* were maintained as clones on *Cryptomonas erosa* v. *reflexa* in glass-fiber-filtered lake water as described elsewhere (Gilbert, 1988). *A. girodi* and *B. calyciflorus* were collected by R. L. Wallace from Green Lake, Green Lake, Wisconsin. *S. pectinata* was collected from Star Lake, Norwich, Vermont. *Strobilidium gyrans* was cultured on *Rhodomonas minuta* in filtered lake water. *Colpidium striatum* Stokes and *Tetrahymena pyriformis* were cultured on *Enterobacter aerogenes* in a grass broth (Gilbert, 1968). *S. gyrans* was collected from Star Lake; *C. striatum* and *T. pyriformis* were obtained from Carolina Biological Supply Co., Burlington, North Carolina. Lengths (± 1 SD) of living *C. striatum*, *S. gyrans*, and *T. pyriformis* were 81 (± 4), 58 (± 9), and 46 (± 5) μm, respectively. Both cryptomonad algae were cultured on a modified MBL medium (Stemberger, 1981). All rotifer, ciliate, and algal cultures were kept at 20 °C on a photoperiod (LD 16:8).

The abilities of the rotifers to prey on these ciliates were determined by incubating known numbers of ciliates with and without rotifers at 20 °C. Clearance rates (CR) (ml rot.$^{-1}$ day^{-1}) and ingestion rates (IR) (cil. rot.$^{-1}$ day^{-1}) were calculated from final ciliate population sizes for each of 3–5 replicate sets of experimental (rotifers) and control (no rotifers) vessels using the formulae:

$$\mathrm{CR} = \frac{V(\ln P_c - \ln P_e)}{TN} \text{ and}$$

$$\mathrm{IR} = \frac{P_c - P_e}{TN},$$

where P_c and P_e are ciliate population sizes in control and experimental vessels at the end of the incubation period, T is the incubation period in days, N is the number of rotifers in the experimental vessel, and V is the volume of medium in the vessels in ml.

In experiment 1, 30 *S. gyrans* were placed in screw-cap vials containing 25 ml medium with or without a single *S. pectinata*, and the vials were rotated (1 rpm for 90 seconds every 10 minutes) on a plankton wheel for 1 day in a photoperiod (LD 16:8). In experiments 2–13, 30 *S. gyrans*, either alone or with 30 *C. striatum* or *T. pyriformis*, were placed in Petri dishes (35 mm x 10 mm) containing 3 ml medium with or without one or two rotifers for 3.4 to 6.5 hours in constant light. Incubation times for control and experimental cultures within each replicate of an experiment never differed by more than 0.5 hour and were averaged. The densities of ciliates used in these experiments (1.2 to 20 ml^{-1}) commonly occur in natural plankton communities (Pace & Orcutt, 1981; Hunt & Chein, 1983; Taylor & Heynen, 1987; Barbieri & Orlandi, 1989; Müller, 1989; Weisse *et al.*, 1990; Wickham & Gilbert, 1991).

The lake water medium contained *Rhodomonas* for the *S. gyrans* and usually *Cryptomonas* for the rotifers. Concentrations of *Rhodomonas* were 1.5×10^4 cells ml^{-1} for experiment 1 and 5×10^3 cells ml^{-1} for all other experiments. *Cryptomonas* was also added to the medium in experiments 4–13 at a concentration of 5×10^3 cells ml^{-1}.

All rotifers used in the experiments were adults. Average body lengths were 491 μm for *A. girodi*, 280 μm for *B. calyciflorus*, and 320 μm for *S. pectinata*. During the experiments there were no rotifer deaths or births to complicate calculations of per capita clearance and ingestion rates. With *A. girodi* and *B. calyciflorus*, births were avoided by using individuals without advanced embryos or attached eggs, respectively. *S. pectinata* deposits its eggs, and so eggs laid during the experiment would not have time to hatch.

In experiments 5–13, rotifers were exposed to two ciliate species – *S. gyrans* and either *C. striatum* or, more commonly, *T. pyriformis*. This design, with *S. gyrans* as an internal standard, makes it possible to compare not only the absolute abilities of each rotifer species to prey on two different ciliates within an experiment but also the relative abilities of the three rotifer species to prey on ciliate species across experiments. The clearance rates of rotifers on two, simultaneously-offered ciliates were compared statistically using Student's t-tests (2-tailed).

In the control vessels, populations of *C. striatum* increased considerably, those of *S. gyrans* usually increased slightly, and those of *T. pyriformis* usually decreased slightly. The *S. gyrans* exhibited pronounced saltations except, for some unknown reason, in experiment 11. These unresponsive individuals were tested to determine if they were more vulnerable to *Brachionus* than normal, responsive individuals.

Results and discussion

Clearance rates of *Synchaeta pectinata* on *Strobilidium gyrans* were 3 to 5 ml $\mathrm{rot.}^{-1}$ day^{-1} at a ciliate density of 10 ml^{-1}(experiments 2–4) and 19 ml $\mathrm{rot.}^{-1}$ day^{-1} at a ciliate density of 1.2 ml^{-1} (experiment 1) (Table 1). The very high clearance rate (19 ml $\mathrm{rot.}^{-1}$ day^{-1}) of *S. pectinata* in experiment 1 could indicate that the incipient limiting concentration is less than 10 *S. gyrans* ml^{-1}, that the ingestion rate of *S. gyrans* increases in the absence of alternative algal food, or both. *Rhodomonas* was the only alga present in this experiment; it probably was not eaten by *S. pectinata*, which ingests such small cells very inefficiently (Gilbert & Bogdan, 1984). In all other experiments, both *Cryptomonas erosa* and *Rhodomonas* were present, and *C. erosa* is readily ingested by *S. pectinata* (Gilbert & Bogdan, 1984).

These clearance rates of *S. pectinata* on *S. gyrans* are 10 to 50 times higher than the highest ones reported for this rotifer on algal food – about

Table 1. Clearance rates (CR) and ingestion rates (IR) of *Synchaeta pectinata* on the ciliate *Strobilidium gyrans* at 20 °C. Values are means ± 1 SD of 3 (experiment 2), 4 (experiments 3, 4) or 5 (experiment 1) replicates.

Experiment no.	Duration (d)	Rotifer density(rot. ml^{-1})	Initial ciliate density (cil. ml^{-1})	CR (ml rot.$^{-1}$ day^{-1})	IR (cil. rot.$^{-1}$ day^{-1})
1	1.00	0.04	1.2	19.4 ± 5.3	24.7 ± 7.1
2	0.16	0.33	10.0	5.6 ± 2.0	50.5 ± 21.3
3	0.20	0.67	10.0	3.1 ± 0.4	34.5 ± 5.7
4	0.22	0.67	10.0	3.2 ± 0.5	36.3 ± 6.1

0.4 ml rot.$^{-1}$ day^{-1} on *Cryptomonas phaseolus* at 3.8 °C and *C. erosa* v. *reflexa* at ~20 °C (Gilbert & Bogdan, 1984). Thus, *S. pectinata* seems to eat some ciliates even more efficiently than large cryptomonads, presumed to be its preferred food.

The clearance and ingestion rates of *S. pectinata*, *Brachionus calyciflorus*. and *Asplanchna girodi* offered mixtures of two different ciliates at equal cell densities (10 ml^{-1}) are shown in Table 2. Clearance rates of *S. pectinata* on *Colpidium striatum* were significantly different from, and 4 to 14 times lower than, those on *S. gyrans* (experiments 7 and 8). The much lower susceptibility of *C. striatum* may be is due to its considerably greater size (81 *vs* 58 μm). The possibility that *Synchaeta pectinata* preys less efficiently on ciliates larger than a certain size was supported by some direct observations showing that it could hold onto but not capture *Strobilidium velox* (Gilbert, unpublished). *S. velox* is broader, although not as long as *S. gyrans*, and may be more difficult to capture. According to measurements of preserved specimens, length by width dimensions of *S. velox* and *S. gyrans* are, respectively, 44 x 44 and 51 x 34 μm.

Clearance rates of *S. pectinata* on *Tetrahymena pyriformis* were significantly different from, and about twice as high as, those on *S. gyrans* (experiments 5 and 6). The lower vulnerability of *S. gyrans* to *S. pectinata* may be due to its somewhat greater size (58 *vs* 46 μm) or, most likely, to its

Table 2. Clearance rates (CR) and ingestion rates (IR) of *Synchaeta pectinata* (S.p.), *Brachionus calyciflorus* (B.c.) and *Asplanchna girodi* (A.g.) in mixtures of two ciliate prey, *Strobilidium gyrans* (S.g.) with either *Tetrahymena pyriformis* (T.p.) or *Colpidium striatum* (C.s.). Conditions: 2 rotifers and 30 ciliates of each species in 3 ml for 0.14–0.27 days at 20 °C. Values are means ± 1 SD of 4 replicates. *, **, and NS indicate significance of difference ($P < 0.05$, < 0.01, and 0.05) between clearance rates on ciliate species within each experiment.

Experiment	Rotifer	Alternative ciliate (cil. x)	CR (ml rot.$^{-1}$ day^{-1})		IR (cil. rot.$^{-1}$ day^{-1})		CR cil. x / CR s.g.
			S.g.	cil. x	S.g.	cil. x	
5	S.p.	T.p.	2.4 ± 0.7	5.4 ± 0.5**	24.3 ± 8.1	50.7 ± 3.3	2.25
6			2.8 ± 1.0	6.1 ± 2.2*	24.9 ± 7.9	28.9 ± 3.5	2.18
7		C.s.	2.8 ± 0.9	0.2 ± 1.0**	23.9 ± 4.8	2.7 ± 22.2	0.07
8			4.4 ± 1.2	1.1 ± 0.9**	40.4 ± 12.1	21.2 ± 16.1	0.25
9	B.c.	T.p.	1.3 ± 0.9	5.0 ± 1.2**	12.3 ± 8.4	33.4 ± 7.5	3.85
10			0.9 ± 0.9	2.5 ± 1.1^{NS}	8.3 ± 8.3	18.5 ± 7.2	2.80
11			3.8 ± 0.1[1]	4.0 ± 0.9^{NS}	29.9 ± 6.9[1]	28.3 ± 5.0	1.05
12[2]		–	1.0 ± 0.4	–	9.9 ± 4.5	–	–
13	A.g.	T.p.	0.4 ± 0.3	5.4 ± 1.3**	3.9 ± 2.8	33.6 ± 7.8	13.5

[1] Individuals non-saltatory.

[2] *Tetrahymena* data unreliable due to very high and variable mortality in control cultures.

saltatory behavior. *S. gyrans* jumps away in response to approaching rotifers, and this response may provide an effective escape (Gilbert & Jack, unpublished).

Brachionus calyciflorus had clearance rates of 2.5 to 5 ml rot.$^{-1}$ day^{-1} on *T. pyriformis* – about the same as those of *S. pectinata* on this ciliate under the same conditions. *B. calyciflorus* also ingested *S. gyrans* less efficiently than *T. pyriformis* (experiments 9 and 10). Clearance rates on the former were about 3 times less than those on the latter but differed significantly from each other in only one of the two experiments (experiment 9). The lower clearance rates on *S. gyrans* almost certainly can be attributed to the escape response of this ciliate. In experiment 11, where *S. gyrans* did not exhibit normal escape responses, clearance rates on *S. gyrans* were much higher than in experiments 9 and 10 and were very similar to those on *T. pyriformis*. When clearance rates of *B. calyciflorus* on *T. pyriformis* relative to those on *S. gyrans* are calculated separately for each replicate, the mean for experiment 11 was significantly higher than that in experiment 9 ($p < 0.05$) but not in experiment 10 ($0.2 > p > 0.1$).

The clearance rates of *B. calyciflorus* on *T. pyriformis* and unresponsive *S. gyrans* (2.5 to 5 ml rot.$^{-1}$ day^{-1}) are somewhat higher than the clearance rates reported for this species on yeast and algal food at very low cell concentrations. *B. calyciflorus* had a clearance rate of 1.2 ml rot.$^{-1}$ day^{-1} on *Rhodotorula glutinis* at a concentration of 10^3 cells ml^{-1} ($\sim$0.03 μg dry weight ml^{-1}) at 28 °C (Starkweather & Gilbert, 1977), and one of $\sim$0.7 ml rot.$^{-1}$ day^{-1} on *Cyclotella meneghiniana* at a concentration of $\sim$0.1 μgC ml^{-1} at 20 °C (Rothhaupt, 1990).

Asplanchna girodi had a clearance rate of 5.4 ml rot.$^{-1}$ day^{-1} on *T. pyriformis* – about the same as those of *S. pectinata* and *B. calyciflorus* on this ciliate under the same conditions. The clearance rate of *A. girodi* on *S. gyrans* was significantly different from, and 13.5 times less than, that of this rotifer on *T. pyriformis*. Thus, the escape response of *S. gyrans* seems to be a very effective defense against *A. girodi*. This conclusion is consistent with other experiments and direct observations with these two organisms (Jack & Gilbert, unpublished).

The results of this study show that *S. pectinata*, *B. calyciflorus*, and *A. girodi* are effective predators on ciliates in the 45–60 μm size range, ingesting up to 50 ciliates rotifer^{-1} day^{-1} (Tables 1 and 2). These and other large rotifers may utilize much of the considerable productivity of such ciliates and may influence the abundance and species structure of ciliates in natural plankton communities.

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