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Prey selection by the copepod *Diacyclops thomasi*[*]

Richard S. Stemberger[**]
Great Lakes Research Division, The University of Michigan, Ann Arbor, MI 48109, USA

Summary. 1. Adult females of the predaceous copepod, *Diacyclops thomasi,* consistently selected for the soft-bodied rotifers *Synchaeta pectinata, Polyarthra major* and *P. remata* when presented various combinations of 8 rotifer species and 2 crustacean species as prey. *Diacyclops* did not select for other small, soft-bodied rotifers such as *P. vulgaris* and *Ascomorpha ecaudis* and, for loricate species such as *Keratella cochlearis, K. crassa* and for large soft-bodied adult *Asplanchna priodonta.* The small cladocerans, *Bosmina longirostris* and *Chydorus sphaericus* also were resistant to predation by this copepod.

2. Increased hunger in *Diacyclops* increased the clearance rates on both vulnerable and *Diacyclops*-resistant prey but did not greatly increase mortality of resistant prey relative to vulnerable prey. Sated *Diacyclops* preferred small, vulnerable prey like *P. major* over larger-bodied *Synchaeta.* This effect may be attributed to limited gut space when food is abundant.

3. When *Diacyclops* was presented different relative proportions of *Keratella* and *Synchaeta* at a constant total prey density (500 prey/L), it selected *Synchaeta* over *Keratella* in all trial proportions. However, *Diacyclops* selected more strongly for *Keratella* (but at a much lower clearance rate than for *Synchaeta*) when the relative abundance of this predator-resistant species was greatest. These results support optimal foraging in this predator.

4. Predator-prey interactions of the kind reported in this study can help identify important food web pathways and can be used to interpret predator-mediated changes in zooplankton communities in nature.

Invertebrate predators selectively modify zooplankton communities. Prey selection is influenced not only by a variety of behavioral and morphological features of the prey such as size, shape, escape responses and taste (Pastorok 1980; Riessen 1980; Williamson 1980; Kerfoot 1977, 1982; Li and Li 1979) but also by predator hunger (Pastorok 1981). The visibility of prey to visually hunting predators also may influence selection (O'Brien et al. 1979; Zaret and Kerfoot 1975; Zaret 1972). Unlike crustacean zooplankton, rotifers are relatively immune to visually feeding fish predators because of their small size (Hrbáček 1962). However, seasonal predation by fish larvae (Siefert 1972; Duncan 1983) and by pelagic filter-feeding fish (Norden 1968; Drenner et al. 1982; Duncan 1984) may have a strong selective influence on limnetic rotifer communities. Nonetheless, most anti-predator adaptations of rotifers appear to be directed against small, tactile-orienting invertebrate predators.

Defensive adaptations of prey increase the time it takes a predator to complete the predation sequence. This is accomplished by interrupting specific steps which lead to ingestion such as recognition, pursuit, attack, capture, handling, and ingestion (Holling 1966; Kerfoot 1978). For example, posterior-spined *Keratella cochlearis* are difficult for cyclopoid and rotifer predators (*Asplanchna*) to manipulate once this prey is captured. These prey increase the predator's handling time or increase the rate of rejection after capture (Stemberger and Gilbert 1984). Large, turgid-bodied forms like *Asplanchna* are difficult for some small, predaceous cyclopoids to capture (Gilbert and Williamson 1978; Williamson 1983). Soft-bodied *Filinia, Polyarthra* and *Hexarthra* may avoid predators with the rapid movement of their spine-like or paddle-like appendages (Gilbert and Williamson 1978; Lewis 1977). These latter species increase the pursuit time or effectively decrease the encounter rate. As a result of these processes, predator-adapted prey are removed from the environment at a lower rate than prey which do not interfere with the predation sequence. The pattern of predation mortality which results forms the basis of selective predation and ultimately affects the species structure of plankton communities.

In this paper, I present results from a variety of experiments designed to test selection of the common cyclopoid copepod, *Diacyclops thomasi,* for rotifer and crustacean prey under different configurations of prey choice, prey proportion and density, and predator hunger level. Knowledge of this predator's prey preferences from laboratory studies can be used to identify important trophic links in the plankton and also to interpret temporal changes in rotifer communities in nature (Stemberger and Evans 1984).

Methods

Diacyclops thomasi (Forbes) (= *Cyclops bicuspidatus thomasi*) was collected from Lake Michigan in June, 1981,

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[**] *Present address:* Dartmouth College, Department of Biological Sciences, Hanover, N.H. 03755

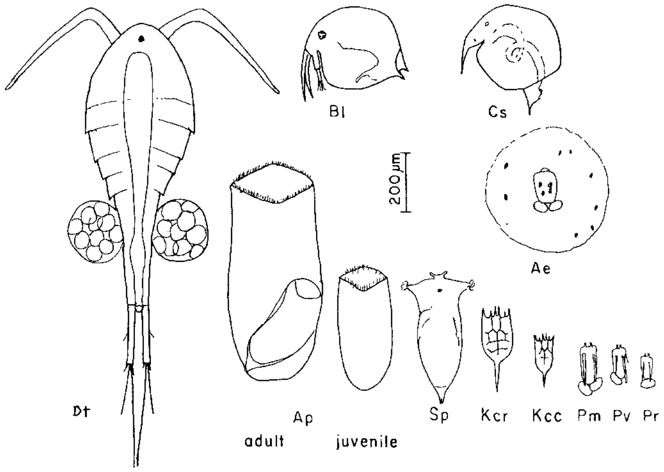

Fig. 1. Zooplankton used in experiments. Dt = *Diacyclops thomasi*; Ap = *Asplanchna priodonta*; Sp = *Synchaeta pectinata*; Kcr = *Keratella crassa*; Kcc = *K. cochlearis*; Pm = *Polyarthra major*; Pv = *P. vulgaris*; Pr = *P. remata*; Ae = *Ascomorpha ecaudis;* Bl = *Bosmina longirostris*; and Cs = *Chydorus sphaericus*

5 km offshore from St. Joseph, Michigan with a 0.5-m, 150 µm mesh net. The copepods were maintained in a 20-L aquarium at 8° C with a single cool-white fluorescent light on a 14:10 LD cycle and fed *Synchaeta pectinata* prey. *Synchaeta pectinata, Keratella cochlearis* f. *typica, K. crassa, Ascomorpha ecaudis, Polyarthra vulgaris, P. major, P. remata* and *Asplanchna priodonta* were cultured in inorganic MBL medium (Nichols 1973) and fed either *Cryptomonas erosa* v. *reflexa* or *Rhodomonas minuta* (Stemberger 1981). The rotifers listed above and the cladocerans, *Bosmina longirostris* and *Chydorus sphaericus* (Fig. 1), were isolated from Lake Michigan and from lakes and ponds in the vicinity of Ann Arbor, Michigan. The cladocerans were reared in 12-L aquaria in Lake Michigan water. Every 3 days *Cryptomonas* and *Rhodomonas* were added sparingly.

Prior to experiments, *Diacyclops* were removed from the aquarium with a sieve and poured into a 25-ml glass dish. Gravid *Diacyclops* females were removed with a 2-mm wide, glass pipette fitted with a suction bulb and about 30 females were placed into a 500-ml, wide-mouth beaker with medium. *Synchaeta pectinata* was added to yield a density of approximately 700/L. The beaker was placed in the incubator (16° C) for 3–4 days under a 14:10 LD cycle. This procedure maintained *Diacyclops* in a sated condition and acclimated them to the experimental temperature (16° C).

In any one experiment, the volume of medium in each of three experimental beakers (150-ml) was adjusted to 100 ml after adding prey and 2 to 6 *Diacyclops*. These beakers and 3 similarly treated controls without *Diacyclops* were placed in the dark at 16° C for a predetermined length of time (<17 h) depending upon the experimental design. At the end of these experiments, the medium was reduced by filtration to 15 ml and *Diacyclops* were removed. The remaining prey were counted under 50 magnifications of a stereomicroscope and then discarded using a mouthpipette.

Clearance rates (ml *Diacyclops*$^{-1}$ h^{-1}) were calculated after Gauld (1951). When predator size, temperature and hunger condition are defined, changes in clearance rates provide a convenient measure of feeding behavior as well as a useful measure of relative prey vulnerability. These rates reflect a predator's ability to harvest different prey. High clearance rates on a prey indicates vulnerability to the predator. Conversely, low clearance rates reflect the prey's ability to interrupt the predation sequence. An electivity index (W_i) was calculated from standardized clearance rates after Vanderploeg and Scavia (1979). This index ranges from a value of 0 (no selection) to 1 (maximum selection) and provides a density-independent measure of selection.

Specific experiments tested *Diacyclops* selectivity for various rotifer and crustacean prey. In one series of experiments, sated *Diacyclops* were presented two prey choices at 1:1 proportions and a total density of either 300 or 500 prey/L. In these experiments, *Synchaeta* was used as a reference prey for six 2-choice combinations with 6 different species of rotifers. Similarly, *Diacyclops* which had been starved for 20 h and 48 h were presented several 2-prey combinations (*K. cochlearis* or *K. crassa* vs. *Synchaeta* and *K. cochlearis* vs. *K. crassa*). These experiments tested the effect of predator hunger on selection. In another series of experiments, sated *Diacyclops* were offered a choice of *S. pectinata* and *K. cochlearis* at different ratios (10:90, 50:50, 90:10) and a constant total density (500 prey/L).

Finally, a series of selection experiments was designed to test selectivity of sated *Diacyclops* when presented 3 to 8 prey species simultaneously. These experiments were designed in the same manner as 2-prey choice experiments except that variable prey ratios were used. Student's t-tests for paired comparisons were applied to 2-prey choice experiments and one-way analyses of variance were done on multiple prey choice experiments. All experimental results were corrected for control treatments before applying the above statistical tests to the treatment means.

Results

Prey selection was assessed by comparing clearance rates of *Diacyclops* and electivity values with *Synchaeta* as the standard reference prey. Even when starved, *Diacyclops* selected *Synchaeta* over *Keratella* when presented a 1:1 ratio of these species (500 total prey/L) (Table 1). If sated *Diacyclops* were presented with only predator-resistant prey, *K. cochlearis* or *K. crassa,* the clearance rate on the former was about 13% of that on *Synchaeta. Keratella crassa* was not eaten at all. However, 48-h starved *Diacyclops* consumed some *K. crassa.* Although 20-h starved *Diacyclops* selected *K. cochlearis* over the larger *K. crassa,* the clearance rate on the former was only 15% of the rate for *Synchaeta* (Table 1). Starved *Diacyclops* moderately increased clearance rates on these prey over sated individuals (Table 1).

Sated *Diacyclops* which were offered different species of *Polyarthra* demonstrated very different selectivites (Table 2). *Polyarthra vulgaris* was least vulnerable to *Diacyclops* predation. Clearance rates on *P. remata* and *Synchaeta* were similar when these species were offered together but *P. major* was consistently preferred over *Synchaeta.* In contrast, *Diacyclops* did not select for the soft-bodied, *Ascomorpha ecaudis.* Mean clearance rates were approximately 6% of the rates for *Synchaeta. Diacyclops* may be repelled after contacting the mucus coating (Stemberger, personal observation).

Sated *Diacyclops*, which were offered *Synchaeta, P. vulgaris* and *P. major* simultaneously (Table 3), selected *P. ma-*

Table 1. Summary of 2-choice selection trials for *Diacyclops* (Dt). Sp = *Synchaeta pectinata;* Kcc = *Keratella cochlearis;* Kcr = *K. crassa*. F = mean clearance rate (ml Dt^{-1} h^{-1}). SE = standard error for 3 experimental replicates. W_i = electivity index. N_i = initial prey density of treatments. N_f = mean final prey density of treatments. N_c = mean final prey density of controls. H = Length of experiment (h). Volume of experiments = 100 ml

	sated		starved		sated		starved	
	20 h				48 h			
Dt/trial		4		4		4		4
Prey	Sp	Kcc	Sp	Kcc	Kcc	Kcr	Kcc	Kcr
N_i	25	25	25	25	25	25	25	25
N_c	25.30	23.0	25.0	23.0	24.0	25.0	24.0	24.0
N_f	6.67	22.3	15.0	22.5	22.0	25.0	18.33	22.33
F	4.38	0.10[a]	6.38	0.28[a]	0.66	0.0[a]	1.12	0.30[a]
SE	1.37	0.12	0.83	0.33	0.39	0.0	0.39	0.16
W_i	0.98	0.02	0.96	0.04	1.00	0.00	0.79	0.21
H		7.6		2.0		4.0		6.0

[a] The null hypothesis that clearance rates are the same for 2-choice trials is rejected at $P = 0.05$

Table 2. Summary of 2-choice selectivity trials for *Diacyclops* (Dt). Pv = *Polyarthra vulgaris;* Pr = *P. remata;* Pm = *P. major*; and Ae = *Ascomorpha ecaudis*. Explanation and symbols as in Table 1

	sated		sated		sated		sated	
Dt/trial		3		4		2		4
Prey	Sp	Pv	Sp	Pr	Sp	Pm	Sp	Ae
N_i	15	15	15	15	15	15	15	15
N_c	15	15	17	15	15	15	16	15
N_f	1.13	11.67	7.67	8.67	12.33	9.0	3.33	13.66
F	4.36	0.42[a]	1.69	1.16	1.35	3.67[a]	3.88	0.23[a]
SE	0.59	0.3	0.60	0.93	0.59	1.65	1.36	0.12
W_i	0.91	0.09	0.59	0.41	0.28	0.72	0.94	0.06
H		10.8		11.8		7.4		10.3

Table 3. Summary of multispecies selectivity trials for *Diacyclops* (Dt). Ap = *Asplanchna priodonta;* Sp = *Synchaeta pectinata;* Pr = *Polyarthra remata;* Pv = *P. vulgaris;* Pm = *P. major;* Kcc = *Keratella cochlearis;* Kcr = *K. crassa;* Ae = *Ascomorpha ecaudis;* Bl = *Bosmina longirostris*

	sated			sated				
Dt/trial		3				4		
Prey	Sp	Pv	Pm	Sp	Ap	Kcr	Kcc	Bl
N_i	10	10	10	10	10	10	10	10
N_c	10.0	9.0	9.0	11.5	13.5	10.0	8.0	8.5
N_f	8.3	8.6	3.0	1.7	11.0	9.7	6.7	7.0
F	0.83	0.20	4.88[a]	3.01[a]	0.32	0.05	0.27	0.30
SE	0.25	0.29	1.95	1.1	0.12	0.04	0.31	0.25
W_i	0.15	0.03	0.83	0.76	0.08	0.01	0.07	0.08
H		7.5				16.0		

[a] The null hypothesis that clearance rates are the same for all prey species is rejected at $P = 0.05$. Explanation and symbols as in Table 1

Table 4. Summary of multispecies selectivity trials for *Diacyclops* (Dt). Kc = *Keratella cochlearis;* Kcr = *K. crassa;* Pm = *Polyarthra major;* Pr = *P. remata;* Pv = *P. vulgaris;* Sp = *Synchaeta pectinata;* Cs = *Chydorus sphaericus;* Ap = *Asplanchna priodonta*

	sated					
Dt/trial	4					
Prey	Sp	Pv	Ap	Kcr	Kcc	Cs
N_i	10	10	10	10	10	10
N_c	10.0	10.0	16.5	10.0	8.0	10.0
N_f	1.0	4.67	13.33	10.0	6.6	8.33
F	3.7[a]	1.27	0.34	0.0	0.32	0.3
SE	0.12	0.53	0.27	0.0	0.3	0.1
W_i	0.62	0.22	0.06	0.0	0.05	0.05
H			15.0			

[a] The null hypothesis that clearance rates are same for all prey species is rejected at $P = < 0.05$. Explanation and symbols as in Table 1

Table 5. Summary of multispecies selectivity trials for *Diacyclops* (Dt). Kcc = *Keratella cochlearis;* Ap = *Asplanchna priodonta;* Pv = *P. vulgaris;* Sp = *Synchaeta pectinata;* Ae = *Ascomorpha ecaudis*

	sated				
Dt/trial	4				
Prey	Sp	Pv	Kcc	Ap	Ae
N_i	15	15	15	5	5
N_c	17.0	15.0	15.0	6.0	5.0
N_f	5.0	12.33	11.33	5.7	5.0
F	2.4[a]	0.38	0.55	0.10	0.0
SE	0.05	0.19	0.09	0.16	0.0
W_i	0.71	0.1	0.16	0.03	0.0
H			17.0		

[a] The null hypothesis that clearance rates are same for all prey species is rejected at $P = 0.05$. Explanation and symbols as in Table 1

jor over *Synchaeta*. The rates on *P. major* were about 6 and 24 times those on *Synchaeta* and *P. vulgaris*, respectively. These results further support the strong selection that *Diacyclops* shows for this species.

In multiple prey choice experiments, the relative selectivities for prey were consistent with results from 2-choice trials (Tables 1–5). Small *Bosmina* and *Chydorus* were about as resistant to predation by *Diacyclops* as *Keratella, Asplanchna*, and *Ascomorpha*. *Synchaeta* was the most highly selected prey in all trials without *P. major*. *Ascomorpha* and *K. crassa* were the least preferred rotifers. *Asplanchna* adults were relatively free from *Diacyclops* predation. However, newborn *Asplanchna*, which are about the size of *Synchaeta*, were vulnerable to predation. Significant reproduction in *Asplanchna* occurred in these experiments as is evident from the increased numbers in the control treatments (Table 4). Thus, size-selective predation on newborn *Asplanchna* may have artificially increased the clearance rates on this species (Table 4).

Diacyclops selected *S. pectinata* over *K. cochlearis* in all trial proportions with constant density (500 prey/L) of these two species (Table 6). At the highest *Synchaeta* proportion (90:10), predation on *Keratella* was not detected. Clearance rates on the former were reduced by a factor of 5 in trials having lower proportions of *Synchaeta*.

Discussion

Selectivity by *Diacyclops* on rotifers is species-specific and could not easily have been predicted based only on prey size, shape, or behavioral response. These results have important implications for the effects of predation by *Diacyclops* on community structure of rotifers. The mechanism of selection has not been the primary focus of this study. However, analyses of results in the light of laboratory observations provide more insight into specific predator-prey outcomes.

Synchaeta and *Keratella* have similar swimming speeds (0.82 and 0.50 mm/s) and therefore contribute about equally to encounter rates with *Diacyclops* (Gerritsen and Strickler 1977; Stemberger, unpublished). Upon contacting *Diacyclops, Synchaeta* contracts into a sphere and slowly sinks. *Diacyclops* usually lunges quickly toward the prey and captures it with its grasping mouthparts. Within 30–90 s, *Diacyclops* ingests the prey completely. When *Keratella* encounters *Diacyclops,* it retracts its ciliated corona into the lorica and also passively sinks. Although *Keratella* is easily captured, the spiny lorica inhibits handling and perhaps ingestion by *Diacyclops* as well. The presence of the posterior spine in *Keratella* confers considerable resistance to predation by small copepods (Stemberger and Gilbert 1984). Successfully eaten prey have portions of the lorica bitten off or have the ventral plate torn away from the dorsal plate. Injured and killed *Keratella* frequently have puncture wounds through the lorica inflicted by the stoutly spined, feeding appendages of *Diacyclops.* Gilbert and Williamson (1978) report that *Mesocyclops* may spend up to 30 min on *Keratella* [*crassa*] before releasing it unharmed. The stiff, well-developed lorica of this species may confer a substantial increase in predation resistance over *K. cochlearis.*

Predator hunger increases the clearance rates on both vulnerable and predator-resistant prey (Table 1). Hunger probably increases encounter rates by directly increasing predator swimming speeds or possibly by decreasing the time to complete some or all steps of the predation sequence. In 2-choice selection experiments (Table 1), electivity did not change with hunger if vulnerable prey were available. However, clearance rates on vulnerable prey were notably higher with increased hunger (Table 1, $P < 0.05$). If *Diacyclops* is offered only predator-resistant prey, it consumes the more vulnerable prey (*K. cochlearis*) at higher clearance rates than it does if *Synchaeta* are present (Table 1). Therefore, the hunger state of the predator has a significant effect on both clearance rates and prey selectivity. However, the effect of predator hunger on mortality of resistant prey remains considerably less than for susceptible prey.

The small, soft-bodied *Ascomorpha ecaudis* are rarely eaten by *Diacyclops* (Tables 2, 5). Upon contacting the mucus sheath, *Diacyclops* stops swimming and makes rapid movements with its feeding appendages, apparently attempting to remove adhering mucus. After several encounters with these sheaths, *Diacyclops* actively avoids them. The mucus confers predation-resistance to *Ascomorpha* through a taste or textural quality which *Diacyclops* avoids. Predation on *Ascomorpha* may occur when the adult swims out of its sheath. However, I never observed predation on this species. *Ascomorpha* lays eggs which hatch within the mucus cavity. The young remain there for several days before they leave the mothers' mucus envelope. Therefore, they receive maternal protection during a portion, if not all, of their pre-reproductive life. Zooxanthellae, which live in the hypodermis and body cavity of this species (de Beauchamp 1932), may possibly produce, or assist in producing these secretions. *Ascomorpha* can quickly secrete copius amounts of mucus if it is rapidly stripped away from the rotifer (Stemberger, unpublished). These selection experiments provide the first evidence supporting an anti-predatory function of mucus in *Ascomorpha.* Mucus envelopes are common to a variety of planktonic rotifers including *Conochiloides* and *Collotheca* and may also have an anti-predatory function. Mucus also may reduce swimming costs by helping the rotifer to maintain position in the water column (Stemberger and Gilbert, in press).

The selectivity of *Diacyclops* for *Polyarthra* was species-specific (Tables 2, 3). Gilbert and Williamson (1978) report that *P. vulgaris* is susceptible to predation by the copepod *Mesocyclops edax* and Brandl and Fernando (1978) report that *Cyclops vicinus* and *M. edax* select for *P. dolichoptera* and *P. major,* respectively. In the Laurentian Great Lakes, *D. thomasi* is the dominant copepod predator (Gannon 1972) and coexists in space and time with *P. vulgaris,* a dominant rotifer (Stemberger 1974; Nauwerck 1978; Stemberger et al. 1979; Stemberger and Evans 1984). *Polyarthra vulgaris* was the least vulnerable rotifer in this genus to predation by *D. thomasi.* However, the larger *P. major* was the most preferred species of all rotifers tested (Table 2, 3). Apparently, *Diacyclops* easily captures *P. major* as suggested by the ease with which this species can be pipetted in contrast to *P. vulgaris* and *P. remata* (Stemberger, personal observation). Thus, resistance may be related to the speed of the escape response.

A possible explanation for the much higher clearance rates (a factor of 2 or 3) for *P. major* than for *Synchaeta* may be related to the hunger condition of *Diacyclops.* Given that both rotifer species encounter *Diacyclops* at about equal rates and that *Synchaeta* also is easily captured and consumed, the high electivity that *Diacyclops* shows for *P. major* may result from satiation. It takes approximately 1 h for a sated *Diacyclops* to evacuate enough space to equal the volume of one *Synchaeta* (Stemberger, unpublished). Because *Polyarthra* is about 1/6 the volume of *Synchaeta,* it would require only about 10 min to create sufficient gut space for this small prey. Thus, if *Diacyclops* fed to maintain a full gut, it would have to reject, or partially consume, prey that were larger than the available gut space. Sated *Diacyclops* will partially consume large *Synchaeta* in the absence of small, vulnerable prey (Stemberger, unpublished). This behavior is analogous to wasteful killing in insect predators (Holling 1966; Johnson et al. 1975). Therefore, at satiating prey densities, *Diacyclops* may favor smaller prey. However, other plausible explanations may be found in the specific, predator-prey interaction. For example, *P. major* may be more easily detected by *Diacyclops* than *Synchaeta,* thus favoring its predation over *Synchaeta.* However, this explanation seems unlikely because *P. major* is much smaller than *Synchaeta.* On the other hand, these results also could be explained if the handling time for *Synchaeta* was much greater than for *Polyarthra.*

Table 6. The effect of constant density (500 prey/L) and variable ratios of vulnerable to resistant prey (*Synchaeta pectinata : Keratella cochlearis*) on *Diacyclops* (Dt) selection. + = the null hypothesis that clearance rates are the same among the 3 treatment ratios is rejected at $P = 0.05$

	Synchaeta : Keratella					
	10:90		50:50		90:10[+]	
Dt/trial	3		4		4	
Prey	Sp	Kcc	Sp	Kcc	Sp	Kcc
N_i	5	45	25	25	45	5
N_c	5.0	45.0	25.3	23.0	45.0	5.0
N_f	3.33	41.33	6.67	22.33	36.67	5.0
F	2.31	0.47[a]	4.38	0.10[a]	0.75	0.0[a]
SE	0.75	0.23	1.37	0.12	0.28	0.0
W_i	0.83*	0.17	0.98	0.02	1.0	0.0
H		6.0		7.6		6.9

[a] The null hypothesis that clearance rates are the same for 2-choice trials is rejected at $P = 0.05$. Explanation and symbols as in Table 1

This interpretation is not consistent with the observation that *Diacyclops* easily captures and rapidly consumes *Synchaeta*. Further study and observation are needed to clarify these results.

The results of the multiple prey selection trials (Tables 3–5) are consistent with the outcome of the 2-prey selection trials. *Diacyclops* selected *Synchaeta* in all trials without *P. major*. With the exception of *P. remata*, most prey generally were either very resistant or very vulnerable to predation by *Diacyclops*.

Diacyclops selected *Synchaeta* over *Keratella cochlearis* as the relative abundance (proportion) of the former prey increased while keeping total prey density constant (Table 6). These results support optimal foraging in *Diacyclops* (Pyke et al. 1977). At a ratio 10:90 (*Synchaeta : Keratella*), *Diacyclops* encounters *Keratella* about 9 times more often than *Synchaeta*. Assuming that *Diacyclops* detects both prey equally, the increased attack and handling on *Keratella* at this ratio may lead to greater mortality and consequently to a decrease in selection for *Synchaeta*. Only about 20% of dead or injured *Keratella* were actually consumed by the end of the experiment which attests to the great difficulty that the lorica poses to this small predator.

In conclusion, within the size range of planktonic rotifers tested (90–750 µm body length) neither prey size nor morphology are dependable predictors of a species' vulnerability to predation by *Diacyclops*. For example, *Keratella cochlearis* and *K. crassa* are 10 and 3 times smaller by volume than *Synchaeta* but are at least 6 times more resistant to predation by *Diacyclops*. The vulnerability of *Polyarthra spp.* to predation by *Diacyclops* is species-specific and may be related to the speed of the escape response. Mucus envelopes in *Ascomorpha* clearly inhibited predation by *Diacyclops*, although the mechanism may involve more than simple mechanical fouling of the feeding appendages. Such secretions commonly occur among planktonic rotifers. Also, starved *Diacyclops* may show increased prey-specific clearance rates over sated individuals. Vulnerable prey are relatively more susceptible to changes in feeding behavior due to predator hunger than are resistant prey. However, satiation may cause a shift in prey selection which favors smaller, vulnerable prey. These predator-prey interactions are valuable not only because they identify potentially important food web pathways in the plankton but also because they provide an experimental framework to help interpret seasonal changes in the species structure and composition of aquatic communities (Stemberger and Evans 1984).

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