

Predator-prey interactions between omnivorous diaptomid copepods and rotifers: The role of prey morphology and behavior¹

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Abstract

Suspension-feeding diaptomid copepods feed selectively on several rotifer species. Predator-prey interactions between *Diaptomus pallidus* and seven species of rotifers were quantified and behavioral probabilities computed. Prey size was a good predictor of the probability of *Diaptomus* avoiding a prey following an encounter but had little or no predictive value in subsequent levels of interaction (capture, ingestion). Three of the rotifers exhibited escape responses which were specifically based on rheotaxis, suggesting they may have evolved primarily in response to selection pressures exerted by suspension-feeding zooplankton. Other prey defense mechanisms included a tough integument and long spines—defense mechanisms often used by crustacean prey in response to large predatory calanoids.

Freshwater calanoid copepods in the family Diaptomidae feed on small particles suspended in the water (Cannon 1928; Vanderploeg and Paffenhöfer 1985) and were classically viewed as being totally herbivorous. A few earlier investigators reported predatory behavior by other freshwater calanoids such as *Heterocope* (Naumann 1923; Burckhardt 1944) and *Epischura* (Main 1962), but it was not until after Brooks and Dodson (1965) focused attention on the potential importance of predation in structuring freshwater zooplankton communities that it became widely recognized that some of the large species of *Diaptomus* are predatory (Anderson 1967, 1970; Dodson 1974; Maly 1976). The predatory behavior and potential impact of many of the larger calanoid species in zooplankton communities have been demonstrated in several studies. These calanoid predators may influence the size structure of their prey communities through selective predation on the smaller prey species (Anderson 1970; Dodson 1974, 1975; Kerfoot 1977; O'Brien et al. 1979). Selective foraging by predatory calanoids may also result in the evolution of prey defense mechanisms which have a profound impact on the morphology, reproductive rates, and seasonal patterns of clonal succession of individual prey species (Kerfoot 1975; O'Brien and Schmidt 1979; Hebert and Loaring 1980; Kerfoot and Peterson 1980).

A more recent study has demonstrated that even the smaller suspension-feeding diaptomids may prey on small animals such as rotifers and that this predation is both intense and selective (Williamson and Butler 1986). This finding raises several fundamental questions as to the impact and mechanisms of predation in these species which have been previously considered to be herbivorous.

I here examine the behavioral interactions between a suspension-feeding diaptomid and seven different species of rotifers representing a wide range of sizes and morphologies. The focus of the study is to examine the relative importance of prey size, shape, and behavior in determining the outcome of an encounter between predator and prey. This approach allows one to examine the level of interaction at which each prey characteristic is effective (or not) in reducing the vulnerability of each species to suspension-feeding predators.

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Methods

Behavioral observations were made on adult individuals of the suspension-feeding freshwater calanoid copepod *Diaptomus pallidus* Herrick and seven species of prey rotifers (Fig. 1). All experimental organisms were collected from Whiteacre Pond in Northampton County, Pennsylvania (40°35'N, 75°22'W). The rotifer species examined are listed in Table 1 along with some

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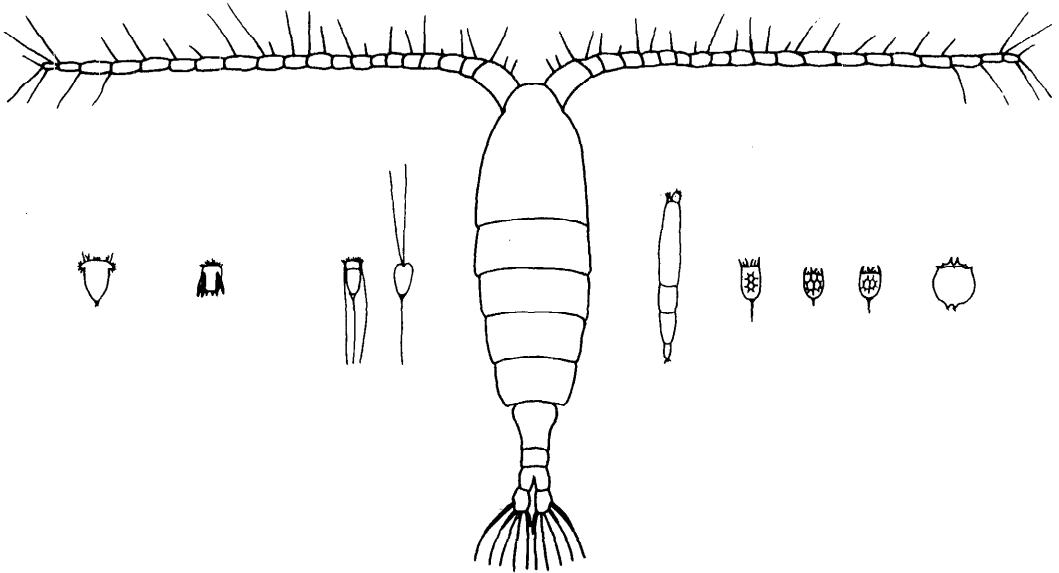


Fig. 1. Scale drawings of an adult female *Diaptomus pallidus* (center) and the seven species of rotifers examined. From left to right: *Synchaeta oblonga*, *Polyarthra major*, *Filinia terminalis* (bristles in normal position when swimming, bristles extended as in escape response), *Rotaria* sp., *Keratella americana*, *Keratella cochlearis* (short-spined, long-spined), and *Brachionus angularis*.

of the critical characteristics of the predator and prey for each experiment. Metasome lengths were 1.1–1.2 mm for adult female *D. pallidus* and 1.0 mm for adult males. The experiments were performed at 25°C in a

2-ml chamber constructed of two opposing 22-mm-square pieces of coverglass with Plexiglas sides and bottom. This chamber size is a compromise chosen to be small enough to enable the complete chamber

Table 1. Experimental conditions and characteristics of prey and predators used in each experiment.

Exp.		Prey				Predator			
		Length (mean \pm SD, μ m)				Sex	Days starved	No. observed	
		Body, not including spines or bristles	Posterior spines or bristles	Anterior spines or lateral bristles	Body, including spines and bristles			Individuals	Encounters
SO	<i>Synchaeta oblonga</i>	130–150	—	—	140	F	0	20	35
SO(+P)	<i>S. oblonga</i> (plus phytoplankton)	130–150	—	—	140	F	0	20	34
SO(M)	<i>S. oblonga</i> (male predators)	130–150	—	—	140	M	0	16	38
PM	<i>Polyarthra major</i>	98 \pm 6.7	—	—	98	F	0	15	140
FT	<i>Filinia terminalis</i>	127 \pm 18.2	280 \pm 26.3	374 \pm 33.2	781	F	0	20	189
KC(SS)	<i>Keratella cochlearis</i> (short-spined)	82 \pm 3.6	29 \pm 4.9	20 \pm 3.7	134	F	0	15	127
KC(SS1)	<i>K. cochlearis</i> (short-spined)	85 \pm 3.3	33 \pm 2.2	21 \pm 2.4	134	F	1	15	116
KC(LS1)	<i>K. cochlearis</i> (long-spined)	89 \pm 7.6	54 \pm 9.6	23 \pm 1.9	165	F	1	15	150
KA	<i>Keratella americana</i>	107 \pm 5.3	83 \pm 10.8	24 \pm 3.5	214	F	0	15	127
BA	<i>Brachionus angularis</i>	150 \pm 1.9	—	—	150	F	0	15	150
RS	<i>Rotaria</i> sp.	500–600	—	—	550	F	0	10	100

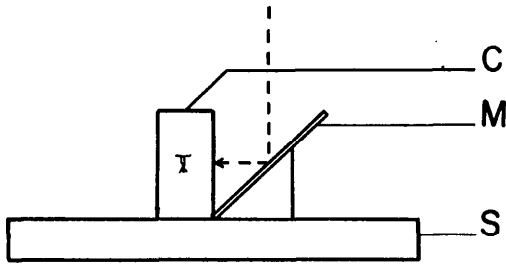


Fig. 2. Side-view diagram of apparatus used to observe behavioral interactions. The path of the fiber-optic illumination is perpendicular to the plane of the paper, while the viewing path from the observer and microscope above is indicated by the dashed line. C—Experimental chamber; M—mirror; S—temperature-controlled stage.

contents to be viewed without having to move the chamber during observation on the one hand and large enough to permit the copepods to swim freely on the other. Similar studies are usually performed with tethered copepods which prevent any whole-body movements but permit higher resolution and filming of the movement of the feeding appendages. A mirror was placed at a 45° angle to permit the chamber to be viewed from the front with a dissecting microscope (Fig. 2). Observations were made with dark-field optics created by oblique illumination with a fiber-optic light source against a dark background. A constant-temperature stage with a circulating water bath was used to avoid changes in temperature during observations.

The standard protocol was to collect and isolate the prey and predators the morning of the experiment and perform the observations the same day starting at 1300 hours. In two experiments the predators were collected and isolated the day before the observations were performed to examine the effects of a day of starvation on behavioral interactions (Table 1). All isolations and experiments were performed in filtered (Whatman 934-AH glass-fiber filters with an effective retention of 1.5 μm) water collected from Whiteacre Pond on the day of the experiment. The exception was one experiment [SO(+P)] performed in water strained through 48- μm Nitex mesh to examine the effects of the presence of natural

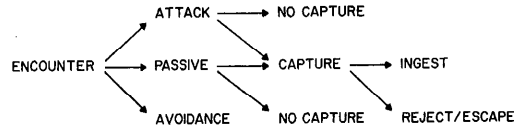


Fig. 3. Flow diagram of the behavior model used to quantify interactions between *Diaptomus pallidus* and its rotifer prey. Each behavior can be expressed as a probability function of any of the preceding behaviors in line.

concentrations of phytoplankton on behavioral interactions (Table 1).

Between 20 and 30 rotifers were placed in the observation chamber and a single copepod predator was added at a time. The copepods were placed gently in the observation chambers with a wide-bore pipet and began actively swimming and feeding in an undisturbed manner within 1 or 2 s. Each predator was given a maximum of 10 encounters with prey or one ingestion, whichever came first. The encounters and resulting behavioral sequences for each encounter were recorded for each predator according to the model outlined in Fig. 3. This model is similar to those previously used for more predatory zooplankton (Gerritsen and Strickler 1977; Kerfoot 1978; Williamson and Gilbert 1980), except that a third behavior (passive response) has been added after the encounter. This addition was necessary because I observed that suspension-feeding calanoids can capture their prey passively as they are brought in on the feeding currents, without any active attack behavior.

The behavioral frequencies were used to compute probabilities for each sequential event by giving each copepod predator equal weight. Handling times were scored to the nearest 0.01 s with a digital stopwatch with four memories. An encounter was defined as any reaction by either prey or predator to the approach of the other organism. An attack was defined as any movement of the copepod in response to a nearby prey that brought the predator and prey into closer proximity. Avoidance was defined as any movement of the copepod in response to a nearby prey which increased the distance between the predator and the prey. When a copepod exhibited no whole-body move-

Table 2. Handling times (mean, SE, max) for *Diaptomus pallidus* on the seven rotifer species. Experimental conditions given in Table 1.

	Exp.	Handling time (s)		
		Mean	SE	Max
<i>S. oblonga</i>	SO	1	0.1	17
<i>S. oblonga</i>	SO(+P)	1	0.1	6
<i>S. oblonga</i>	SO(M)	3	0.8	18
<i>P. major</i>	PM	<1	<1	<1
<i>F. terminalis</i>	FT	2	0.8	4
<i>K. cochlearis</i>	KC(SS)	2	1.2	21
<i>K. cochlearis</i>	KC(SS1)	12	3.7	60
<i>K. cochlearis</i>	KC(LS1)	2	0.7	51
<i>K. americana</i>	KA	2	1.1	48
<i>B. angularis</i>	BA	2	0.7	51
<i>Rotaria</i> sp.	RS	4	1.9	77

ments (jumps, turns) in response to an approaching prey, the response was scored as being passive. These passive responses often involved distinct changes in the motion of the feeding appendages and thus were passive only in terms of the lack of any movement of the body of the copepod as a whole. Passive does not imply that the copepod was unaware of the presence of the prey. Captures were defined as a grasping of the prey by the feeding appendages of the predator. Ingestions were scored as ingestion of the prey in its entirety; partial ingestions, although rare, were scored as half of a total ingestion.

In the present study the advantages of high resolution offered by high-speed microcinematography (Alcaraz et al. 1980; Vanderploeg and Paffenhöfer 1985) were sacrificed for the ability to observe a large number of replicate encounters on several different rotifer species. More than 1,200 encounters and 176 predators were observed in the 11 experiments performed (Table 1). The significance level of differences between behavioral probabilities was determined with the Kruskal-Wallis non-parametric rank test. Least-squares linear regressions were performed to examine the relationship between prey size (body length, bristle/spine length, and total length) and the success of the predators at each level of interaction. Arcsin square-root transformations of the behavioral data either slightly reduced or did not influence either the

predictive power or the significance level of the regressions and therefore were not used.

Results

Diaptomus spent most of the time alternating between two activity phases: one which was a primarily stationary phase in which the feeding currents of the animals seemed to offset any gravitational forces and keep them oriented in a vertical to slightly diagonal angle in the water (see also Strickler 1982), and one which consisted of short hops of up to a few millimeters. Encounters with prey generally occurred as prey organisms were brought in toward the feeding chamber of the copepod on water currents created by the rapidly vibrating feeding appendages. The currents (and prey) came in from the anterior, anterolateral, and anteroventral directions in a manner very similar to that described for *Diaptomus sicilis* by Vanderploeg and Paffenhöfer (1985). When prey were entrained in the feeding currents, the feeding appendages of *Diaptomus* often fluttered as if to sample either the prey or the water immediately surrounding the prey before responding. The finer details of these flutterings were not resolvable due to their short duration (<1 s) and high speed, but they appeared to consist primarily of a change in the beating pattern of the feeding appendages, which caused the appendages to extend slightly beyond their normal range of movement. These flutterings did not involve any movement of the swimming legs or cause any obvious whole-body movements of the copepods.

Attacks were initiated primarily by contact between the prey and any portion of the first antennae of the copepods, although in many instances attacks were observed at distances <0.5 mm, before actual contact between the prey and predator occurred. The attacks consisted of short jumps, turns, and orientation responses accompanied by grasping motions of the feeding appendages. These attacks were not as vigorous as the leaps and pounces often observed in cyclopoid copepods such as *Mesocyclops edax* (Williamson and Gilbert 1980; Williamson 1983). Once captured, the prey was either ingested immediately in its entirety, or rap-

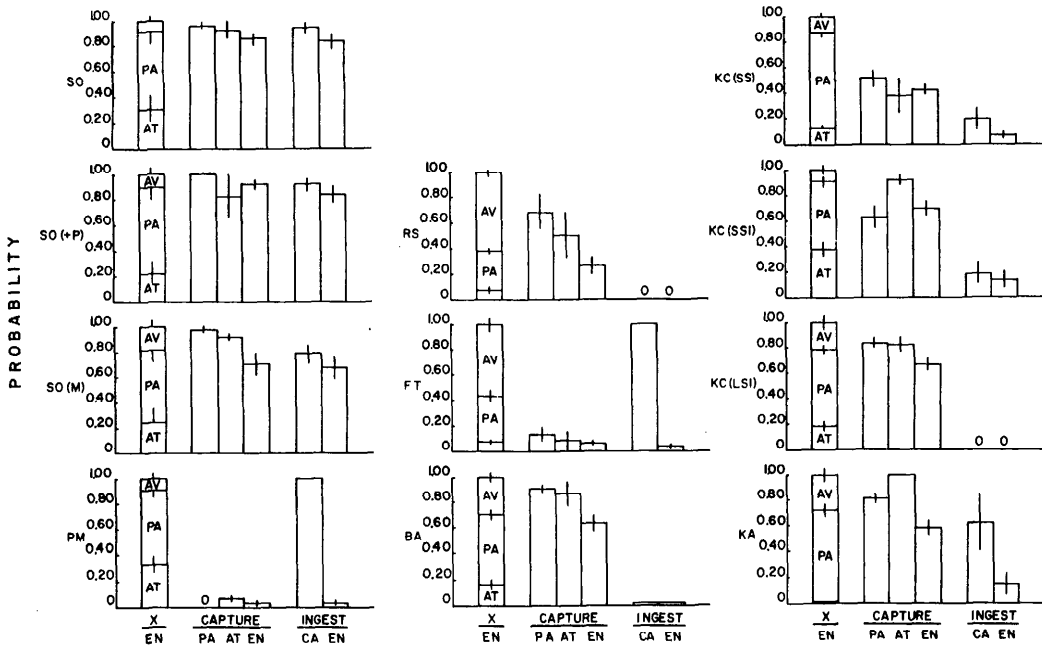


Fig. 4. Behavioral probabilities (means and SE) for interactions between *Diaptomus pallidus* and its rotifer prey. EN—Encounter; AV—avoidance; PA—passive; AT—attack; CA—capture. X refers to corresponding probability after encounter. Explanation of experimental conditions given in Table 1.

idly turned, shifted, and reoriented during a brief handling period of generally < 4 s (Table 2), after which the prey was either ingested or rejected. Ingestion consisted of disappearance of the prey within the feeding chamber of the copepod. Due to the transparency of *D. pallidus*, the prey organisms could frequently be seen passing down the esophagus.

This generalized behavioral sequence was observed with all of the rotifer prey species. However, the success rate of the predator in each phase was highly variable (Fig. 4). Many of the rotifers possessed morphological and behavioral characteristics that drastically reduced their vulnerability to predation.

The rotifer that was most vulnerable to *Diaptomus* predation was *Synchaeta oblonga*, a small, soft-bodied rotifer with no effective defense mechanisms against *Diaptomus*. There were no significant differences ($P > 0.5$) between behavioral probabilities for adult female *Diaptomus* preying on *Synchaeta* in the presence vs. the absence of

natural phytoplankton [experiments SO vs. SO(+P), Fig. 4]. *Diaptomus* males exhibited similar encounter responses and capture probabilities to those of females, but the ingestion probabilities were somewhat lower for males than for females, with the probability of ingestion after capture being significantly different [$P = 0.05$, experiments SO vs. SO(M), Fig. 4]. All of the capture and ingestion probabilities for adult female *Diaptomus* preying on *Synchaeta* were above 0.8, and the probability of avoidance after encounter was low (0.10). This gave an overall probability of ingestion after encounter of 0.84 for this species (Fig. 4, exp. SO). The probability of ingestion after encounter was < 0.2 for all other species of rotifers examined (Fig. 4), due to a variety of defense mechanisms.

Two rotifer species, *Polyarthra major* and *Filinia terminalis*, had movable appendages that significantly ($P < 0.001$) reduced their probability of capture after encounter (0.03, 0.06 respectively) compared to all other species (0.26–0.92, Fig. 4). In both

Polyarthra and *Filinia* the escape mechanisms involved rapid elevation of lateral appendages. These responses were generally exhibited as the prey were brought in on the feeding currents of *Diaptomus*, before actual contact with the copepod. *Polyarthra* has lateral appendages (paddles, Fig. 1) which serve to propel the rotifer up to 10 times its body length during an escape response from a predator (Allen 1968; Gilbert and Williamson 1978). *Polyarthra* exhibited this escape response, successfully evading capture, in 129 out of 140 (92%) of the observed encounters with *Diaptomus*. When captured however, *Polyarthra* was immediately ingested (Table 2, Fig. 4).

Filinia terminalis has three long bristles, one that is caudal and fixed and two that are lateral and movable (Fig. 1). As *Filinia* became entrained in the feeding currents of *Diaptomus* it was brought toward the feeding chamber anterior end first (due apparently to the viscous drag on the trailing bristles). Shortly before, or occasionally just after contact with the predator, *Filinia* elevated its lateral bristles into a position such that they were directed anteriorly, roughly parallel to the caudal bristle. This response by the prey did not cause the body of the rotifer to move any substantial distance, but rather presented the *Diaptomus* with two long bristles that either got caught in the feeding chamber of the copepod or caused the rotifer to continue to flow past the copepod apparently undetected (passive response scored). When the bristles contacted the copepod, the predator responded by fluttering its feeding appendages in an apparent attempt to grasp the prey. This was followed by an almost immediate slight to strong hop in a direction away from the prey (avoidance response scored) wherein the prey was rejected. The avoidance response was similar to that shown by *Diaptomus* when non-food objects were encountered. Occasionally a copepod succeeded in grasping a *Filinia*, in which case it was ingested within 4 s (Table 2, Fig. 4).

The small, soft-bodied rotifers tested (*Filinia*, *Polyarthra*, and *Synchaeta*) were more easily ingested after capture (probabilities were 0.94, 1.00, and 1.00 respectively) than

were the similarly sized species with hard loricae (*Brachionus angularis*, *Keratella americana*, short- and long-spined *Keratella cochlearis*, probabilities were 0.01, 0.62, 0.20, and 0.00 respectively, Fig. 4). The capture probabilities were moderate to high for these loricate species (0.38–1.00: Fig. 4). A few captured individuals of each of these species were ingested. Juvenile individuals were ingested whole, lorica and all; the loricae of adults were often mangled, but rarely ingested. More often the loricate species were rejected unharmed following capture and resumed active swimming within a few seconds of release. After each ingestion the copepods were removed from the chamber and their guts examined under a compound microscope. Loricae were frequently observed in their guts.

Keratella cochlearis, in addition to its hard lorica, exhibited a swimming escape response that consisted of a rapid acceleration of its swimming speed for a brief (<1 s) period when it became entrained in the feeding currents of *Diaptomus*. This escape response was not as effective as the skipping escape response of *Polyarthra*, but it did enable *K. cochlearis* to swim out of the feeding currents of *Diaptomus* and escape capture in 29 out of 127 (23%) of the observed encounters [experiment KC(SS)].

After a day of starvation *Diaptomus* exhibited significant increases in its probabilities of attack after encounter ($P < 0.001$), capture after attack ($P < 0.003$), and capture after encounter ($P < 0.002$) [experiments KC(SS) vs. KC(SS1), Fig. 4]. No significant differences were observed in the probabilities of capture after a passive response ($P = 0.19$), ingestion after capture ($P = 0.88$), or ingestion after encounter ($P = 0.65$) following starvation.

Both long- and short-spined morphs of *K. cochlearis* were tested to examine the effect of spine length on the ability of *Diaptomus* to prey on rotifers [experiments KC(SS1) vs. KC(LS1)]. The results showed that *Diaptomus* was more likely to attack ($P < 0.006$) and somewhat less likely to avoid ($P = 0.07$) the short- vs. the long-spined *K. cochlearis* after an encounter (Fig. 4). The short-spined forms were also more

likely to be ingested after capture ($P < 0.006$) or after an encounter ($P < 0.006$) compared to the long-spined forms. *Keratella americana* has spines which are even longer than those of the long-spined *K. cochlearis* (Table 1). The longer spined *K. americana* was less likely to be attacked ($P < 0.001$) and somewhat more likely to be avoided ($P = 0.064$) after encounter than the long-spined *K. cochlearis* (Fig. 4). Spine length was not important in reducing ingestion probabilities for *K. americana* compared to the long-spined *K. cochlearis* and apparently yielded to some more subtle interspecific differences, perhaps related to the integrity of the lorica (Fig. 4).

The regressions of predator success on prey size gave a significant relationship only for the probability of avoidance after encounter (Table 3). The coefficient of determination was low for the regression on bristle/spine length alone ($r^2 = 0.28$, $P < 0.05$), somewhat higher for the regression on body length alone ($r^2 = 0.46$, $P < 0.01$), and highest for the regression on total prey length (body plus bristles/spines, $r^2 = 0.81$, $P < 0.001$). The soft-bodied prey (*Filinia*, *Polyarthra*, and *Synchaeta*) and the short-spined *K. cochlearis* values sorted out below the regression line for size on total body length, while the values for the species with

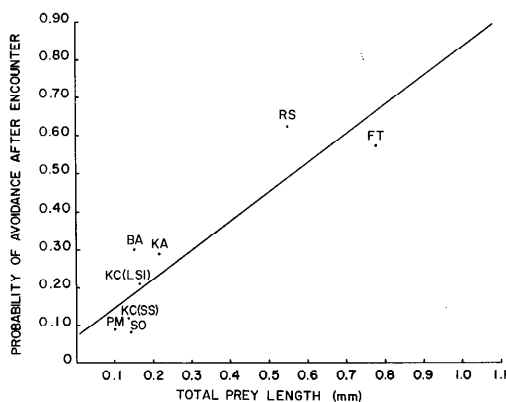


Fig. 5. Regression line for the probability of avoidance after encounter vs. total prey length (body plus bristle/spine length, in mm). Regression equation is $y = 0.76x + 0.073$; $r^2 = 0.81$, $P < 0.001$. Abbreviations explained in Table 1.

tougher loricae (*Brachionus*, *K. americana*, *Rotaria*) and the long-spined *K. cochlearis* sorted out above the regression line (Fig. 5). The coefficients of determination for prey size vs. the probability of avoidance after encounter were 0.27, 0.42, and 0.88 for the regressions on bristle/spine length alone, body length alone, and total prey length.

Prey size was not very effective in explaining the variation observed in some of the other behavioral probabilities tested; in

Table 3. Statistics for least-squares linear regressions of behavioral responses of adult female *Diaptomus pallidus* on three size parameters of the seven rotifer species tested. Bristles/spines refers to extended bristles for *Filinia*, while total refers to the sum of body length plus bristles/spines.

Behavioral probability	Size parameter length (mm)	Regression equation	r^2	P
Avoidance after encounter	Body	$y = 0.91x + 0.13$	0.46	<0.01
	Bristles/spines	$y = 0.50x + 0.23$	0.28	<0.05
	Total	$y = 0.76x + 0.07$	0.81	<0.001
Attack after encounter	Body	$y = -0.15x + 0.17$	0.002	>0.2
	Bristles/spines	$y = -0.20x + 0.16$	0.13	>0.1
	Total	$y = -0.22x + 0.20$	0.21	>0.1
Capture after encounter	Body	$y = -0.39x + 0.51$	0.04	>0.2
	Bristles/spines	$y = -0.62x + 0.51$	0.21	>0.05
	Total	$y = -0.66x + 0.62$	0.29	>0.05
Ingestion after capture	Body	$y = -1.12x + 0.66$	0.14	>0.05
	Bristles/spines	$y = 0.89x + 0.37$	0.18	>0.05
	Total	$y = 0.27x + 0.40$	0.02	>0.5
Ingestion after encounter	Body	$y = -0.25x + 0.18$	0.02	>0.4
	Bristles/spines	$y = -0.25x + 0.17$	0.04	>0.4
	Total	$y = -0.30x + 0.22$	0.07	>0.2

all cases the coefficient of determination was below 0.30 and the relationship not significant at the 0.05 level (Table 3).

The largest rotifer examined was *Rotaria*, with a body length of 500–600 μm and width of about 50 μm . This species has a retractable foot which, when extended, can increase the total body length of the rotifer up to three times its retracted length (longer than the *Diaptomus*). As these rotifers were brought in on the feeding currents of the copepods, they were occasionally attacked but more frequently avoided by a jump of the predator away from the prey. Captured *Rotaria* was consistently grasped by one end or the other, never by the middle. These rotifers were handled for a few seconds (up to 77 s in one case, Table 2) and “nibbled on” by the predator before being rejected. Although no observable ingestion took place, and the rotifers generally swam away apparently unharmed, examination of the *Rotaria* under a compound microscope after the experiment revealed several dead individuals with severe damage to their coronas.

Discussion

Diaptomus pallidus was able to capture all seven of the rotifer species examined, but only five were ever ingested. The vulnerability of the various rotifer species to *Diaptomus* predation was extremely variable and resulted from a variety of types of prey defense mechanisms enacted at several different levels of interaction (Fig. 4).

Prey size has been of particular importance in explaining patterns of selective predation in zooplankton communities: visual predators prefer larger prey species, while tactile invertebrate predators prefer smaller prey species. In the present study I found that prey size appears to be an important factor in determining the initial response of an omnivorous suspension-feeder to various rotifer prey but is of diminished importance at the subsequent levels of interaction (capture and ingestion, Table 3, Fig. 5). The low coefficients of determination for the regressions of the probability of ingestion after encounter on the three prey size parameters (0.02–0.07; Table 3) indicate that

size is not an important overall determinant of the selectivity of *Diaptomus* for the various rotifer species tested.

Rotifers are faced with a different sort of a problem when defending themselves against omnivorous suspension-feeders like *Diaptomus* compared to more specialized invertebrate predators such as *Cyclops* and *Mesocyclops* which attack rotifers with a vigorous leap or a pounce (Williamson and Gilbert 1980; Williamson 1983). In the former case the rotifers must use subtle cues related to changes in the microcurrents surrounding them in order to escape being swept into the feeding chamber of suspension-feeders. Three of the seven rotifer species tested exhibited escape responses that demonstrated such rheotactic capabilities. *Keratella*'s swimming escape response and the appendage elevation responses of *Filinia* and *Polyarthra* were all frequently elicited while these rotifers were entrained in the feeding currents of *Diaptomus*, before any contact was made with the predator. It seems likely that these rheotactic responses would also be effective against some of the large species of *Daphnia* which can damage rotifers entering their feeding chambers (Gilbert and Stemberger 1985).

Diaptomus seems to be able to collect a substantial amount of information on the nature of an encountered prey item in the short time available before it must respond. Whether the prey item is avoided is highly dependent on prey size (Table 3, Fig. 5). If we use the regression line in Fig. 5 to represent the “expected” values for avoidance probabilities, the fact that the long-spined morphs of *K. cochlearis* fall above this line suggests that they are more likely to be avoided than expected on the basis of size alone, while the short-spined morphs, which fall below the line, are less likely to be avoided. Similarly, the other loricate rotifers all fall above the regression line or are more likely to be avoided than expected, while the soft-bodied rotifers all fall below the regression line and are therefore less likely to be avoided than would be expected on the basis of size alone. These data suggest that *Diaptomus* also has some information on the spine length and integument of a prey

species before taking it into the feeding chamber. Differences in the attack and avoidance probabilities following encounter for *Diaptomus* feeding on *K. americana* and long- vs. short-spined *K. cochlearis* (Fig. 4) also suggest that the copepods have some information on the spine length of their prey before capture. The sensory basis of this information is not clear, but *D. pallidus* has mechanoreceptors on its first antennae and contact chemoreceptors on its feeding appendages (mandibles, mandibular palps, first and second maxillae: Friedman and Strickler 1975; Friedman 1980). A combination of these two sensory modes may be involved in prey discrimination.

The active vs. passive nature of prey selection by invertebrate planktivores has been variously defined in recent years. Gilbert (1980) suggested that the key difference between active and passive selection is that in the former the predator makes a decision to avoid potentially ingestible prey. This definition requires the investigator to be able to distinguish between prey that have been detected but ignored by the predator vs. those that were never detected. Detailed information on the flow patterns generated by each prey organism as well as the threshold signal amplitude necessary to stimulate an attack by the predator makes application of this definition theoretically possible (Kirk 1985).

In calanoid copepods the concept of active and passive selection has taken on a slightly different meaning. Calanoids use two different mechanisms to capture small vs. large particles suspended in the water. The existence of these two separate feeding mechanisms in calanoids has been recognized for some time (Conover 1956, 1966; Gauld 1966), while the specifics have been described in more recent studies with high-speed microcinematography (Price et al. 1983). In a detailed microcinematographic study of the feeding of *D. sicilis*, Vanderploeg and Paffenhöfer (1985) separated and defined these two mechanisms: one as being passive, and the other active. They stated that during a passive capture "... the continuous low amplitude vibrations of the second maxillae remain unaltered by the pres-

ence of the algae" (p. 875); while an active capture "... always involved flaps of the swimming legs and second maxillae..." (p. 877). These definitions are very similar to the ones used here (see methods), but precise comparison is difficult because Vanderploeg and Paffenhöfer used tethered *Diaptomus* and I did not. An active capture (=attack) as defined here (involving whole-body movements such as jumps and turns) is not possible for a tethered copepod. However, the flaps of the swimming legs and second maxillae described by Vanderploeg and Paffenhöfer during active captures would inevitably cause whole-body movements in untethered copepods (e.g. Koehl and Strickler 1981; Paffenhöfer et al. 1982), while the continuous low amplitude vibrations by which they characterized a passive capture would not cause any sudden whole-body movements. The definitions of active and passive captures used here for untethered *D. pallidus* feeding on rotifers are thus approximately equivalent to those used by Vanderploeg and Paffenhöfer for *D. sicilis* feeding on algae.

Passive captures were, by definition, exhibited only when the prey organisms were brought directly in toward the feeding chamber of the copepod so that no whole-body movement was necessary for the copepod to grasp the prey. Active captures were exhibited both when the prey were brought in distal to the chamber and when they were brought in directly toward the chamber. The similarity in the success rate of active vs. passive captures for most prey species (Fig. 4) suggests that *Diaptomus* is quite good at reorienting itself during active captures so that the subsequent capture probability approaches that for the passive captures.

Vanderploeg and Paffenhöfer (1985) have referred to *Diaptomus* as being a "small-particle specialist" due to the fact that it does not turn off the continuous, low-amplitude vibrations of the second maxillae during large-particle capture as does *Epi-schura pileatus* (Price et al. 1983). The fact that *Diaptomus* exhibits clearance rates on rotifers that are 5-6 times greater than its clearance rates on algae (Williamson and

Butler 1986), however, suggests that this "enhanced" ability of *Diaptomus* to feed on small particles (Vanderploeg and Paffenhöfer 1985) does not inhibit its ability to feed efficiently on large particles.

The effectiveness of a tough lorica and long spines in reducing predation by suspension-feeding diaptomids on rotifers suggests that rotifers use mechanisms similar to those of many crustacean zooplankton to defend themselves against the larger, more predatory calanoids (Kerfoot 1975; O'Brien and Schmidt 1979; O'Brien et al. 1979; Hebert and Loaring 1980). The presence of rheotactic escape responses in several of the rotifer species, and their effectiveness in reducing vulnerability of the rotifers to predation by *Diaptomus*, suggests that these responses may have evolved specifically in response to predation pressures from suspension-feeding zooplankton. I am currently examining the relative effectiveness of these rheotactic escape responses in defending against some of the more predatory calanoid species.

The high clearance rate of *D. pallidus* on vulnerable rotifers such as *S. oblonga* gives this copepod the potential to remove all of the rotifers from a body of water in a single day at natural concentrations of predators and prey (Williamson and Butler 1986). The intense and selective nature of predation by *D. pallidus* on rotifers suggests that this calanoid has the potential to severely affect rotifer populations. Knowledge of existing rotifer defense mechanisms thus may help us to better understand the role of diaptomid predation in the structure of rotifer communities in nature. Simultaneously it may provide insight into the nature of the evolutionary responses of some of the smaller prey species that are potentially most vulnerable to diaptomid predation.

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