THE FEEDING ECOLOGY OF *HYDRA* AND POSSIBLE IMPLICATIONS IN THE STRUCTURING OF POND ZOOPLANKTON COMMUNITIES

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ABSTRACT

Although most invertebrate predators are size-selective, two species of *Hydra*, *H. oligactis* and *H. pseudoligactis*, are not. A marked preference for *Daphnia pulex* over *Simocephalus vetulus*, similarly sized prey items, is observed in feeding trials. *S. vetulus* is virtually ignored and swims among the tentacles of *Hydra*, whereas *D. pulex* is rapidly attacked and captured. However, normal feeding responses are induced in the presence of homogenates of both *Daphnia* and *Simocephalus*. This suggests that the lack of response to live *Simocephalus* as prey items may be due to defense mechanisms evolved during the course of long-term coexistence in the shallow, weedy littoral zone of lakes and ponds. Such mechanisms could involve reduced activation of nematocysts, immunity to the toxin, or lack of penetration of nematocysts through the carapace of *Simocephalus*. The impact on the structure of the zooplankton community of this differential susceptibility to predation by *Hydra* is discussed.

INTRODUCTION

In the past 20 years it has become apparent that both vertebrate (Brooks and Dodson, 1965) and invertebrate (Dodson, 1974) predators are important in structuring zooplankton communities. In most instances only the larvae of the midge *Chaoborus* and copepods are considered as dominant invertebrate predators on pond zooplankton. Recently, however, other invertebrates, such as notonectids (O'Brien and Vinyard, 1978), dystiscids (Arts *et al.*, 1981), odonates (Johnson, 1973; Johnson and Crowley, 1980), and flatworms (Maly *et al.*, 1980; Schwartz and Hebert, 1982), have been recognized as having possible roles in shaping zooplankton communities. All of these invertebrate predators have been deemed 'size-selective' (Zaret, 1980) in that each demonstrates a marked preference for prey of a particular, usually small, size. By preferring small prey the predators constitute a selective pressure favoring species or individuals larger than the preferred feeding range (Zaret, 1980).

The cladoceran genera *Simocephalus* and *Daphnia* are commonly represented in pond habitats throughout the temperate zone. Although species of the two genera often co-exist, *Daphnia* tend to be most abundant in ponds lacking vegetation, while *Simocephalus* predominates in macrophyte-filled ponds. It has been argued that *Daphnia* avoid these latter habitats because of the presence of toxins released by the plants (Hasler and Jones, 1949; Pennak, 1973) or due to interference with swimming behavior from the vegetation (Porter, 1977), but the role of predation has not been critically assessed. The abundance of *Simocephalus* might simply reflect the presence of substrates for attachment or alternatively the resistance of this species to predators common in macrophyte-filled habitats.

In an effort to understand the factors governing the distribution of these two genera, we set up a number of aquaria containing *Daphnia pulex* and *Simocephalus vetulus*. In agreement with the results of earlier laboratory studies (Frank, 1952), we found that *Daphnia* rapidly displaced *Simocephalus*. There is little doubt that *Simocephalus* is competitively inferior to *Daphnia* even in small containers in which the surface area:volume ratio is large. However, when *Hydra* were added to the aquaria the *Daphnia* population declined rapidly and *Simocephalus* became the numerical dominant. As adult *Daphnia* and *Simocephalus* are of similar size, it was clear that the *Hydra* were selecting prey not on the basis of size but on some other criteria. This initial observation led to the present research, the goals of which were to: 1) determine the selectivity of two *Hydra* species on cladoceran species of different behavior and size and 2) establish the basis of selection.

Stimulation for feeding and the feeding mechanics are both well known for *Hydra* (reviewed by Lenhoff, 1968). Predation is cued by an initial chemical stimulus which sensitizes the nematocysts. When the trigger, or cnidocil, is subsequently given mechanical stimulus the nematocyst is fired and the prey paralyzed and trapped (Lentz, 1966). For the species of *Hydra* studied here, two types of nematocysts were most frequently observed: piercing stenoteles and entangling desmonemes. By means of synchronous tentacular flexing and contraction (referred to as a concert), the prey is brought toward the mouth and slowly engulfed. The entire process takes less than two min for small prey such as *Artemia* nauplii (Rushforth and Hofman, 1972). Though this process is well understood there is sparse literature concerning the implications of *Hydra* feeding on natural prey assemblages and prey community structure (Cuker and Mozley, 1981; Schroeder and Callaghan, 1982).

MATERIALS AND METHODS

Two species of *Hydra* were used in the feeding trials: *H. oligactis* and *H. pseudoligactis*. *Hydra oligactis* was collected at Fish Lake, Lagrange County, Indiana, from an extensive bed of *Elodea* in water less than a meter deep. *Hydra pseudoligactis* was collected at Rondeau Provincial Park, Kent County, Ontario, in a shallow (less than 1 m), well-shaded forest pool. Species identifications were made using Hyman's key (1959) with the lengthwise coiling of the filament in the holotrichous isorhiza and lack of nipples on the testes clearly distinguishing *H. oligactis* from *H. pseudoligactis*. Populations of these species were established in synthetic pond water (Hebert and Crease, 1980) and fed a mixture of *Daphnia* and *Ceriodaphnia* at two day intervals. M solution, the frequently used medium for *Hydra*, was not used as it was found to be lethal to the cladocerans. The prey species used in the trials were all common cladocerans at Rondeau Park and included *Daphnia pulex*, *Daphnia laevis*, *Ceriodaphnia reticulata*, *Scapholeberis kingi*, and *Simocephalus vetulus*. The two larger species, *D. pulex* and *S. vetulus*, were divided into adult and juvenile size classes to provide two additional prey groups. All cladocerans were also cultured in synthetic pond water.

Feeding trials were conducted on laboratory reared *Hydra* by placing one *H. oligactis* (8–10 mm when fully extended) or two *H. pseudoligactis* (5–8 mm total length) in a 120 ml plastic cup with 100 ml synthetic pond water, a depth of 4 cm. Two individuals of *H. pseudoligactis* were used due to their smaller size. The *Hydra* were starved at least 24 h prior to the addition of 20 prey items to each cup. Trials were conducted with 8 replicates and two controls. At the end of 12 h at 20°C in constant light the remaining live prey were counted in each cup. In addition, selectivity was tested by providing 10 juveniles of both *D. pulex* and *S. vetulus* in similarly conducted trials.

TABLE I

ANOVA for feeding trials with Hydra.

	df	ms	F
Hydra oligactis			
Among prey	6	33.78	11.37**
Within prey	42	2.97	
Total	48		
Hydra pseudoligactis			
Among prey	6	246.57	23.51**
Within prey	42	10.49	
Total	48		

** $p < .0001$.

Behavioral responses were observed in 3-depression slides. Single *Hydra* were presented with several individuals of a prey species and the response noted over a 5 min interval. Different *Hydra* were used for each prey item. To observe the feeding response in the absence of behavioral differences in prey species, trials were conducted in which homogenates of prey species (produced by crushing a single individual of a prey species in a drop of synthetic pond water) were introduced into the region of the *Hydra* tentacles. Response to the homogenate was also observed during a 5 min interval. As a certain background rate of concerting may occur, two 5 min observation periods preceded every behavioral response trial. In the event that the background rate of concerting exceeded 1/min, that particular *Hydra* was discarded.

RESULTS

Feeding ecology

The results of feeding trials with two species of *Hydra*, fed 8 different species or combinations of prey species, are presented in Tables I and II. No prey items died in the control containers during the course of their feeding trials. The rank order of mean numbers of prey surviving to the end of the trial was the same for both *Hydra* species, indicating similar prey preferences, and showed no concordance with ranking of the prey items by length. Thus, these species of *Hydra* are not size-selective predators. No distinction was made between prey which had been actively consumed and those killed coincidentally as the result to the prey population is the same.

The prey species could be divided into two or more distinct groups based on their relative vulnerability to predation by *Hydra* (Table II, Duncan's multiple range test, $p < .05$). *Daphnia pulex* adults and juveniles and *Ceriodaphnia* proved to be very vulnerable to attack, whereas *Simocephalus vetulus*, adults and juveniles, and *Scapholeberis* were relatively immune. The response to *Daphnia laevis* differed for the two *Hydra* species: *H. pseudoligactis* preyed upon *D. laevis* with an intensity intermediate between the two groups described above, while *H. oligactis* attacked *D. laevis* as intensely as *Ceriodaphnia* and *D. pulex*. Both *Hydra* species attacked *D. pulex* juveniles at a rate approximately twice that for juvenile *S. vetulus* when presented with a choice of the two prey species (t = 8.98 and 5.625 for *H. oligactis* and *H. pseudoligactis*, respectively, $p < .0001$).

<div align="center">TABLE II</div>

Mean length of prey times, mean number of prey items remaining alive at the end of feeding trials for two species of Hydra *and their grouping by Duncan's multiple range test (p < .05).*

Prey	Age Class	Mean (±s.e.) Length (mm)	Mean (±s.e.) Number of prey alive			
			H. pseudoligactis	Group	H. oligactis	Group
Simocephalus vetulus	A	1.70 ± .02	19.6 ± .2	a	20	a
Simocephalus vetulus	I	.66 ± .01	18.2 ± .5	a b	20	a
Scapholeberis kingi	A	0.80*	18.1 ± .5	a b	19.3 ± .2	a
Daphnia laevis	A	1.58 ± .03	15.4 ± .6	b	17.2 ± .5	b
Ceriodaphnia reticulata	A	.69 ± .01	10.2 ± 1.0	c	17.2 ± .9	b
Daphnia pulex	A	1.88 ± .03	7.7 ± .7	d	15.6 ± .8	b
Daphnia pulex	I	1.20 ± .02	5.7 ± 1.2	d	15.0 ± .5	c
Daphnia pulex and Simocephalus vetulus	I		4.2 ± .5		6.1 ± .6	
			9.7 ± .1		9.6 ± .2	

* Length data from Brooks, 1959.
Means with the same letter are not significantly different. A = adult, I = immature.

Behavioral responses

Responses of the *Hydra* to the various prey items fell into three distinct categories. The immediate response of a *Hydra* to the introduction of *D. pulex* individuals was the gentle waving of its tentacles in the approximate direction of the prey. As soon as the prey contacted one or more of the tentacles, its swimming movements slowed and the animal appeared to be quickly paralyzed. The *Hydra* then either directed the prey toward the mouth by tentacular movements, or occasionally the prey dropped out of reach and was ignored. When the homogenate of a crushed daphniid was introduced near the *Hydra* tentacles, there was an initial burst of concerts, followed by a steady decline in rate of concerting over the 5 min period of observation, the average rate being 5–6 concerts/min.

In contrast was the response of *Hydra* when *Scapholeberis* was presented as prey, where rapid and rather spasmodic tentacular concerts were induced. These did not appear to be focused in the direction of the prey, as they were with *D. pulex*, and were not accompanied by an opening of the mouth or any other feeding response. If *D. pulex* were then provided to the *Hydra* that already had *Scapholeberis* available as prey, the *Hydra* did not attempt to feed on the *Daphnia*. Thus, there appears to be an initial induction of a powerful tentacular concert, with a possible inhibition of the subsequent feeding response. *Scapholeberis* homogenate caused two types of responses: 1) immediate writhing followed by weak concerts with a higher frequency of concerts toward the end of the observation period, and 2) a few weak concerts and several whole body contractions.

When *Simocephalus* were provided to *Hydra* as prey items there was a very striking absence of response. *Simocephalus* adults can swim near and even among the tentacles and evoke no visible response, in much the same fashion as the clown fish can swim among the tentacles of the sea anemone. Occasionally, several nematocysts (desmonemes) will entangle an antenna of *Simocephalus*, but in a few seconds the cladoceran will be seen to shake off this tenuous attachment and swim away unharmed. When offered *D. pulex* subsequent to the *Simocephalus*, the *Hydra* quickly attacked the *Daphnia*. The homogenate of *Simocephalus*, as well as that of the remaining cladocerans studied, did evoke the feeding concert response in *Hydra* at a rate similar to that produced by the homogenate of *D. pulex*.

The pattern of concert behavior differed with *Simocephalus* in a marked manner. After introduction of the homogenate, there was frequently no response for the first minute of observation, followed by a burst of concerts, then a gradual decline in the rate of concerting. Thus, although intact, *Simocephalus*, particularly the adults, rarely elicit any attack by *Hydra*. There was no apparent inhibition of the glutathione-mediated feeding response when crushed prey were presented. This suggests that the differential response to the prey may be occurring at the site of nematocyst activation.

DISCUSSION

The results of our research indicate that both species of *Hydra* used in our investigations could conceivably be important predators in pond communities. Unlike other invertebrate predators, however, *Hydra* are not size-selective but appear to select prey on other characteristics. This result conflicts with Cuker and Mozley (1981) who found that *Hydra* in arctic ponds prefer small prey items, such as *Cyclops* species and *Bosmina*. The difference in results may be due to the inclusion in our study of other than limnetic cladocerans though Schroeder and Callaghan (1982) saw no evidence of prey selectivity among an array of limnetic cladocerans and copepods. In the present study limnetic zooplankton species, such as *Daphnia* and *Ceriodaphnia*, suffered high mortality regardless of size, while zooplankton species more often associated with the shallow littoral zone were not preyed upon extensively. Observations of behavior together with feeding trials suggest that those species living in close association with the *Hydra* seem to have evolved some means of defense.

The defense mechanisms of these cladocerans may include one or more of the following features: 1) an exoskeleton thick enough to prevent the penetration of *Hydra* nematocysts, specifically stenoteles; 2) an immunity to the toxin released from the nematocysts; 3) biochemical characteristics which could inhibit firing of the nematocysts (Lubbock, 1979), and 4) patterns of swimming behavior and location in the water column that result in different encounter and escape probabilities and hence varying vulnerabilities to predation. It should be emphasized that the evolution of any of these characteristics may not have been primarily in response to selection caused by *Hydra* but may be pre-adaptations.

All of these mechanisms may be present to some extent in *Simocephalus*. When nematocysts are fired at *Simocephalus*, as evidenced by the threads attaching the tentacles to the prey, the *Simocephalus* will often sit for a moment and then swim off, unharmed. This would suggest that the exoskeleton is not allowing penetration of the nematocysts or that the *Simocephalus* are immune to the toxin. The only other documented instance of apparent immunity to *Hydra* nematocysts is the chydorid cladoceran, *Anchistropus*, that actively preys on *Hydra* (Borg, 1935). But the observation that nematocysts are rarely fired even when the *Hydra* are in contact with this prey (*i.e.*, providing mechanical stimulation) suggests that the *Simocephalus* possess a cloaking mechanism such that the *Hydra* do not respond to their presence.

This is not to say that *Hydra* will not capture and feed on *Simocephalus*. Immature individuals, especially first instars, are readily preyed upon by larger *Hydra*. It may be that younger individuals have thinner carapaces, greater susceptibility to the toxin, or lack of strength to break from the threads of the nematocysts. In a mixed population, however, adults are usually ignored and the immature individuals taken only occasionally. *Daphnia* adults and juveniles are preyed upon to a much greater extent.

The nematocysts of several other coelenterates have been shown to have associated chemosensory cells (Mariscal and Bigger, 1976; Satterlie and Case, 1978) in addition to the mechanosensory cnidocils. Coelenterate nematocysts and/or sensory cells appear to be capable of distinguishing between and responding to surfaces of different chemical composition (Lubbock, 1979), even to the extent that inter-clonal differences of the anemone *Anthopleura elegantissima* can be recognized (Francis, 1973). Chemical substances associated with the carapace of *Simocephalus* may differ in some subtle manner from those of other cladoceran genera such that the response induced in the chemosensory cells of *Hydra* may be below a threshold level and nematocysts are not discharged. Enzyme inhibitors have been shown to reduce nematocyst discharge in *Hydra* in the presence of appropriate chemosensory stimuli (Lentz and Barnett, 1962; Lentz, 1966). Such inhibitors may be associated with the *Simocephalus* carapace surface, thereby preventing threshold levels of chemosensory stimulation from being reached.

The release of glutathione from wounded prey stimulates the feeding response in *Hydra* (Loomis, 1955). Any slowing of the response by the tentacles (which generally involves further entanglement of the prey and additional encounters with nematocysts) will allow increased escape time. Such a factor could be a substrate which competes with glutathione receptors and would account for the apparent delay in concert response with *Simocephalus* homogenate.

Though living in close proximity with *Hydra*, *Simocephalus* will only occasionally come in contact with the predator, as individuals spend much of their time attached to some substrate and swim only when disturbed. Clearly, this behavior decreases the number of encounters with *Hydra* and partially explains the results of the feeding trials. However, the small volume of the cups and large number of prey/cup ensured numerous opportunities for contact between predator and prey. Behavioral characteristics may also explain the reduced susceptibility of *Scapholeberis*. Individuals of this genus live in or near the surface film. Although *Hydra* have been observed attached to the roots of such floating vegetation as *Lemna*, and will float from the surface under adverse conditions (Lomnicki and Slobodkin, 1966), large areas of open water reduces the likelihood of *Scapholeberis* encountering *Hydra*.

Neither *D. pulex* nor *Ceriodaphnia* appear to have any defense against predation of *Hydra*. These two species are inhabitants of open water and would, therefore, encounter *Hydra* infrequently in the natural environment. Pressure to evolve a defense mechanism against *Hydra* may have been slight.

Community composition may thus be radically affected by the presence or absence of *Hydra*. *Daphnia* spp. were eliminated in our laboratory aquaria, but these have relatively large surface area:volume ratio such that *Hydra* were found on at least five of the six surfaces. The *Daphnia* thus had little room for error. In a natural environment the volume of open water may be considerably greater thereby reducing encounter frequency to a level permitting coexistence of *Hydra* and *Daphnia*. However, the cladoceran community would be expected to be dominated by *Simocephalus* and *Scapholeberis* regardless of volume of water where *Hydra* is in common abundance.

In conclusion, we have shown that *Hydra* feed differentially on commonly available cladoceran prey. The criteria for selection remain unknown, but it is clear that mechanisms protecting individuals exist in those potential prey species living in closest proximity to *Hydra*. We hope this initial research will lead to a better understanding of both *in situ* feeding ecology of *Hydra* and the role of "minor" predator groups in structuring pond zooplankton communities.

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