Early warning lowers risk of stonefly predation for a vulnerable mayfly

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Behavior of *Baetis bicaudatus* (Ephemeroptera; Baetidae) was video taped in a western Colorado, USA stream to identify the specific stimuli eliciting noncontact responses to predatory stoneflies (*Kogotus modestus;* Plecoptera; Perlodidae). In situ behavioral and feeding trial experiments were also conducted to assess the effect of removal of *Baetis* cerci on these responses to predators, on measured reactive distances, and on the vulnerability of *Baetis* to stonefly predation. Predatory stimuli tested included live stoneflies (tethered and untethered), stonefly models (plasticized), excised fresh stonefly antennae, and wires. Intact *Baetis* primarily turned their cerci (tail curl behavior) with similar frequencies toward live or model stoneflies that were between 1 and 2 cm downstream, and primarily moved when stoneflies were within 1 cm even before contact. Removal of *Baetis'* cerci reduced the frequency of tail curl responses and the reactive distance, but increased the frequency of movement responses to noncontact with *Kogotus*. Neither intact nor cerciless *Baetis* showed much response to *Kogotus* antennae and wires. These results suggest that stimuli associated with the whole stonefly, such as visual or more probably hydrodynamic cues, cause *Baetis* tail curl behavior. However, movement behavior was uniformly high after contact with all predator treatments, and the pattern of movement (swim, drift or crawl) varied with predator stimulus, suggesting that *Baetis* can discriminate live or model *Kogotus, Kogotus* antennae, and wires using chemotactile or tactile cues.

Removal of *Baetis* cerci resulted in increased encounter rates (contact) with live, untethered *Kogotus,* higher capture success, and greater predation rates than on intact *Baetis.* When touched by all predator treatments, *Baetis* usually swam, a behavior that stimulates stonefly attacks, but after noncontact tail curl responses, *Baetis* most often remained stationary. Thus, cerci were apparently effective as an early warning system, enabling *Baetis* to detect *Kogotus* before contact, thereby reducing the incidence of dangerous swimming escape behavior, and the susceptibility to predation.

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Introduction

Although much has been written about the importance of prey-generated water wave disturbances as cues for detection or selection by aquatic or semiaquatic predators (Markl et al. 1973, Kerfoot 1978, Giguère and Dill 1979, Lang 1980, Young et al. 1981, Kolmes 1983, Bleckmann and Barth 1984, Buskey 1984, Kirk 1985, Formanowicz 1987), little is known about the use of such cues by prey as an early warning system against aquatic predators. *Baetis bicaudatus,* a stream-dwelling mayfly, laterally flexes its abdomen and turns its cerci toward predaceous stoneflies (tail curl behavior: Peckarsky 1983, 1987), presumably detecting pressure wave disturbances created by their movement patterns (Peckarsky 1987). This behavior occurs with lowest frequency when stoneflies are upstream from *Baetis,* reducing the probability that vision or chemical cues are a primary

Tab. 1. Mean ± 2 s.e. head capsule widths (mm) of predators (*Kogotus*) and prey (*Baetis*) used in behavioral experiments. Sample sizes are given in parentheses. Mean prey sizes did not differ between intact and cerciless individuals (Student's t-test).

Year	Trial	*Kogotus*	*Baetis*
1984	Behavioral	2.53±0.14 (4)	1.00±0.04 (32)
1985	Behavioral	2.49±0.08 (5)	0.92±0.04 (59)
1987	Predation	2.62±0.06 (17)	1.01±0.06 (69)
1988	Predation	2.36±0.14 (24)	0.86±0.04 (72)

stimulus, although the visual field of *Baetis* has not been determined. After these tail curl responses, behavior is different from that after contact encounters with predators. *Baetis* swims or drifts away almost exclusively after being touched by a stonefly (Peckarsky 1980). This hydrodynamically conspicuous behavior decreases after tail curl responses to noncontact predator-prey encounters (Peckarsky 1987).

The objectives of this paper were to (1) identify the specific stimuli eliciting noncontact responses of *Baetis* to predators, (2) define the reactive distance of *Baetis* to predaceous stoneflies, (3) assess the effect of removal of *Baetis* cerci on the reactive distance and responses to different predator stimuli, and (4) determine whether the presence of cerci and the tail curl behavior affect the vulnerability of *Baetis* to stonefly predation.

Materials and methods

Experiments were carried out at Benthette Brook, a first-order tributary of the East River at 2940 m elevation, near the Rocky Mountain Biological Laboratory in western Colorado. Late instars of *Baetis bicaudatus* (Baetidae) were collected from this stream (sizes in Tab. 1) and held in flow-through chambers while cerci were amputated from half the individuals. Specimens were held out of water briefly as cerci were removed with surgical scissors, and returned to chambers for observation. No individuals showing obvious effects of trauma associated with handling were used in experiments.

Either 15 intact or 15 cerciless *Baetis* were then placed in flow-through observation boxes (illustrated in Peckarsky and Penton 1989) constructed of plexiglass with 10×20 cm floors having sides sloped outward for more effective viewing from above. Upstream and downstream ends consisted of nitex (800 µm mesh) windows that allowed flow. Nitex was also glued to the floor and sides of the boxes for use by insects as a foothold and for use by observers as a grid for measuring predator or prey sizes. Trials were recorded in the field with an RCA TC-20 55 video camera fitted with a Vivitar zoom macrolens, and a JVC BR-6200U video cassette recorder.

Kogotus modestus (Perlodidae) is one of two stonefly species that consumes *Baetis* as its primary mayfly prey item in the East River and its tributaries and readily eats *Baetis* in observation boxes (Peckarsky and Penton 1989). During August 1984 and 1985 behavior of intact and cerciless *Baetis* was recorded in the presence of five different predator treatments in replicate 10-min trials. (1) Live *Kogotus* individuals were allowed to forage within observation boxes (N = 7); (2) using a nontoxic glue, abdomens of live *Kogotus* were tethered ventrally to thin wires (N = 7); (3) preserved *Kogotus* were "plasticized" by spraying them with a clear enamel paint the day before trials and were tethered as in treatment 2 (N = 7); (4) *Kogotus* antennae were excised from fresh-caught specimens and tethered to wires (N = 4); and (5) thin wires were used as a predator stimulus (N = 4). Replication was reduced for treatments (4) and (5) since noncontact responses to these two stimuli were very rare. *Baetis* responses were recorded as either movement (crawl, swim or drift) or tail curl behavior. Attempted tail curl behavior of cerciless *Baetis* could be observed as lateral abdominal movement.

To identify the specific stimuli eliciting noncontact responses of *Baetis* to predators (Objectives 1 and 3), the frequencies of tail curl and movement responses were arcsine transformed and compared among all predator treatments using a three-way ANOVA [five predator treatments (live *Kogotus*, tethered-live *Kogotus*, model *Kogotus*, *Kogotus* antennae and wires) ×

Tab. 2. Information gained from pairwise comparison between treatments.

| Comparison	Information
Predator treatments	
Live untethrered vs live-tethered *Kogotus*	Artifacts of tethering *Kogotus*
Live (tethered or untethered) vs model *Kogotus* and *Kogotus* antennae vs wires	Importance of chemical or chemotactile stimuli to prey responses
Live (tethered or untethered *Kogotus*) vs *Kogotus* antennae and model *Kogotus* vs wires	Importance of visual or hydrodynamic cues to prey responses
Stimulus	
Contact vs noncontact encounters	Importance of tactile or chemotactile stimuli to prey responses
Prey treatments	
Intact vs cerciless *Baetis*	Role of cerci in predator detection
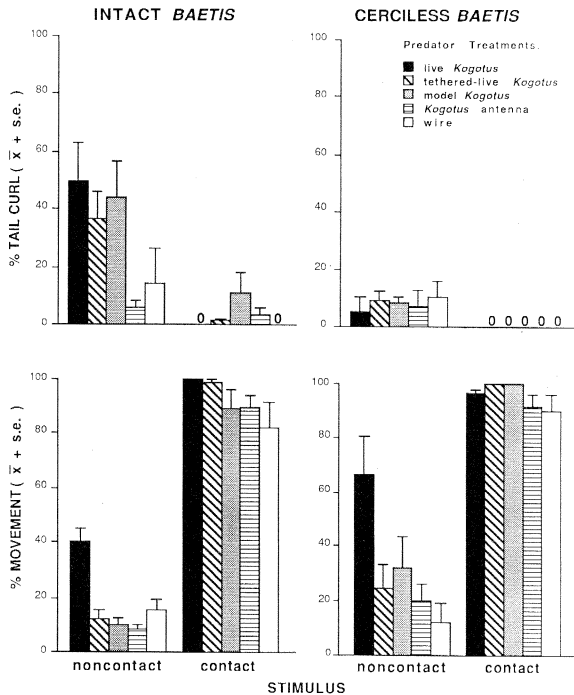
Fig. 1. Percentage of the total noncontact and contact responses by intact and cerciless *Baetis* to five predator treatments ($\bar{x} \pm 1$ s.e., n = 4–7 trials, percentages based on an average of 30 encounters per treatment per trial). Absence of histogram indicates mean and standard error of zero for that treatment. Upper = tail curls; lower = movement. Data analyzed by 3-way ANOVA (see Tab. 3) and a posteriori paired t-tests (see Results).

two prey treatments (intact or cerciless *Baetis*) × two stimulus types (contact or noncontact)]. A posteriori pairwise comparisons between specific treatments were made with paired t-tests. Null hypotheses were rejected at reduced alpha levels ($\alpha = 0.05/n$, n = number of pairwise comparisons per experiment) to compensate for experimentwise error. Information gained from each pairwise comparison is summarized in Tab. 2.

In 1985, observations were made on a 1 × 1 cm grid underlying the flow-through boxes, so that precise measurements of reactive distance could be made (Objectives 2 and 3). The live, untethered *Kogotus* treatment was omitted, since responses by *Baetis* could not be methodically measured without tethering stoneflies. An observer manipulated the tethered stonefly, antenna or wire approaching each *Baetis* (if possible) in the following methodical fashion. The predator stimulus was moved longitudinally with respect to current along grid-lines starting downstream or upstream from each *Baetis* individual beginning at coordinates about 4 cm away, both laterally and longitudinally. Since *Baetis* individuals are positively rheotactic, most were oriented facing upstream during these experiments. Successive longitudinal passes were made by decreasing the lateral

distance in 1 cm increments until the final pass was made directly in the line of flow with *Baetis*. Initial responses, defined as the first distance (to the nearest 0.5 cm) at which *Baetis* either tail curled or moved, and subsequent responses were noted from videotapes and used as a basis for defining reactive distances. Since prey responses to *Kogotus* antennae and wires at 2–4 cm were rare or absent, experimental effort was concentrated within 1 or 2 cm of *Baetis*. For all treatments, effort was also concentrated downstream of the prey, because previous work had shown that *Baetis* responses were higher when predators were in this location (Peckarsky 1987).

The distances at which *Baetis* individuals reacted to the four predator treatments were examined in two ways. First, at each distance tested, the probability of a tail curl or movement response was calculated by dividing the total number of noncontact responses (initial and subsequent) of all *Baetis* individuals by the total number of predator passes (responses + no responses). General trends in response probability with predator distance and predator treatment were inspected graphically. Second, the spatial pattern of *Baetis* responses was statistically analyzed. Chi-square or Fisher's Exact Probability tests (when sample sizes were very low) were used to compare the noncontact response frequencies of intact and cerciless *Baetis* at distances > 1 cm and ≤ 1 cm, upstream and downstream from the four predator stimuli (Objectives 2 and 3).

To test the effects of *Baetis* cerci on its vulnerability to *Kogotus* predation (Objective 4), during summers 1987 and 1988 24 replicates of a predation trial were conducted in Benthette Brook. Plexiglass boxes 20 × 10 × 10 cm with stainless steel mesh (800 μm) ends were filled with standardized natural materials as substrate (as in Peckarsky and Penton 1989) and placed in 7–8 cm of water. Half of the boxes received 15 intact *Baetis* and the other half *Baetis* with excised cerci (as above). For control purposes, intact *Baetis* were handled similarly to cerciless ones before trials. A single 24-h starved *Kogotus* was placed in half the boxes containing intact or cerciless *Baetis* (the other half of which served as controls), and allowed to feed from 0500 PM (MDT) until 0700 AM, two days later. This time period (38 h) was chosen from previous experiments as adequate for measuring the differences between *Kogotus* feeding rates on intact and cerciless *Baetis*. *Baetis* mortality rates (m) were calculated using the equation $N_f = N_o e^{-mt}$, where N_f = final prey density (corrected for losses from controls), N_o = initial prey density (15), and t = duration of trial (1.58 d) (Dodson 1975). Prey mortality rates were compared between intact and cerciless *Baetis* using Students' t-tests.

Mechanisms explaining differences in vulnerability to *Kogotus* predation between intact and cerciless *Baetis* were examined by recording the results of contact encounters between live, untethered *Kogotus* and intact or cerciless *Baetis*. Encounter rates, attacks per encounter,

Tab. 3. Results of three-way analysis of variance with 5 predator treatments (live *Kogotus*, live-tethered *Kogotus*, model *Kogotus*, *Kogotus* antenna, and wire), 2 prey treatments (intact and cerciless *Baetis*), and 2 stimuli (noncontact and contact).

Source	df	Percent tail curl			Percent movement		
		Sum of squares	F value	Probability	Sum of squares	F value	Probability
Predator treatment	4	0.22	2.18	0.079	1.90	8.28	<0.001
Prey treatment	1	0.44	17.18	<0.001	0.35	6.09	0.016
Predator treatment × prey treatment	4	0.25	2.46	0.052	0.15	0.64	0.633
Stimulus	1	0.77	30.37	<0.001	27.12	473.84	<0.001
Predator treatment × stimulus	4	0.17	1.66	0.167	0.75	3.29	0.015
Prey treatment × stimulus	1	0.26	10.33	0.002	0.07	1.26	0.265
Predator treatment × prey treatment × stimulus	4	0.20	1.93	0.114	0.37	1.61	0.180
Total	19	2.63	5.44	<0.001	34.64	31.85	<0.001

capture success (as a percentage of attacks) and handling times (seconds to complete consumption) by *Kogotus* were compared between intact and cerciless *Baetis* (Mann-Whitney U Tests).

Finally, to test whether tail curl behavior affected *Baetis'* vulnerability to *Kogotus* predation (Objective 4), we considered tail curl responses a behavioral bioassay of noncontact *Baetis-Kogotus* interactions. The behavior immediately after tail curl (noncontact) responses to predators was recorded for intact *Baetis* and compared, using chi-square analysis, with behavior that occurred after contact by each predator treatment. Cerciless *Baetis* responses were not included in this analysis since they so rarely responded to *Kogotus* without contact.

Results

Stimuli eliciting responses to predators

Without contact, intact *Baetis* tail curled at higher frequency to live, (untethered and tethered) and model *Kogotus* than to *Kogotus* antennae and wires (Fig. 1, upper left). Cerciless *Baetis* tail curled rarely (significantly less often than intact *Baetis*) and with equal frequency toward all predator treatments (Fig. 1, upper right). When contacted, intact and cerciless mayflies rarely or never tail curled (Fig. 1, upper) and almost always moved (Fig. 1, lower) with no significant differences among predator or prey treatments. Without contact, movement of both intact and cerciless *Baetis* occurred significantly more often in the presence of live, untethered *Kogotus* than in all other predator treatments (Fig. 1, lower). While intact *Baetis* showed higher frequencies of tail curl responses overall (Fig. 1, upper), cerciless *Baetis* showed higher overall frequencies of

movement responses without predator contact (Fig. 1, lower). See Tab. 3 for summary of 3-way ANOVA.

This analysis shows that tail curls predominated as a response by intact *Baetis* to noncontact encounters with predators. Since tail curl responses by intact *Baetis* to whole *Kogotus*, whether live or plasticized, tethered or untethered, did not differ and were significantly higher than those toward *Kogotus* antennae and wires, stimuli associated with whole *Kogotus* are implicated as causal
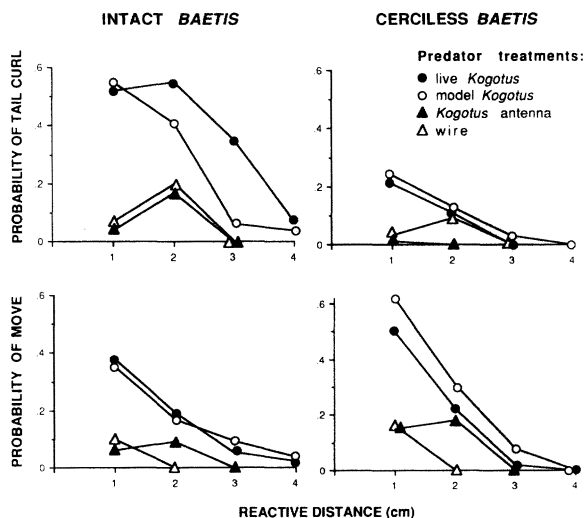

Fig. 2. Probability [responses/total approaches (responses + no responses)] that *Baetis* tail curled (upper) and moved (lower) at each distance from four predator treatments. (Frequencies based on an average of 35 encounters per treatment.) Intervals were assigned with distance (d) from *Baetis* as follows. 1: 0 < d < 1 cm (note: this interval does not include contact encounters); 2: 1 ≤ d < 2 cm; 3: 2 ≤ d < 3 cm; 4: 3 cm ≤ d < 4 cm. Left = intact *Baetis;* right = cerciless *Baetis*.

Fig. 3. Percentage of the total noncontact responses (based on an average of 25 encounters per treatment) by intact and cerciless *Baetis* occurring within 1 cm (including responses at 1 cm, inner box) and outside 1 cm (outer box) when predator treatments approached from upstream (above) or downstream (below) of *Baetis*. Left = tail curl responses, right = movement.
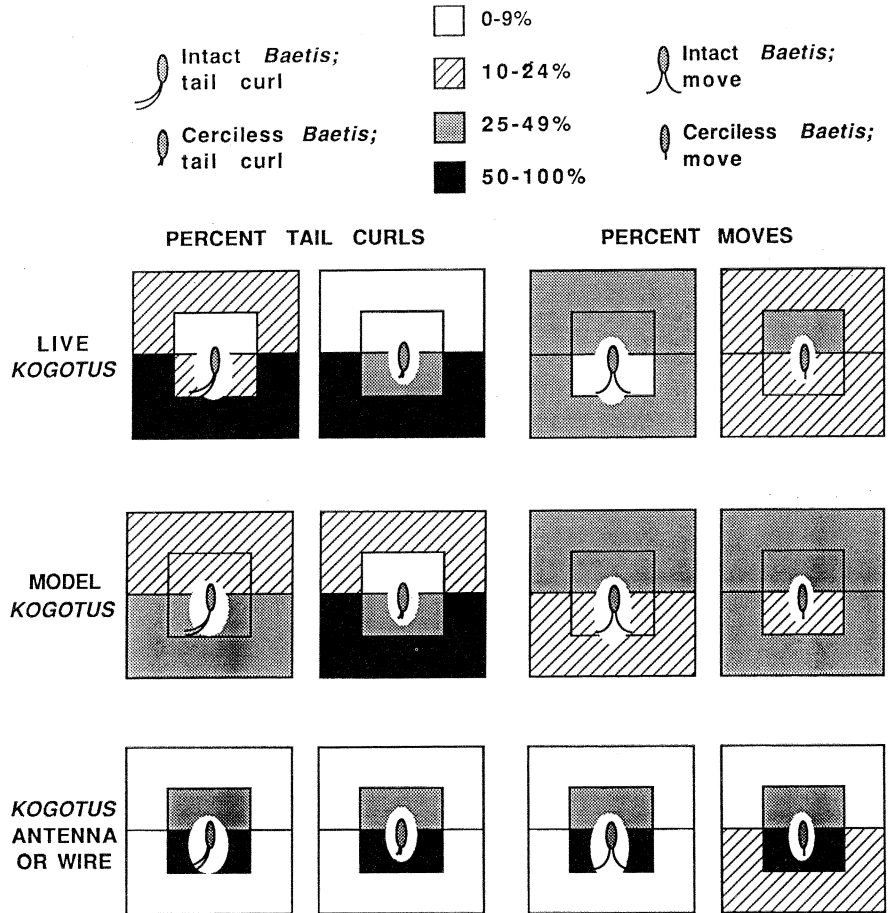
to tail curl behavior (Tab. 2). Movement occurred most commonly after contact between intact or cerciless *Baetis* and any predator treatment, or before contact with a live, untethered *Kogotus* only. These results suggest that although cerci are important for *Baetis'* tail curl responses, this is not the case for movement responses; and that while removal of cerci disrupted the normal pattern of responses to noncontact encounters, it did not affect responses to contact encounters between predators and prey.

Reactive distances

Graphic analysis of the reactive distances of intact and cerciless *Baetis* to four predator treatments shows that *Baetis* rarely (intact: < 10%) or never (cerciless) responded to live-tethered or model *Kogotus* at a distance of greater than 3 cm away in any direction and never responded to *Kogotus* antennae or wires at a distance of greater than 2 cm away (Fig. 2). *Baetis* generally showed an increased probability of response as the predator got closer. As in the previous experiment in-

tact *Baetis* showed a higher tendency to tail curl than to move, and cerciless *Baetis* responses most often involved movement. Responses occurred with very low frequency (usually < 20%) to *Kogotus* antennae or wires, even at the closest distances.

More detailed comparisons from Fig. 2 show that tail curl reactive distances to live and model *Kogotus* were always greater for intact *Baetis* than cerciless *Baetis*. In other words, predators could get much closer to cerciless *Baetis* before these would turn their abdomens as if to tail curl. This was not the case for movement responses, however. The probability of cerciless *Baetis* movement was similar or even higher at each distance than that of intact *Baetis*. This trend reflects the general tendency for cerciless *Baetis* to move more than intact *Baetis* without contact with predators (Fig. 1, lower). Further, peak tail curl frequency of intact *Baetis* toward live *Kogotus*, *Kogotus* antennae or wires was not necessarily at the closest distance measured. That is, intact *Baetis* responded with equal or greater probability when these stimuli were ≥ 1 cm than when they were at < 1 cm. Also, distances at which *Baetis* responded to live and model *Kogotus* generally did not differ, with
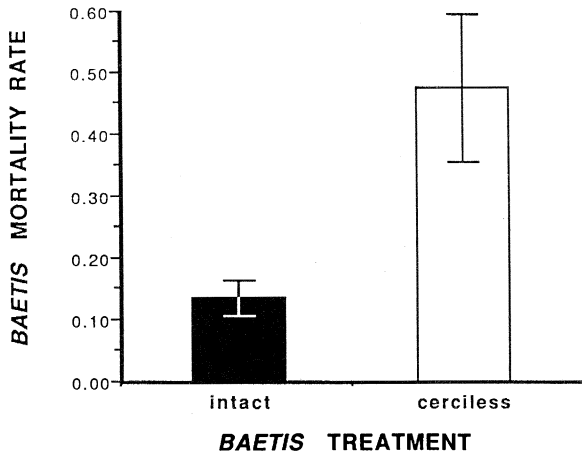
Fig. 4. Mean $\pm$ 1. s.e. mortality rate of intact and cerciless *Baetis* during predation trials with *Kogotus* present, corrected for numbers missing from control boxes without *Kogotus* (N = 24).

the exception that intact *Baetis* tended to react by tail curl when farther away from live *Kogotus*. Likewise, *Baetis* responded at similar distances from *Kogotus* antennae and wires, and to these with consistently lower probability than to the whole stoneflies. These differences further suggest that stimuli triggering *Baetis* responses were most prevalent in whole *Kogotus*, whether live or plasticized.

The statistical analysis of *Baetis* reactive distances showed that tail curl responses were more common when *Kogotus* was downstream of intact *Baetis*, while movement was the more frequent response to upstream *Kogotus* (live-tethered *Kogotus*: χ^2_{1df} = 10.13, p < 0.01; model *Kogotus*: χ^2_{1df} = 4.87, p < 0.05) (Fig. 3). Combining upstream and downstream responses, tail curl (χ^2_{1df} = 22.29, p < 0.001) and movement responses (Fisher's p = 0.001) of intact *Baetis* occurred more frequently at > 1 cm than at $\leq$ 1 cm from live *Kogotus*, occurred at equal frequencies > 1 cm and $\leq$ 1 cm from model *Kogotus* (χ^2_{1df} = 0.36, p > 0.05, Fisher's p = 0.13, tail curl and movement, respectively), and were more frequent within 1 cm of *Kogotus* antennae or wires (χ^2_{1df} = 7.12, p < 0.01, Fisher's p = 0.02, tail curl and movement, respectively). Cerciless *Baetis*, on the other hand, responded with equal frequencies to live (Fisher's p = 0.62) and model (Fisher's p = 0.38) *Kogotus* $\leq$ 1 cm and > 1 cm away, and never (tail curl, Fisher's p = 0.002) or rarely (move, χ^2_{1df} = 11.99, p < 0.001) responded unless the *Kogotus* antennae or wires were within 1 cm.

Vulnerability to predation

Results of predation trials showed that cerciless *Baetis* had significantly higher mortality rates than intact *Baetis* (Student's t-test, p < 0.05) (Fig. 4). Thus, the vulnerability of cerciless *Baetis* to *Kogotus* predation was

higher than that of intact *Baetis*. Mechanisms underlying this pattern were identified by examining results of contact encounters between live, untethered *Kogotus* and intact vs cerciless *Baetis* (Fig. 5). Although *Kogotus* encountered more cerciless than intact *Baetis*, predators attacked more intact than cerciless *Baetis* (nonsignificant trend) during six 10-min trials (Fig. 5, upper). Capture success was significantly higher on cerciless than on intact *Baetis*, and there was no significant difference between handling times, although it took *Kogotus* somewhat longer to consume *Baetis* with than without cerci (Fig. 5, lower). Thus, although cerciless *Baetis* were attacked less frequently per encounter, they were encountered more often and were significantly more vulnerable to capture once attacked by *Kogotus* than were intact *Baetis*.

Finally, the analysis of responses by *Baetis* after tail curl behavior (as a behavioral bioassay of noncontact *Baetis-Kogotus* interactions) compared with responses after contact with predator treatments enabled us to make further inferences about the effect of tail curl behavior on *Baetis'* vulnerability to predation. There was a significant difference between the behavioral response frequencies of *Baetis* after tail curls (noncontact) and after contact with each predator treatment (Fig. 6). For all predator treatments, after tail curls swim-drift behavior was reduced and freezing (no response) behavior was higher than expected when compared with behavior after contact (p < 0.05, significant cells test, Fagen and Mankovich 1980). For all but tethered *Kogotus*, crawling behavior was also lower than expected after tail curls. Thus, for all predatory stimuli, tail curl
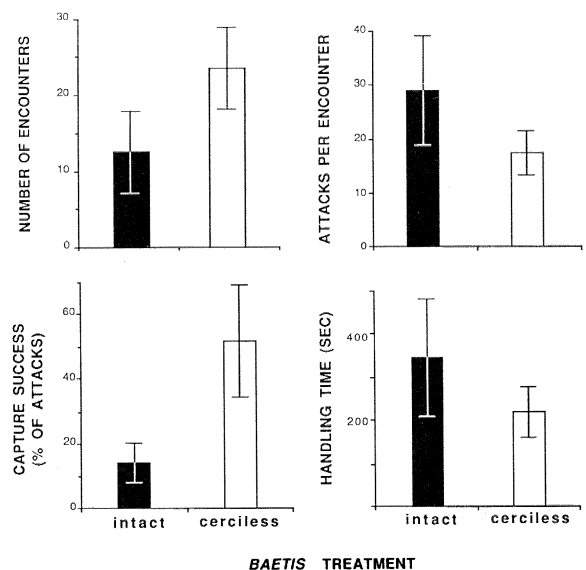

BAETIS TREATMENT

Fig. 5. Number of encounters, attacks per encounter, capture success (percentage of attacks) and handling time by live, untethered *Kogotus* of intact and cerciless *Baetis* during 10-min behavioral trials ($\bar{x}$ $\pm$ 1. s.e., n = 6).
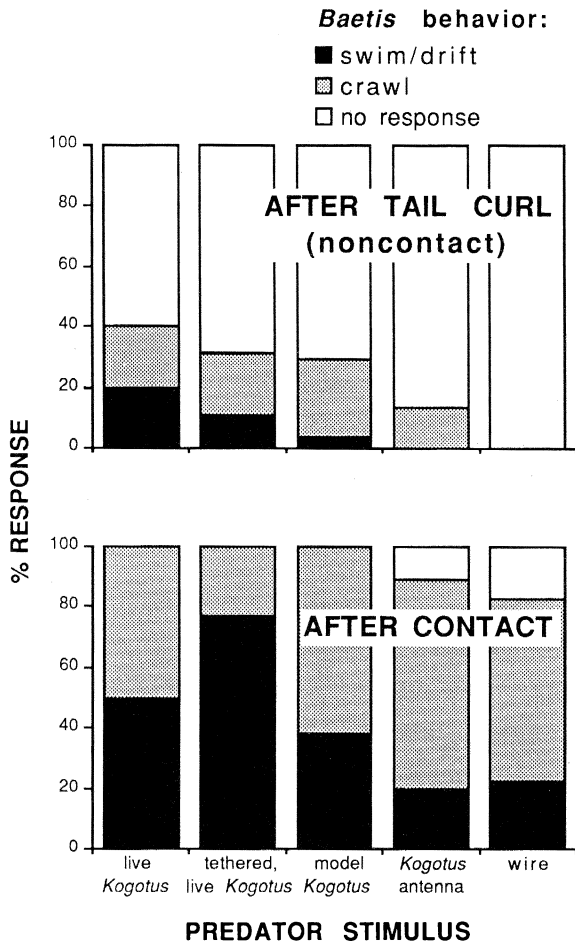
Fig. 6. Swim-drift, crawl or no response (freeze) by intact *Baetis* as a percentage of total interactions (average of 50 per treatment) involving noncontact (tail curls) or contact with five predator treatments.

behavior resulted in a reduction of movement, most notably swim-drift behavior, which is hydrodynamically attractive to stonefly attacks (Peckarsky and Penton 1989, Peckarsky and Wilcox 1989) and an increase in the frequency of the least hydrodynamically conspicuous behavior (freezing or no movement). These trends are similar to those reported earlier (Peckarsky 1987) for responses of *Baetis* to *Kogotus,* but are more dramatic here since this study used more accurate recording methods and more replication.

Response frequencies after tail curls were homogeneous across all predator stimuli ($\chi^2_{4df} = 7.81$, $p > 0.05$), but differed after contact with different predator stimuli (Fig. 6) ($\chi^2_{4df} = 38.69$, $p < 0.001$). *Baetis* swam or drifted in frequencies higher than expected and crawled with lower frequency than expected when touched by live-tethered *Kogotus.* Crawling was the most frequent response to contact with model *Kogotus, Kogotus* antennae and wires. This result suggests that *Baetis* can

distinguish among contacts with the different predator treatments.

Discussion

Tail curl responses were most prevalent when whole stoneflies were used as stimuli rather than excised stonefly antennae or wires (Fig. 1, upper). Since such responses occured with the same frequencies to live-free, live-tethered, and model-tethered stoneflies, we did not greatly alter *Baetis* tail curl behavior by using tethered *Kogotus,* and the shape of the stonefly, not its chemistry, was the key factor causing *Baetis* responses. Since the incidence of tail curl behavior was very low when the predators were upstream of *Baetis* (Fig. 3), the implication is that visual stimuli were less important than hydrodynamic stimuli in alerting *Baetis* that a stonefly was in the vicinity. However, neither the visual field nor the acuity of *Baetis* nymphs are known. We also do not know whether the hydrodynamic wave pattern of *Kogotus* was significantly altered by tethering or plasticizing the stoneflies.

While tethering *Kogotus* did not affect the frequency of tail curl responses (Fig. 1, upper), it did affect the frequency of movement responses by *Baetis* after noncontact encounters with *Kogotus* (Fig. 1, lower). This difference in response may be due to the restriction in normal motion caused by attaching the stonefly to a wire. Interestingly, *Baetis* moved away before contact with untethered *Kogotus,* the treatment with the highest risk of predation, more frequently than with any of the other predator treatments. Frequency of movement also increased when *Kogotus* was upstream of *Baetis* (Fig. 3), and thus could be a result of visual detection of the predators or detection of upstream wave disturbances by *Baetis* antennae, which bear numerous sensory receptors (Martínez 1987). Differences in movement patterns of *Baetis* after contact with live vs model *Kogotus* or *Kogotus* antennae vs wires (Fig. 6), implicate potential discrimination of these stimuli using chemotactile cues. Avoidance after contact with a chemical extract of *Kogotus* by *Baetis* has been previously demonstrated (Martínez 1987).

Removal of *Baetis* cerci almost eliminated tail curl behavior, but increased the frequency of movement responses without contact by predators (Fig. 1). Reduction of tail curls could be due to the subtlety of lateral abdominal movement (indicating attempted tail curl) when cerci were absent. More probably, loss of receptors on the cerci could explain the virtual elimination of the tail curl response and the reduction of *Baetis's* reactive distance to predators. Scanning electron micrographs show that *Baetis* cerci have nearly identical receptors to those of antennae (Martínez 1987). Thus, cerci may be important sensory structures enhancing this mayfly's ability to detect hydrodynamic cues. The cercal movement behavior (tail curl) may indicate activation of mechanoreceptors used to detect pressure

wave disturbances created by stoneflies, as has been shown to occur in crayfish antennal vibration receptors (Tautz 1987), and those on the head of mosquito larvae (Magnuson and Baerwald 1987).

Although reactive distances to prey have been measured for aquatic predators, mostly fish (Luecke and O'Brien 1981, Hairston 1982, Dunbrack and Dill 1984, Li et al. 1985, Hoekstra and Janssen 1986)) a few insects (Giguère and Dill 1979, Jamieson and Scudder 1979, Formanowicz 1987), and crustaceans (Kerfoot 1978), response distances of aquatic prey to their predators have not been previously reported. Here, *Baetis* responded with high probability (75% combining tail curl and movement) to live predaceous stoneflies at distances between 1 and 2 cm, but rarely before predators were within 2 cm (Fig. 2). Once a predator was within 1 cm of *Baetis,* the probability of a prey response was 90%. Thus, only 10% of the time, *Baetis* allowed tethered predators to get close enough to contact them. Removal of *Baetis* cerci reduced the reactive distance; that is, intact *Baetis* responded to predators at greater distances than did cerciless *Baetis.*

If *Baetis* used its cerci to detect predaceous stoneflies without contact, its vulnerability to predation should increase when cerci are removed, which effect was observed during predation trials with *Kogotus. Baetis* without cerci were encountered (contacted) more frequently and captured with significantly greater success than were intact *Baetis.* Higher predator-prey encounter rates with cerciless mayflies may have been due to the disruption of *Baetis'* early warning system associated with cerci. Interestingly, intact *Baetis* were attacked more per encounter and were slightly more difficult to handle than were cerciless *Baetis.* Although these were nonsignificant trends, lower attack rates may be due to a change in the usually conspicuous swimming pattern of *Baetis* by removal of its cerci. Once attacked, cerciless *Baetis* were easier to capture and, thus, more vulnerable to predation. A similar finding was documented by Otto and Sjöström (1983) upon removal of stonefly cerci.

Analysis of *Baetis'* behavior after tail curl responses provides a possible mechanism for the effect on predation risk of reducing predator-prey encounters. When mayflies avoided predator contact, the frequency of hydrodynamically conspicuous behavior consequent to predator contact also declined. *Baetis* almost always moved when contacted by stoneflies (Fig. 1), and the most common type of movement after such encounters was the conspicuous swim-drift motion (Fig. 6). If mayflies moved after tail curl responses or before contact with stoneflies, they usually crawled forward or sideways from the predators, a behavior that did not attract attacks. Most often, however, they did not move, but they froze or remained stationary after having presumably used their cerci to detect a predator. Rarely did they swim-drift without having been actually contacted by predators.

With regard to the objectives of this study, we summarize and interpret the data as follows: (1) the specific stimulus eliciting tail curl responses by *Baetis* was most probably a hydrodynamic cue resulting from pressure wave disturbances created by the movement of a predaceous stonefly, rather than visual, chemical or chemotactile stimuli. However, these latter cues may have played a role in stimulating movement patterns by *Baetis* before or after contact with predators. (2) *Baetis* reacted to predaceous stoneflies at distances greater than 1 cm, but rarely beyond 2 cm. (3) Removal of *Baetis* cerci significantly reduced the frequency of tail curl responses and the distance at which *Baetis* responded to *Kogotus.* (4) Tail curl behavior was an early warning system reducing contact encounters between predators and the *Baetis* individuals that showed this response. Individuals that tail curled exhibited less hydrodynamically conspicuous behavior in the vicinity of predators than did those individuals that were contacted by stoneflies. Removal of cerci reduced the extent of sensory receptors available to *Baetis* for noncontact detection of stoneflies, thereby increasing their vulnerability to capture and subsequent mortality by stonefly predation.

References

Bleckmann, H. and Barth, F. G. 1984. Sensory ecology of a semi-aquatic spider (*Dolomedes triton*). II. The release of predatory behavior by water surface waves. – Behav. Ecol. Sociobiol. 14: 303–312.

Buskey, E. J. 1984. Swimming pattern as an indicator of the roles of copepod sensory systems in the recognition of food. – Mar. Biol. 79: 165–176.

Dodson, S. I. 1975. Predation rates of zooplankton in arctic ponds. – Limnol. Oceanogr. 20: 426–433.

Dunbrack, R. L. and Dill, L. M. 1984. Three-dimensional prey reaction field of the juvenile coho salmon (*Oncorhynchus Kisutch*). – Can. J. Fish. Aq. Sci. 41: 1176–1182.

Fagen, L. M. and Mankovich, N. J. 1980. Two-act transitions, partitioned contingency tables, and the significant cells problem. – Anim. Behav. 28: 1017–1023.

Formanowicz, D. R., Jr. 1987. Foraging tactics of *Dytiscus verticalis* larvae (Coleoptera: Dytiscidae): prey detection, reactive distance and predator size. – J. Kansas Ent. Soc. 60: 92–99.

Giguère, L. A. and Dill, L. M. 1979. The predator responses of *Chaoborus* larvae to acoustic stimuli, and the acoustic characteristics of their prey. – Z. Tierpsychol. 50: 113–123.

Hairston, N. G., Jr. 1982. Fish vision and the detection of planktonic prey. – Science 218: 1240–1242.

Hoekstra, D. and Jansson, J. 1985. Non-visual feeding behavior of the mottled sculpin, *Cottus bairdi,* in Lake Michigan. – Environ Biol. Fish. 12: 111–117.

Jamieson, G. S. and Scudder, G. G. E. 1979. Predation in *Gerris* (Hemiptera): reactive distances and locomotion rates. – Oecologia (Berl.) 44: 13–20.

Kerfoot, W. C. 1978. Combat between predatory copepods and their prey: *Cyclops, Epischura,* and *Bosmina.* – Limnol. Oceanogr. 23: 1089–1102.

Kirk, K. L. 1985. Water flows produced by *Daphnia* and *Diaptomus:* implications for prey selection by mechanosensory predators. – Limnol. Oceanogr. 30: 679–686.

Kolmes, S. A. 1983. Ecological and sensory aspects of prey capture by the whirligig beetle *Dineutes discolor* (Coleoptera: Gyrinidae). – J. New York Ent. Soc. 91: 405–412.

Lang, H. H. 1980. Surface wave discrimination between prey and nonprey by the back swimmer *Notonecta glauca* L. (Hemiptera, Heteroptera). – Behav. Ecol. Sociobiol. 6: 233–246.

Li, K. T., Wetterer, J. K. and Hairston, N. G., Jr. 1985. Fish size, visual resolution, and prey selectivity. – Ecology 66: 1729–1735.

Luecke, C. and O'Brien, W. J. 1981. Prey location volume of a planktivorous fish: a new measure of prey vulnerability. – Can. J. Fish. Aq. Sci. 38: 1264–1270.

Magnuson, L. J. and Baerwald,R. J. 1987. Water current trichobothria on the larvae of *Toxorhynchites rutilus* (Diptera: Culicidae). – Ann. Ent. Soc. Am. 80: 637–641.

Markl, H., Lang, H. and Wiese, K. 1973. The accuracy of orientation of the backswimmer *Notonecta glauca* toward the source of surface waves. – J. Comp. Physiol. 86: 359–364.

Martínez, L. A. 1987. Sensory mechanisms underlying the predator-prey interaction between perlodid stonefly nymphs and their mayfly nymph prey. – Ph.D. thesis, Cornell Univ., Ithaca, NY.

Otto, C. and Sjöström, P. 1983. Cerci as antipredatory attributes in stonefly nymphs. – Oikos 41: 200–204.

Peckarsky, B. L. 1980. Predator-prey interactions between stoneflies and mayflies: behavioral observations. – Ecology 61: 932–943.

– 1983. Use of behavioral experiments to test ecological theory in streams. – In: Barnes, J. R. and Minshall, G. W. (eds), Stream ecology. Plenum, New York, USA, pp. 79–97.

– 1987. Mayfly cerci as defence against stonefly predation: deflection and detection. – Oikos 48: 161–170.

– and Penton, M. A. 1989. Mechanisms of selective predation by stream-dwelling stonefly nymphs. – Ecology (in press).

– and Wilcox, R. S. 1989. Stonefly nymphs use hydrodynamic cues to distinguish between prey. – Oecologia (Berl.) (in press).

Tautz, J. 1987. Water vibration elicits active antennal movements in the crayfish, *Orconectes limosus.* – Anim. Behav. 35: 748–754.

Wetterer, J. K. and Bishop, C. T. 1985. Planktivore prey selection: the reactive field volume model vs. the apparent size model. – Ecology 66: 457–464.

Young, S. R. et al. 1981. Responses of the medicinal leech to water waves. – J. Comp. Physiol. 144A: 111–116.