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## INVERTEBRATE PREDATION AND LOTIC PREY COMMUNITIES: EVALUATION OF IN SITU ENCLOSURE/EXCLOSURE EXPERIMENTS<sup>1</sup>

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**Abstract.** The influence of the stonefly *Kogotus nonus* on prey communities was assessed by varying the predator density within small enclosures in a first-order stream in southwestern Alberta. Experimental containers with natural densities of prey, standardized substrate and detritus, and zero, one, two, or three *Kogotus* were buried in a riffle for 10 d during three periods: July 1981, June 1982, and July 1982. *Kogotus* depressed the densities of *Thienemaniella* and some other Orthocladiinae, but had no effect on the densities of *Corynoneura* (Orthocladiinae), *Stempellinella* (Tanytarsini), and *Baetis tricaudatus* (Ephemeroptera). Significant reduction of the densities of *Thienemaniella* and other Orthocladiinae occurred only when these prey items were present at high densities. The extent to which prey densities were depressed was found to be dependent on predator density within the enclosures: increased predator densities resulted in lower prey densities. However, when predator density in the containers exceeded that commonly observed in the riffle, predator efficiency dropped, probably because of interference between predators, the existence of prey refuges, or changes in predator search effort.

An experimental design in which containers that excluded predators were compared with controls accessible to predators was used to determine if results would be similar to results from the enclosure experiments. Using this design, observed results could not clearly be attributed to the presence or absence of the predator, and were more likely due to differences in abiotic conditions between the experimental and control containers. It was concluded that observation of predator effects in field manipulative experiments may be strongly dependent on the selection of an experimental design in which predator effects are not confounded with container effects.

**Key words:** enclosures; exclosures; predation; predator-prey interactions; stonefly.

### INTRODUCTION

Conflicting views have been presented on the importance of predation in structuring aquatic communities. Predators have been reported to influence prey species diversity (Paine 1966), species composition (Hall et al. 1970, Dodson 1974), distribution (Macan 1965, Sih 1979, Peckarsky and Dodson 1980), feeding and activity levels (Stein and Magnusson 1976) and production rates (Benke 1976). Conversely, Thorp and Bergey (1981), Choat and Kingett (1982), and Allan (1982b) have concluded that predators do not significantly affect aquatic prey communities.

The importance of predation has been inferred from community surveys (Hildrew and Townsend 1976) and gut-content analysis (Siegfried and Knight 1976). Recently, field experiments manipulating predator densities and, occasionally, prey densities have become popular, since the results can be interpreted directly in terms of predator effects. In a few lentic environments, it has been possible to remove a predator from or add it to an ecosystem (Macan 1965, Hall et al. 1970) or an artificial ecosystem (Morin 1981, 1983). However, in most aquatic systems, large-scale manipulation is not feasible; thus, experiments have taken place within enclosed, representative portions of ecosystems.

Two different approaches have been employed in field manipulative experiments, and they sometimes produce results that are apparently contradictory. In the first approach, changes in the densities of prey populations in areas excluding predators are compared with changes in the densities of natural populations in undisturbed control areas (exclosure-only experiments). In studies using this approach, fish were found not to influence the densities of marine invertebrates (Choat and Kingett 1982), or of benthic invertebrates in lakes (Thorp and Bergey 1981) or in streams (Allan 1982b). Results from this type of experiment have been criticized, since the effects (or lack of effects) may be due to the presence of the experimental device used to exclude predators rather than to the absence of the predators (Hulberg and Oliver 1980). The second approach avoids this problem by using experimental containers that both include a known predator density and exclude all other predators (enclosure/exclosure experiments). Since enclosure effects are constant in all treatments, differences between treatments including and excluding predators can be unambiguously attributed to the presence or absence of the predator. Results from studies using this method have shown that fish and crabs depress marine infaunal densities (Virnstein 1977, Kneib and Stiven 1982), plecopteran predators reduce lotic macroinvertebrate densities (Peckarsky and Dodson 1980), and fish reduce total prey biomass as well as mean prey size (Crowder and Cooper 1982).

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There has been little use of field manipulative experiments to investigate biotic interactions in temperate streams, partly because of the importance of factors such as discharge and temperature fluctuations, unstable substrate, and patchy substrate and detritus, and partly because of the difficulty of adequately controlling experimental conditions. At present, the work of Peckarsky and Dodson (1980) is the only experimental test of the importance of a stream invertebrate predator in the field. However, since their results were reported as a community effect (all potential prey species combined), and since prey response is species specific (Peckarsky 1980), there is a need for studies that consider effects at the species level and at prey and predator densities that approximate natural levels.

The first objective of our study was to investigate the influence of the predator *Kogotus nonus* (Plecoptera: Perlodidae) on the densities of its prey in a small stream. The following three questions were posed: (1) Does the presence of the predator influence the composition of the prey community within an enclosure when the prey are allowed to enter and leave the enclosure? (2) Does the observed effect vary if predator density is varied? (3) Does the observed effect vary if background prey density varies?

The second objective was to determine if the results of field manipulative experiments in streams are dependent on the experimental design (enclosure/exclosure vs. exclosure-only experiments). To fulfil this objective, the results from the above experiments were compared with results from a second experimental design in which enclosed areas without predators were compared with unenclosed areas accessible to predators.

Benthic invertebrate communities are strongly influenced by physical factors such as the velocity of the current and the composition of the sediment, detritus, and substrate (e.g., Rabeni and Minshall 1977, Rosenberg and Wiens 1978, Reice 1980). It was therefore considered important to standardize or measure abiotic parameters carefully, so that any treatment differences could be unambiguously attributed to the presence or absence of the predator.

#### STUDY SITE

Experiments were conducted in an unnamed, first-order tributary of Big Hill Creek, located 30 km northwest of Calgary, Alberta, Canada. The stream is spring fed, which results in a relatively uniform discharge throughout the year, and a stable substrate. Water temperatures in the summer (June to August) reach an average maximum of 10.5°C daily and drop to an average of 5.5° at night.

Experiments were conducted in a 2 × 5 m riffle located ≈ 3 km downstream from the stream source. The riffle has an annual mean water depth of 10 cm, a current velocity of 25–35 cm/s, and a substrate predominantly of pebble and small cobble interspersed

TABLE 1. Density of all invertebrates present in the benthic community of the experimental riffle.

Invertebrates	Density (no./100 cm <sup>2</sup> ± SE)	
	June 1982	July 1982
<b>Predators</b>		
<i>Kogotus</i>	1.96 ± .49	1.50 ± .67
<i>Rhyacophila</i>	.33 ± .20	.49 ± .32
<i>Polycelis</i>	10.75 ± 2.76	14.43 ± 6.30
<b>Detritivores</b>		
<i>Baetis tricaudatus</i>	1.78 ± .49	7.01 ± 1.67
<b>Orthoclaadiinae</b>		
<i>Thienemaniella</i>	131.56 ± 32.21	443.78 ± 63.67
<i>Corynoneura</i>	17.33 ± 8.46	43.46 ± 11.59
other Orthoclaadiinae	79.11 ± 30.61	791.46 ± 193.10
<b>Tanytarsini</b>		
<i>Stempellinella</i>	74.67 ± 22.62	73.31 ± 25.17
<b>Large-particle detritivores</b>		
Nemouridae	39.11 ± 7.76	43.62 ± 15.48
Tipulidae	1.30 ± .49	1.48 ± .75

with gravel and sand. Detritus input upstream was primarily from balsam poplar (*Populus balsamifera* L.) and willow (*Salix* sp. L.); grasses were the primary riparian vegetation adjacent to the study riffle. Discharge during the experimental periods ranged from 0.03 to 0.04 m<sup>3</sup>/s, the pH of the water was 8.5, its total alkalinity (as CaCO<sub>3</sub>) was 180 mg/L, and it was 100% oxygen saturated.

#### BENTHIC INVERTEBRATE COMMUNITY

The benthic community is relatively simple in this stream, and so is easily manipulated (Table 1). The composition of the natural community was obtained from five benthic samples taken with a cylinder sampler (12.5 cm in diameter) in the experimental riffle at the end of the June and July experimental periods in 1982. The invertebrate predators that were present were the numerically dominant perlodid stonefly *Kogotus nonus* Needham and Claassen, the caddisfly *Rhyacophila* sp. Pictet, and the triclad *Polycelis coronata* Girard. *Baetis tricaudatus* Dodds was the only mayfly species present. During June and July, the Chironomidae included both Orthoclaadiinae and Tanytarsini. The other components of the community were members of the families Nemouridae and Tipulidae.

In the study stream, *Kogotus* is univoltine and emerges from June to early September at sizes of 14–20 mg dry mass. Nymphs used in the experiments averaged 10.4 ± 0.5 mg ( $\bar{x} \pm \text{SE}$ ) in mass, and ranged from 1.5 to 1.8 mm in head-capsule (intraocular) width. Allan (1982a) reported that, in Colorado, *Kogotus modestus* feeds on both mayfly and chironomid larvae. From preliminary gut-content analyses ( $n = 25$ ), it was found that, in our stream, *Kogotus nonus* nymphs also

consumed larvae of both *Baetis tricaudatus* and Chironomidae.

Although chironomids were present throughout the summer, the relative contribution each species made to the composition of the community differed between the two months (Table 1). In June, the Tanytarsini made up 25% of the total number of chironomids, and *Stempellinella* composed >95% of this group. *Stempellinella* lives in a sturdy tube that it constructs out of sand grains. In July, however, the Orthoclaadiinae made up 95% of the entire chironomid community, about half of which were the free-living *Thienemanniella* and *Corynoneura*. Most of the other Orthoclaadiinae live in thin mucus tubes. A full range of *Baetis* nymphal instars were present in June and July.

## METHODS

### *Experimental design*

*Enclosure/exclosure experiments.*—The effects of *Kogotus* on prey populations were determined by varying predator densities in experimental containers buried in the stream. The considerable difference in the composition of the chironomid prey community between June and July provided an ideal opportunity to test for the effect of the same-sized predators on different densities of prey. When the potential prey consisted of high densities of Orthoclaadiinae and lower densities of Tanytarsini (July 1981 [S. J. Walde, *personal observation*], 1982 [Table 1]), experiments with zero and two predators per container (1981) and zero, one, two, and three predators per container (1982) were conducted. When Orthoclaadiinae were less abundant and Tanytarsini more numerous (June 1982), experimental treatments were zero, one, and two predators per container.

Various enclosure sizes have been used in predator-manipulation experiments. We felt that enclosures should be a size that allowed (1) minimization of variability within and among enclosures, (2) adequate replication, (3) establishment of a representative prey community, and (4) observation of predator effects at natural ratios of predator to prey. The average benthic density of *Kogotus* in June and July was 1 *Kogotus*/45 cm<sup>2</sup> (Table 1); aggregation occasionally produced local patch densities of up to 3 *Kogotus*/45 cm<sup>2</sup>. Containers that were ≈45 cm<sup>2</sup> in area (7.5 cm in diameter) and that included zero, one, two, or three *Kogotus* were therefore the logical choice, provided, of course, that they met the above criteria.

These experiments were designed to test the effect of a predator within a patch, so it was important to view the enclosures as single microhabitat patches of stony substrate. A small enclosure allowed better control over abiotic variables both within and among containers, since large containers are far more likely to have internal heterogeneity of abiotic conditions. In addition, the small size allowed sufficient replication

for statistical testing even after containers that differed greatly in measured abiotic factors were discarded.

Each enclosure contained a representative distribution of the natural streambed substrate, which prey readily colonized in high numbers. Prey were not found clinging to the sides of the containers. Despite the small size of the containers, the surface area of the walls in any case represented <15% of the habitable surface area provided by the substrate. At the end of the experiments, the species abundance within the containers was similar to that in the neighboring benthos (see Fig. 4).

At least two biotic interactions may be present in a predator-prey experiment of this type: the interaction between predator and prey, and the interaction between predators. Since *Kogotus* has exhibited quite aggressive behavior in our laboratory, a treatment that eliminated interference between predators was deemed important. Since the average benthic density was 1 *Kogotus*/45 cm<sup>2</sup>, use of a container 7.5 cm in diameter made this possible. Higher predator-density treatments, which were representative of observed benthic aggregations, reflected both types of interaction. Almost all of the mortality of *Kogotus* in the experiments was in treatments containing two or three predators, suggesting that *Kogotus* does not easily tolerate confinement with conspecifics.

Connell (1974) suggested that minimizing disturbance, establishing adequate controls, and replicating treatments and controls were the keys to successful field experiments. We attempted to satisfy these conditions by establishing as natural a community as possible in small enclosures and by manipulating one variable at a time.

*Exclosure-only experiments.*—In the exclosure-only experiments, the containers that excluded all *Kogotus* were compared with two types of controls, both of which were accessible to predators. In the first type of control, containers with identical substrate, detritus, and prey to those excluding predators were buried in the riffle without screens on top (July 1981). The second type of control consisted of benthic samples from the experimental riffle taken at the conclusion of the exclosure experiments (June and July 1982).

### *Experimental procedure*

Three weeks prior to initiation of the experiments, substrate from a gravel bar was placed in wire baskets in the stream to permit microbial colonization. The experimental enclosures were plastic containers (200 mL in volume, 7.5 cm in diameter, 7 cm deep) with two side windows (4 × 8 cm, 230-μm mesh) to allow water flow, and with removable top screens (1.5-mm mesh) to allow only prey immigration/emigration. The size of the substrate used in the experiments approximated the size distribution of the natural streambed (10% of the substrate, by volume, was 2–4 mm in size; 20% was 4–9.5 mm; 35% was 9.5–16 mm; and 35%

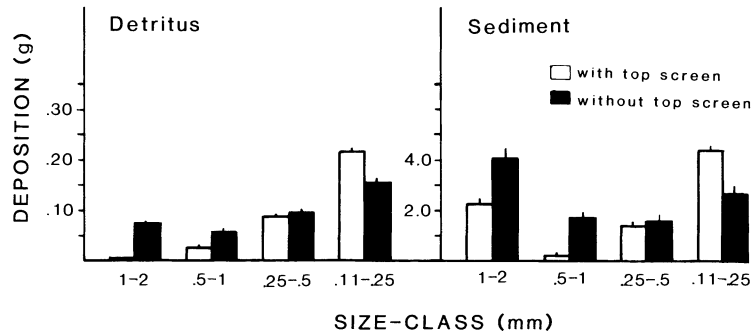


FIG. 1. Detritus and inorganic sediment deposition in experimental containers with and without top screens (July 1981). Error bars are standard errors.

was 16–32 mm). For each replicate, each substrate size-class was measured volumetrically. After macroinvertebrates and detritus were removed, the mixture was placed into an enclosure.

Quantitative benthic samples were taken with a cylinder sampler (12.5 cm in diameter and with 230- $\mu$ m mesh). All predators were removed, and the samples were placed in a cone subsampler (Wrona et al. 1982). A subsample based on previous analyses was placed in each container so that natural, background quantities of detritus and densities of prey would be produced. Five to eight subsamples were preserved for later estimation of initial prey densities. It was found that for species with an abundance of >20 per subsample, standard errors were always <10% and usually <5% of the mean.

In each experiment, screened containers with various densities of *Kogotus* predators and unscreened containers with only a single predator were buried flush with the substrate surface in a uniform portion of the riffle. All treatments were arranged in a completely randomized design (eight replicates per treatment). A Marsh McBirney Model 21 flow meter was used to measure the current velocity 1 cm above the substrate. Water depth and current velocity were measured over every second container at the beginning of each experiment, and water temperature was measured continuously with an immersible thermograph. To ensure that periphyton growth did not hinder colonization or emigration, we scrubbed the top screens of the containers every second day.

After 10 d, containers were removed, and animals and detritus were immediately preserved in 10% formaldehyde. Containers in which predators had died or undue sediment deposition had occurred (ash mass >10 g) were not included in the analysis. Invertebrates of the remaining four to six replicates per treatment were sorted under 10 $\times$  magnification and identified. Organic and inorganic sediments were sieved into four size-classes (106–250  $\mu$ m, 250–500  $\mu$ m, 500–1000  $\mu$ m, 1–2 mm), were dried at 90° to constant mass, and were

ashed at 500° to constant mass. The ash mass and ash-free dry mass of each size-class were determined.

For each experiment, treatments were compared by using analysis of variance and Student-Newman-Keuls multiple range test (Zar 1974). A log ( $x + 1$ ) transformation was performed on the data to stabilize the variance (Elliott 1977). Differences were termed significant at  $P < .05$ .

## RESULTS

### *Physical parameters*

In the enclosure/exclosure experiments, no significant differences in total amounts of detritus or inorganic sediment (<2 mm) deposition were observed among the three experimental periods, although minor differences occurred in size distributions. Comparison among treatments within each experiment showed no significant differences in detritus and sediment quantities or in size distributions. Current velocity (25–33 cm/s), depth measurements (8–12 cm), mean daily maximum water temperatures (10.4°), and mean minimum water temperatures (5.4°) were not significantly different among experimental periods.

In the exclosure-only experiments, however, while containers that allowed ingress and egress of free predators (no screened tops) accumulated approximately the same amount of sediment and detritus in total, there was more coarse and less fine material than in the screened containers (Fig. 1). Benthic samples taken from the same riffle (same current velocity, depth, and temperature) had significantly less fine (<0.5 mm) and more coarse (>1 mm) detritus per unit area than did the experimental containers that excluded predators (Fig. 2).

### *Predator effects*

*Enclosure/exclosure experiments.*—In July 1982, densities of *Thienemaniella* were reduced by 30% in containers with one *Kogotus*, in containers with two predators, densities were lowered by 64%; but there

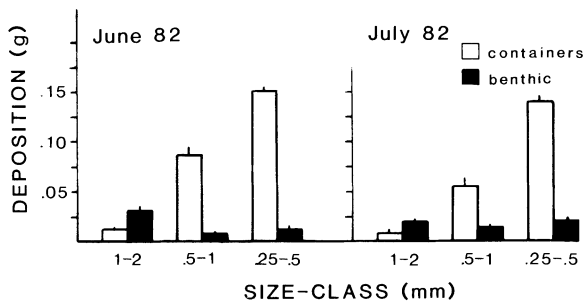


FIG. 2. Comparison of detritus in experimental containers with top screens that excluded predators, vs. the natural benthos. Error bars are standard errors.

were no additional effects in containers with three predators. In the previous year, containers with two predators had a 69% reduction in *Thienemaniella* densities. *Corynoneura* and *Stempellinella* showed no response to the predator in either year. Other Orthocladiinae were relatively rare in 1981 and showed no response to *Kogotus*. However, in 1982, when densities of other Orthocladiinae were high, one predator had no effect, but both two and three *Kogotus* per container reduced prey densities significantly (Fig. 3).

In June 1982, when benthic densities of *Thienemaniella* were only one-third those of July 1982, *Kogotus* had no significant effect on the abundance of *Thienemaniella*, *Corynoneura*, other Orthocladiinae, or *Stempellinella* (Fig. 3). The mortality of *Kogotus* in June was 50%, but in July it was 18%.

*Baetis* was rare in all experiments. There were never more than four *Baetis* per container, and densities were not significantly different among the treatments in any experiment (Fig. 3). Of the other predators in the stream, *Rhyacophila* was absent from the experimental containers, and *Polycelis* densities did not vary significantly among treatments. Densities of the other taxa (Nemouridae, Tipulidae) found in the experimental containers also did not vary among treatments.

*Exclosure-only experiments.*—In the exclosure-only experiments, containers that excluded *Kogotus* were first compared with control containers that permitted *Kogotus* to enter and exit at will (July 1981). In the controls, no significant differences were found in *Thienemaniella* or *Baetis* densities, but there was a decrease in *Corynoneura* densities, a fourfold increase in other Orthocladiinae densities, and a ninefold increase in *Stempellinella* densities (Fig. 4). Additionally, prey densities in containers excluding *Kogotus* were compared with natural densities in the experimental riffle. In both June and July 1982, the natural benthos had lower densities of *Corynoneura* than did the containers excluding predators. No significant differences were observed in *Thienemaniella*, other Orthocladiinae, or *Baetis*. In June 1982, the natural benthos also had fewer *Stempellinella* than the containers had (Fig. 4).

## DISCUSSION

### Standardization of physical parameters

It is critical to any experiment comparing treatments such as predator densities that all other parameters be consistent among treatments. This is particularly difficult to establish in lotic habitats, since current velocity and sediment and detritus deposition regimes may vary drastically within an apparently uniform riffle. In these experiments, even with current velocity and depth as uniform as possible, several replicates were not included in the analysis, because fine-sediment deposition varied. Testing for differences in physical parameters among treatments is imperative, and random placement of containers in an apparently homogeneous riffle does not guarantee consistency.

Comparison of experimental periods is also dependent on consistent physical parameters. In this study, current, temperature, and deposition regimes were very similar in all enclosure/exclosure experiments, and substrate size was standardized among experimental periods as well as among treatments. However, in the exclosure-only experiments, which compared containers with screened tops (predator exclusion) to containers without tops (predator access), absence of the screened tops caused a change in the deposition regime. The quantities of benthic detritus were also very different from the quantities of detritus in experimental containers; thus, neither control in this experimental design was good in terms of physical parameters.

### Exclosure-exclosure experiments

The time needed to conduct a stream colonization experiment has been the subject of considerable debate

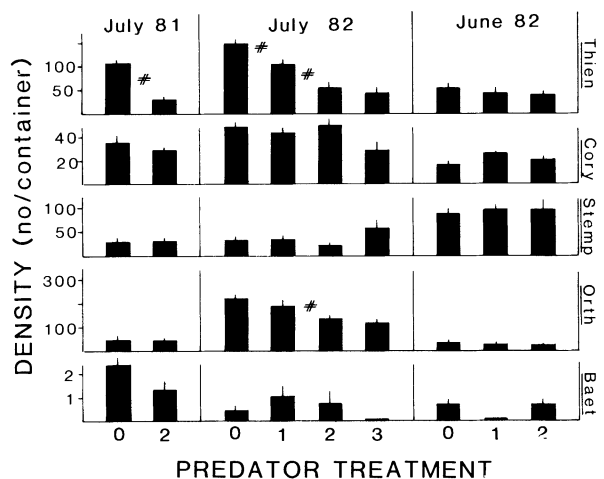


FIG. 3. Response of prey (*Thienemaniella*, *Corynoneura*, *Stempellinella*, other Orthocladiinae, *Baetis*) in predator enclosure/exclosure experiments. Treatments are number of *Kogotus* per container. Error bars are standard errors. # indicates a significant difference ( $P < .05$ ) between adjacent treatments.

(Allan 1975, Nilsson and Sjöström 1977, Shaw and Minshall 1980), since the rapid change in community composition due to species-specific differences in life cycles makes the time needed for adequate colonization difficult to determine. In the present experiment, this problem was circumvented by placing animals into the containers at natural benthic densities. Thus, the changes with time were not due to inadequate initial colonization, but to cumulative predator effects, to changes in life-history patterns occurring naturally in the benthos, or to changes in the detritus and sediment regimes within the containers. Since changes due to life-history patterns and detritus and sediment regimes were the same in treatments excluding and including predators, differences among treatments could clearly be attributed to the predator.

The consistent depression of *Thienemaniella* densities in July 1981 and 1982 suggests that *Kogotus* is likely to influence *Thienemaniella* densities in natural prey patches either by consumption or by increasing dispersal due to predator disturbance or prey avoidance behavior. The fact that three predators per container were not more effective in lowering *Thienemaniella* densities than two predators per container may be due to one or more of the following: (1) increased interference among predators countering the effects of increased predator density, (2) a set number of prey refuges in the containers, below which the prey population could not be depressed, or (3) a fixed encounter rate below which the predator did not actively search for prey. This type of experiment does not permit clear differentiation among these possibilities, but the drop in predator effectiveness (at three per container) does correspond to the limit of commonly observed benthic predator patch densities. Both informal laboratory observation and higher mortality of predators in treatments of high predator density suggest that interference, perhaps similar to that described by Baker (1980, 1981) for zygopteran nymphs, may be an important factor with respect to these species. The fact that a very similar final prey density was observed with two to three predators in July 1981 and 1982, and in all treatments in June 1982, tends to lend support to the prey-refuge or predator-search-rate hypotheses. Benke (1978), using dragonfly larvae, and Crowder and Cooper (1982), using bluebills, similarly found that changes in the structure of prey communities were mediated by the complexity of the habitat or by the presence of refuges.

*Kogotus* did not affect *Stempellinella* densities in any of the experimental periods, even when *Stempellinella* densities were high and other prey were scarce. Thus, it appears that *Kogotus* either does not recognize the *Stempellinella* tube as containing an animal or is unable to extract the animal. The high predator mortality in June, despite high *Stempellinella* densities, further supports the suggestion that *Kogotus* is unable to utilize

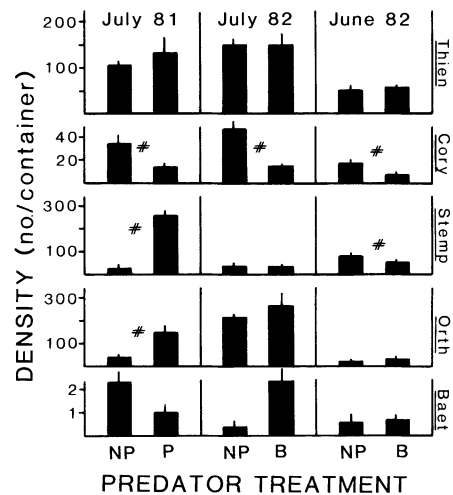


FIG. 4. Response of prey in predator exclusion-only experiments. Predator treatments were: no predator in container (NP), predator allowed access to container (P), and the benthos (B). Error bars are standard errors. # indicates a significant difference ( $P < .05$ ) between adjacent treatments.

this chironomid as a food source. Densities of *Stempellinella* are similar with or without *Kogotus*, which also indicates that *Stempellinella* does not respond to disturbance by this predator by moving out of the area.

The effect on other Orthoclaadiinae seems to be a function of their density, since no predator effects were observed at low prey densities (July 1981, June 1982), but two or more *Kogotus* per container significantly lowered densities in July 1982 (Fig. 3). *Thienemaniella* and the other Orthoclaadiinae showed the same qualitative trend as predator density increased. However, the steeper slope in the case of *Thienemaniella* suggests either higher utilization or a higher disturbance by the predator on this species. The absence of an effect at low prey densities could be due either to a lack of predator response or to a refuge effect.

*Baetis* was not significantly affected in any experiment, despite the fact that preliminary investigation showed it to be an important prey item. This may have simply been due to the extremely low densities observed, and to the difficulty of obtaining significant differences at these levels. On the other hand, *Baetis* may have been responding more strongly to some factor other than the presence of the predator.

Since these experiments were carried out in single-habitat patches, the results cannot be directly interpreted in terms of effects on the entire community. From these experiments we know that *Kogotus* influenced the density of some of its prey within a patch, but whether this effect would be seen over the whole stream bottom in terms of changes in either density or distribution remains a matter for conjecture. The next logical step would be to determine the effect of the

predator on prey densities in areas containing more than one patch.

#### *Exclosure-only experiments*

In the literature there is a trend for predator enclosure/exclosure experiments to show positive predator effects (Virmstein 1977, Peckarsky and Dodson 1980, Kneib and Stiven 1982), while predator exclosure-only experiments show no effects (Thorp and Bergy 1981, Allan 1982b, Choat and Kingett 1982). This can be interpreted in one of two ways. First, the use of enclosures may increase the apparent effect of predation by changing predator or prey behavior, inappropriately selecting predator density, or restricting the predator to a single substrate patch over an unrealistic period of time. In the above experiments, predator density was carefully selected to reflect natural densities. Thus, although it is unlikely that in the natural community the same predator would stay in one patch for ten days, on average there would always be one predator in that patch. The unknown factor in these experiments, as in any experiment that manipulates predators, is whether predator and prey behavior are modified by the enclosure, and therefore, as discussed above, positive results cannot easily be interpreted in terms of effects on entire prey populations.

The second possible interpretation is that unenclosed areas of the riffle may not be adequate controls for treatments that use experimental devices to exclude predators. Since any physical barrier changes the physical environment, and since the extent of predation in open control areas is often difficult to assess, it becomes difficult to attribute results to the absence of predators or to the effects of the enclosure. This has been suggested by marine researchers (Virmstein 1977, Hulberg and Oliver 1980), and the criticism appears equally valid for freshwater ecosystems.

It appears, then, that in predator enclosure/exclosure experiments, there may be some difficulty in interpreting the results in terms of the entire community, but if enclosures are used only to exclude predators, it is difficult to determine if the observed results are even valid in themselves.

In the exclosure-only experiments presented in this paper, containers excluding predators were first compared with containers that allowed free access to unenclosed predators. Since these containers were prepared in exactly the same way as those excluding predators, they were thought to represent the closest possible control. The results, however, if interpreted in terms of predator effects, approach the nonsensical. A ninefold increase in *Stempellinella*, a species apparently not consumed by the predator, as well as a fourfold increase in other Orthocladiinae, would have been attributed to the presence of *Kogotus*, when, in fact, the density differences were probably due to differences in current, detritus, or sediment. Furthermore, no impact on *Thienemaniella* was observed, whereas there was a highly

significant effect in the enclosure/exclosure experiments.

When containers excluding predators were compared with benthic samples from the same riffle, the same trend of no effect on *Thienemaniella* was seen. The consistently higher densities of *Corynoneura* inside containers with top screens, regardless of the number of predators present, suggests that this species responded to the enclosures. *Baetis* densities were not significantly different inside or outside the enclosures.

In general, then, exclosure-only experiments produced very different results from the enclosure/exclosure experiments. Potential prey either were not significantly different inside and outside the enclosures, possibly indicating a low level of visitation by the predator, or showed effects attributable to the presence or absence of the enclosure.

#### CONCLUSIONS

In summary, a lotic invertebrate predator has been shown to lower the abundances of some of its prey (*Thienemaniella* and some other Orthocladiinae) in patches of high prey density. A drop in predator efficiency, probably due to predator interference, prey refuges, or changes in search effort, occurred at a density larger than that corresponding to natural predator patch densities. The predator's effectiveness in reducing prey density was dependent on background prey density, which in turn was dependent on prey life histories. Differences in predator influence were observed between experiments conducted only one month apart, with predators of similar size, and even greater differences would be expected in fall and winter when not only are the prey species different but the predator is smaller.

This experiment has also demonstrated the importance of testing for consistent abiotic parameters. Variable current, substrate, and deposition of inorganic sediment and detritus may obscure or eradicate predator effects, as well as making comparison between experiments difficult. Lack of a comparable abiotic regime in treatments and controls is likely a primary problem with exclosure-only experiments, often making observed results uninterpretable in terms of predator effects.

Caution, therefore, needs to be exercised when interpreting results of field manipulative experiments. Observed differences in results reported in the literature may be due to real differences in the importance of predation among communities, or to variations in experimental procedure or the time of year the experiment was conducted. Experimental designs in which predator effects are not confounded with enclosure effects should be used, whenever possible, to permit straightforward interpretation of experimental results.

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