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INVERTEBRATE PREDATOR-PREY INTERACTIONS

AND STREAM COMMUNITY STRUCTURE

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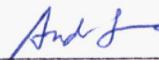
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## ABSTRACT

The importance of an invertebrate predator-prey interaction in structuring a stream community was investigated in a small, spring-fed stream in southwestern Alberta, Canada. Kogotus nonus (Plecoptera: Perlodidae) is a univoltine predator, which while small (July - November) consumes only orthoclads, but feeds on both orthoclads and Baetis tricaudatus (Ephemeroptera) for the remainder of its life cycle.

To determine if Kogotus could influence within patch densities (microdistribution) of its prey, Kogotus density was manipulated in a series of short-term (10 d) field experiments (June and July, 1981-1983). Orthoclad densities were consistently depressed by Kogotus in the July experiments, and Baetis showed a significant response once, indicating that Kogotus could potentially influence prey distributions. However, the absence of any significant effects in the June experiments demonstrated that the influence of Kogotus varies seasonally.

A model suggesting that predator effects are reduced by increasing the harshness of the physical regime was tested by increasing the level of fine sediment in further field predator manipulations. Predator effects were eliminated by the sediment in two experiments, but contrary

to the predictions of the model, addition of sediment actually enhanced the effect of Kogotus on prey densities in one experiment. Consideration of the assumptions underlying the model revealed that the expected outcome is dependent on how the environmental harshness is perceived by the predator relative to the prey. It was concluded that there is no reason to expect harsh regimes to consistently eliminate predator effects unless the regime is harmful to the predator but leaves the prey unaffected.

Behavioral experiments indicated that Kogotus responds to differences in prey density by altering its movement rate. That this response did not lead to a correspondance between predator and prey distributional patterns in the field was attributed to mutual interference between predators and to prey mobility. Close proximity of conspecifics significantly reduced the number of captures by Kogotus, and thus aggregating in prey patches would actually lower capture rates. It was also shown that even a low degree of prey mobility would effectively remove any evidence of attempted aggregation by the predator. It was concluded, therefore, that although there is some response by Kogotus to the distribution of its prey, effective aggregation is prevented by avoidance of other predators and by movement of the prey itself.

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## CHAPTER 1

## INTRODUCTION

There is currently considerable controversy as to what factors determine the structure of ecological communities (eg. Strong et al. 1984). For the purposes of this thesis, a community is defined as an assemblage of species that co-exist in time and space and therefore have the potential to interact with each other. The structure of a community involves the numbers and types of species present, the relative abundance of these species and the distribution of the individuals of each population.

Much of the debate about community structure has centered on the question of whether physical factors or biotic factors (species interactions) are more important in determining community patterns. In a sense this is a false dichotomy since the physical environment sets the template for all communities, limiting the species composition to those species that can tolerate a particular physical regime. Since species can only exist within certain ranges of physical factors, the abiotic environment structures all communities at least to the extent that it eliminates many species. The real question in this debate is whether the communities we see are structured only by these physical

factors, possibly with slight variation due to historical accidents such as colonization events, or whether the community is significantly modified within this framework by species interactions such as competition, predation and mutualism. Modification of community structure can, of course, involve any aspect of structure, addition or deletion of species, changes in relative abundance or alteration of distributional patterns.

Stream communities have traditionally been considered to be structured by physical factors. The majority of stream research to date has consisted of studies that correlate the macro- and microdistribution of stream invertebrates with factors such as temperature, current, discharge regime and substrate size (Reice 1977, 1980; Wise and Molles 1980; Sweeney and Vannote 1978). Even a relatively recent attempt to make generalizations about stream community structure, the river-continuum-concept (Vannote et al. 1980), incorporates only one interaction, detritus processing by invertebrates, completely ignoring the potential effects of predation or competition.

Demonstrating that such species interactions do influence community structure is a two step process. First, it must be shown that the interaction actually occurs, and secondly, that the community would be altered if the interaction were removed. Although there has been some

controversy over the existence of competitive interactions in streams (Hart 1983), there is no question that numerous predator-prey interactions are present. However, there is very little evidence either for or against the suggestion that removing a predator species would significantly affect the remainder of the community. Most experimental field studies of fish predation have failed to show significant community effects (Allan 1982; Reice 1983; Flecker and Allan 1984; Culp pers. comm.). There are two studies to date testing the effect of stream invertebrate predators (Peckarsky and Dodson 1980a; Oberbdorfer et al. 1984), and these experiments showed that plecopteran and trichopteran predators may influence the distribution of their prey, but that the effect varies with locality and season.

There is the potential for two significant interactions in any predator-prey relationship, 1) the predator may influence the prey community (as above) and 2) the prey may influence the predator population. The latter interaction has also received little attention in streams. The effects of prey distribution on the distribution of predators has been investigated indirectly by correlational analyses (Sheldon 1980; Malmqvist and Sjostrom 1984; Hildrew and Townsend 1982), and directly by experimental manipulation only once (Peckarsky and Dodson 1980b). Although food-limitation has been shown to occur for

herbivores (Hart 1981), there have been no attempts to determine if lotic predators are food-limited.

A predator-prey interaction may significantly affect community structure by influencing the density and/or the distribution of the species involved. The work presented in this thesis will concentrate on predator and prey-induced distributional effects, coupled with behavioral responses that have the potential to affect distributional patterns. The stream selected as a study site, Big Hill Springs Creek, has a fairly low number of species present in the benthic community, but is highly productive in terms of species abundances. In addition, it is small enough that in situ experiments were feasible. Kogotus nonus Needham and Claassen (Plecoptera: Perlodidae) was selected as the focal predator species since it was both abundant in the stream and amenable to both field and laboratory manipulation.

The overall objective of this study was to determine if the structure of the benthic community present in Big Hill Springs Creek is significantly influenced by the invertebrate predator, Kogotus. Initially, a sampling program was set up to determine the life cycle of the predator, and the seasonal variation in its diet (Chapter 2). The potential that Kogotus has to influence the distribution and behavior of its prey was then tested in

field and laboratory experiments (Chapter 3), and the outcome of the interaction between these predator effects and an abiotic disturbance was determined in further field experiments (Chapter 4). The possibility that Kogotus was responding to the distribution of its prey was investigated by observing field distributional patterns and predator behavior (Chapter 5), and additional investigations of predator foraging behavior are presented in Chapters 6 and 7.

The statistical tests used in this thesis are described for each set of experiments, and in each case differences are termed significant at  $\alpha = 0.05$ . The abbreviations SE and SD are used for standard error and standard deviation, respectively.

## CHAPTER 2

THE LIFE CYCLE AND DIET OF KOGOTUS  
IN BIG HILL SPRINGS CREEK

## 2.1. The Study Site

Big Hill Springs Creek is a first order (1-2 m wide), spring-fed tributary of Big Hill Creek, located in the transition zone between prairies and foothills in southwestern Alberta (51°15' latitude, 114°23' longitude). It was selected because of its small size and relatively stable discharge regime, the result of draining a small watershed (approx. 5 km<sup>2</sup>). Measured summer discharges varied from .02 to .04 m<sup>3</sup>/s, with winter discharge slightly lower. Summer pH of the water was 8.5, total alkalinity (as CaCO<sub>3</sub>) was 180 mg/l, and the water was 100% oxygen saturated. Temperature was measured continuously with an immersible Ryan thermograph, and mean monthly maxima (average of daily maxima) varied from near 1°C in December and January to over 10°C in June and July (Fig. 2.1). Summer diel temperature fluctuations were on the order of 5°C.

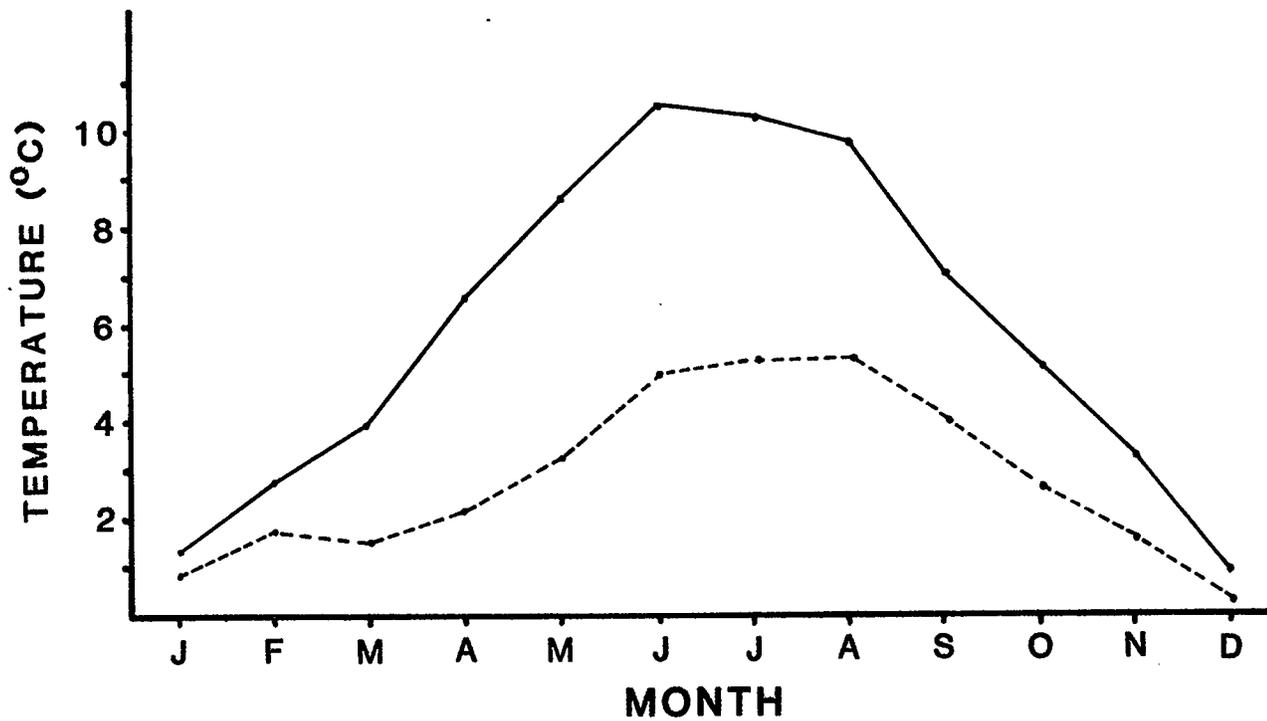


Fig. 2.1. Average monthly maximum and minimum water temperature of Big Hill Springs Creek.

## 2.2. Sampling Program

A benthic sampling program was conducted from June 1981 to June 1984 in the lower 500 m of the 3.5 km stream. Five to ten benthic samples were taken from three riffles (Fig. 2.2) using a cylinder sampler of 12.5 cm diameter and a mesh size of 0.23 mm. Samples were collected to a depth of approximately 8 cm, swirled to remove the heavy inorganics, and quick-frozen in the field with dry ice. Macroinvertebrates were sorted in the laboratory at 12X magnification and the ash-free dry wts of three categories of sediment (.25-.5 mm, .5-1 mm, 1-2 mm) were determined by drying at 90°C to constant wt and ashing at 500°C to constant wt. During the first year (1981-1982) samples were taken semi-monthly during the summer (May - August) and monthly during the remainder of the year. Thereafter, samples were taken monthly during the summer and every three months through the winter. To compare average substrate size ( $\phi$ ), two samples of the complete substrate (8 cm depth) were taken from each riffle. Mean  $\phi$  was calculated as follows:

$$\text{mean } \phi = (\phi[16] + \phi[50] + \phi[84])/3$$

where 16, 50 and 84 are cumulative % by wt.

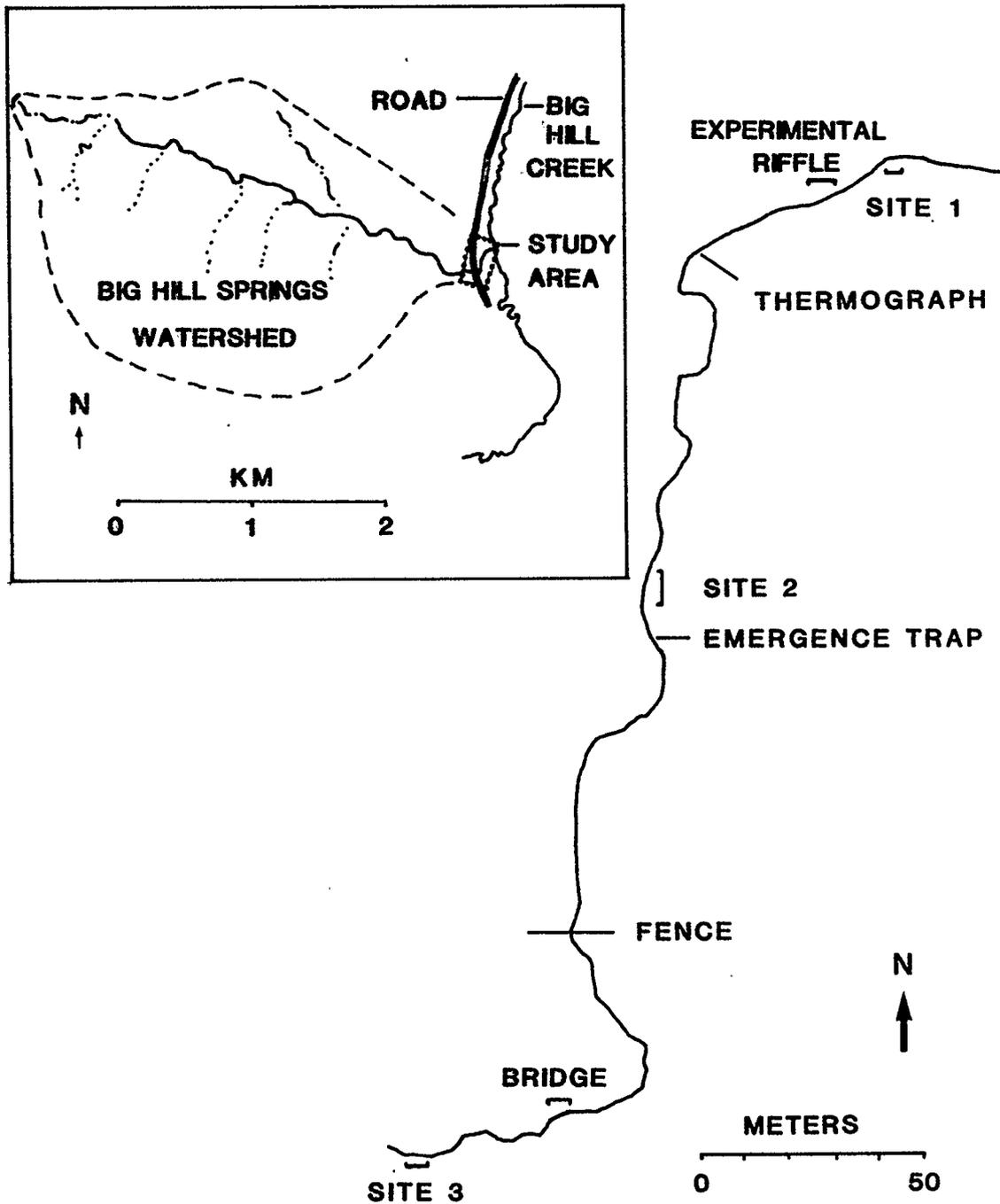


Fig. 2.2. Study area at Big Hill Springs Creek, showing the location of the sampling sites and the experimental riffle.

The upstream riffle (Site 3) was located in aspen (Populus tremuloides L.) forest, while the downstream two sites were in fairly open rangeland, bordered by only a few trees. Despite a nearly closed canopy during the summer, detritus levels were lowest at Site 3 throughout the year (Table 2.1). Site 2 had the coarsest substrate, with both the largest average stone size and lowest amount of fine inorganic sediment (<1 mm). Sites 1 and 3 had similar average substrate sizes, but Site 1 had higher levels of fine sediment.

Site 3 was the only site that was completely ice-free throughout the winter. Site 2 had a number of gaps (0.5-1 m across) in the ice cover, and Site 1 was completely frozen over. All the water in the stream did not freeze during the winter, and the 30 to 50 cm layer of ice and snow was separated from the water by a 10 to 15 cm air space.

Table 2.1. Substrate and detritus characteristics of the three sampling sites.

	SITE		
	3	2	1
Average substrate size (phi)	-3.53	-5.02	-3.27
Fine sediment (<1 mm)			
% of total	21	5	13
kg/m <sup>2</sup>	18.8	5.8	8.3
Detritus (g/m <sup>2</sup> )			
October	13.1	25.9	--
January	16.4	20.5	23.2
April	14.7	29.5	26.7
June	16.5	27.9	23.2

### 2.3. Life Cycle of Kogotus

The predator selected for this study was Kogotus nonus (Plecoptera: Perlodidae), the most abundant insect predator in Big Hill Springs Creek. Larval life cycle information was derived from measurements of head (interocular) width and thorax length of the animals collected in the benthic samples. To determine the numerical relationship between these measurements and body wt, additional Kogotus were collected, wet wt determined alive, the animals quick frozen, measured, dried at 40°C and weighed. The data were fitted to power functions by regressing log(wt) on log(linear measure), and thorax length was found to be the best predictor of dry wt (Fig. 2.3) and of wet wt (Fig. 2.4). A linear relation was obtained for dry versus wet wt (Fig. 2.5).

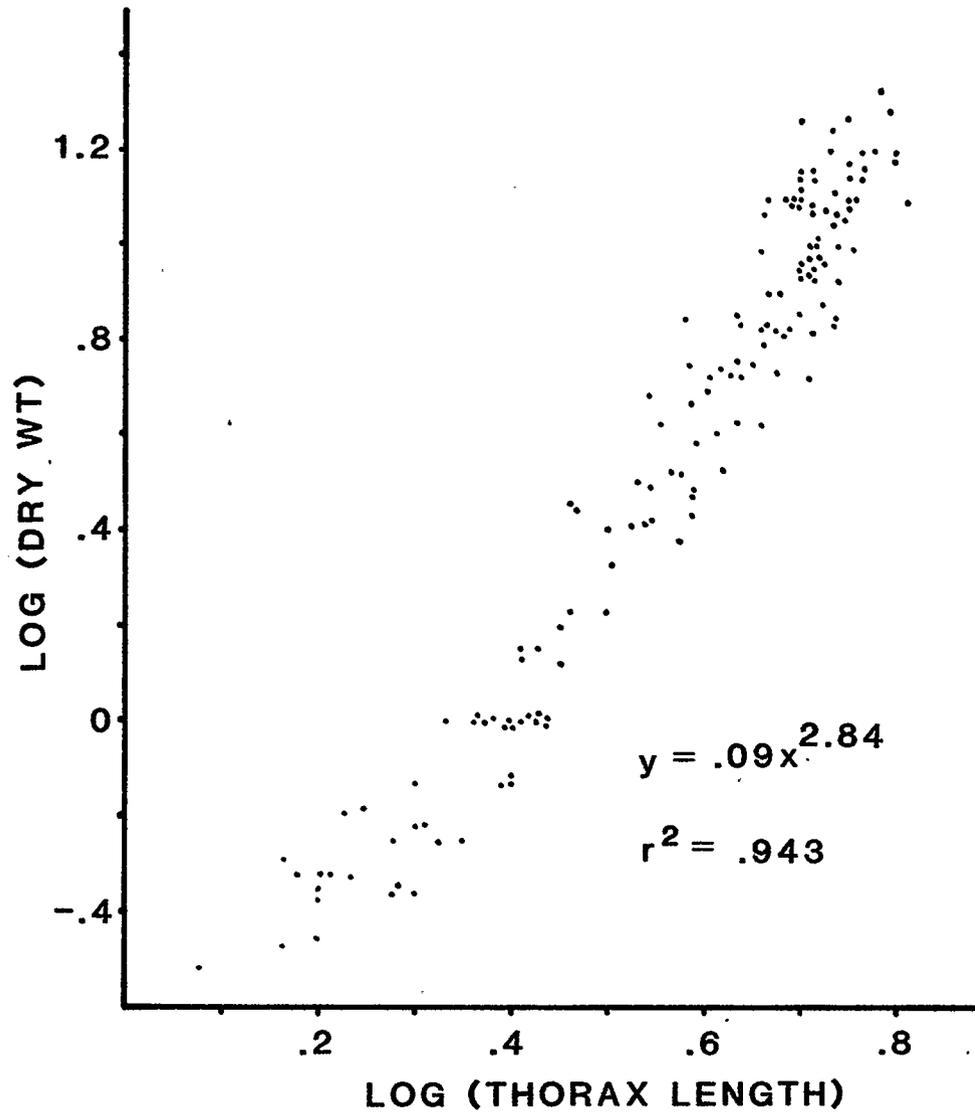


Fig. 2.3. Plot of log [thorax length (mm)] versus log [dry wt (mg)] for 150 *Kogotus*, and fitted power function for thorax length (x) versus dry wt (y).

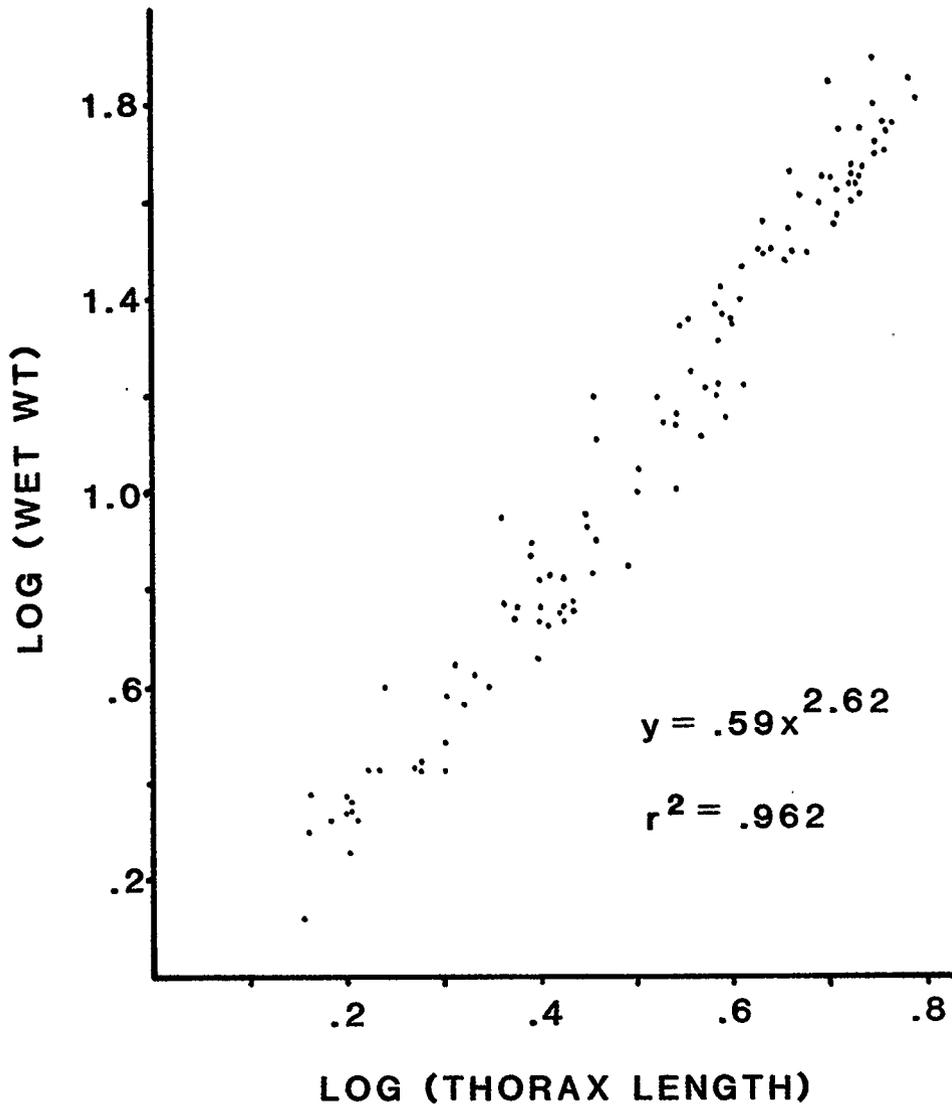


Fig. 2.4. Plot of log [thorax length (mm)] versus log [wet wt (mg)] for 100 *Kogotus*, and fitted power function for thorax length (x) versus wet wt (y).

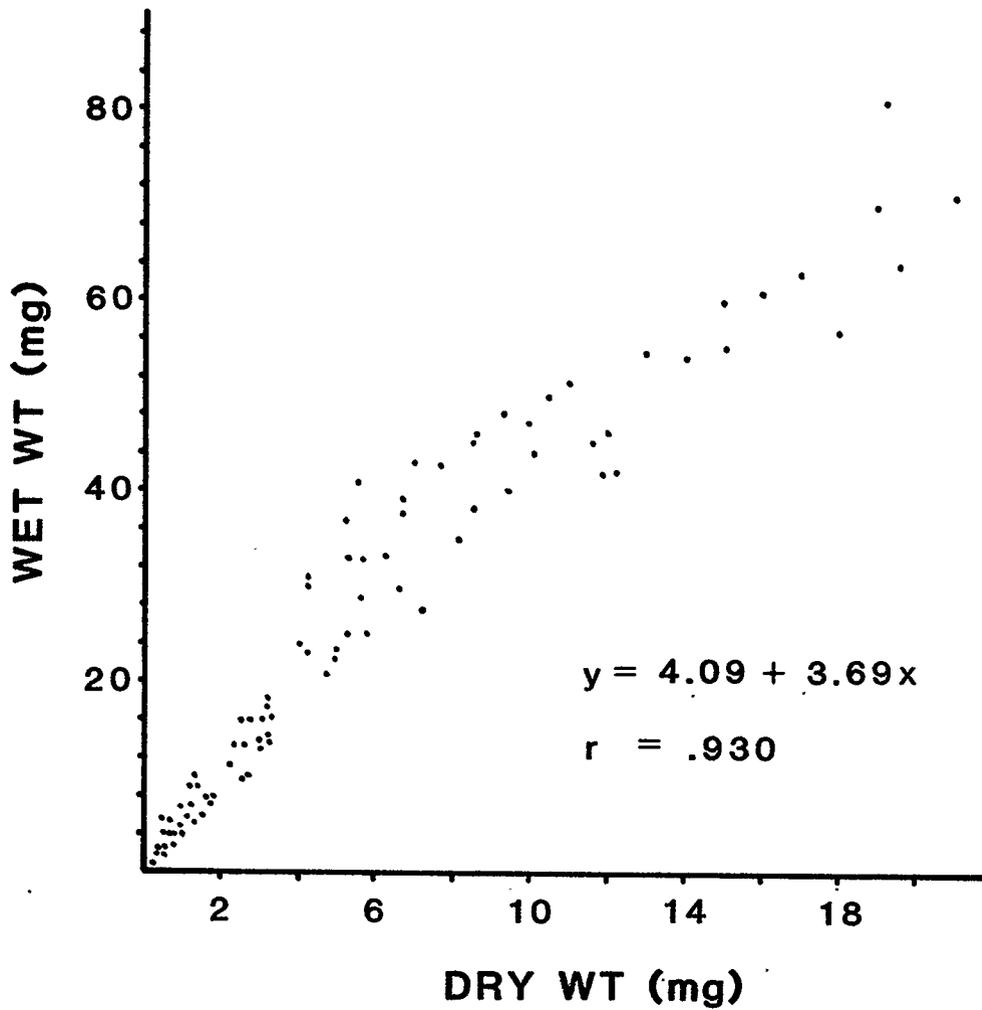


Fig. 2.5. Plot of dry wt (x) versus wet wt (y) for 100 Kogotus.

Kogotus is univoltine, emerging from June to August in Big Hill Springs Creek (Fig. 2.6). The ratio of adult males to females did not vary significantly from unity (chi-squared test with 70 animals,  $p > .10$ ). Early instar larvae grew rapidly from July to October, increasing their wt by more than 10 fold (Table 2.2). During the winter, larval growth rates were much lower, increasing as temperatures increased in spring. Larval size did not vary significantly between sites (Fig. 2.7).

Although first instars started to hatch in summer, peak benthic densities of Kogotus were reached in December at the upstream site, and progressively later in the season at sites further downstream (Fig. 2.8). Furthermore, while Kogotus was collected from Site 3 as early as July, it did not appear at Site 2 until October, and at Site 1 until December (Fig. 2.8). This pattern cannot be attributed to later hatching at the downstream sites, since downstream Kogotus were of similar size to those found upstream. A possible explanation is that the major oviposition and hatching sites are upstream, and that there is a net displacement of larvae downstream throughout the year. While downstream displacement by drift has been proposed as part of a colonization cycle (Muller 1982), there is no documentation in the literature to date that a net downstream displacement actually occurs.

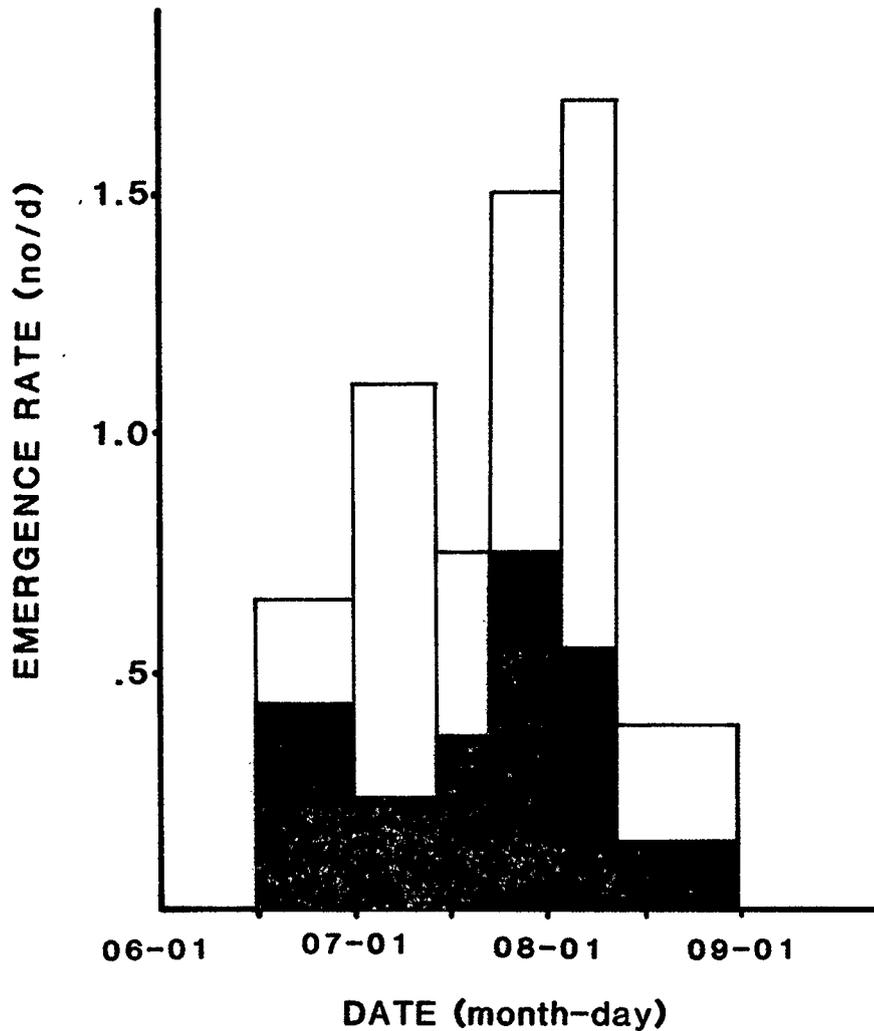


Fig. 2.6. Pattern of *Kogotus* emergence as determined from bankside emergence trap collections. Shaded areas are males, clear areas females. No *Kogotus* adults were found in collections prior to 06-15 or after 09-01.

Table 2.2. Seasonal change in growth rate of Kogotus absolute increase (mg gained/day) and increase relative to original body size (mg gained/mg body wt) per 3 month period, with average maximum and minimum temperature ( $^{\circ}\text{C}$ ) over each time period.

MONTH	ABSOLUTE INCREASE				RELATIVE INCREASE	AV. TEMP	
	81/82	82/83	83/84	AV		MAX	MIN
07-10	.003	.002	.001	.002	10.6	8.18	4.52
10-01	.003	.004	.003	.003	2.7	2.48	1.36
01-04	.007	.007	.010	.008	2.4	3.63	1.57
04-05	.026	.011	.022	.020	4.8	7.65	2.65
05-06	.093	.101	.065	.086		9.57	4.09
06-07	.031	.051	--	.041		10.33	5.09

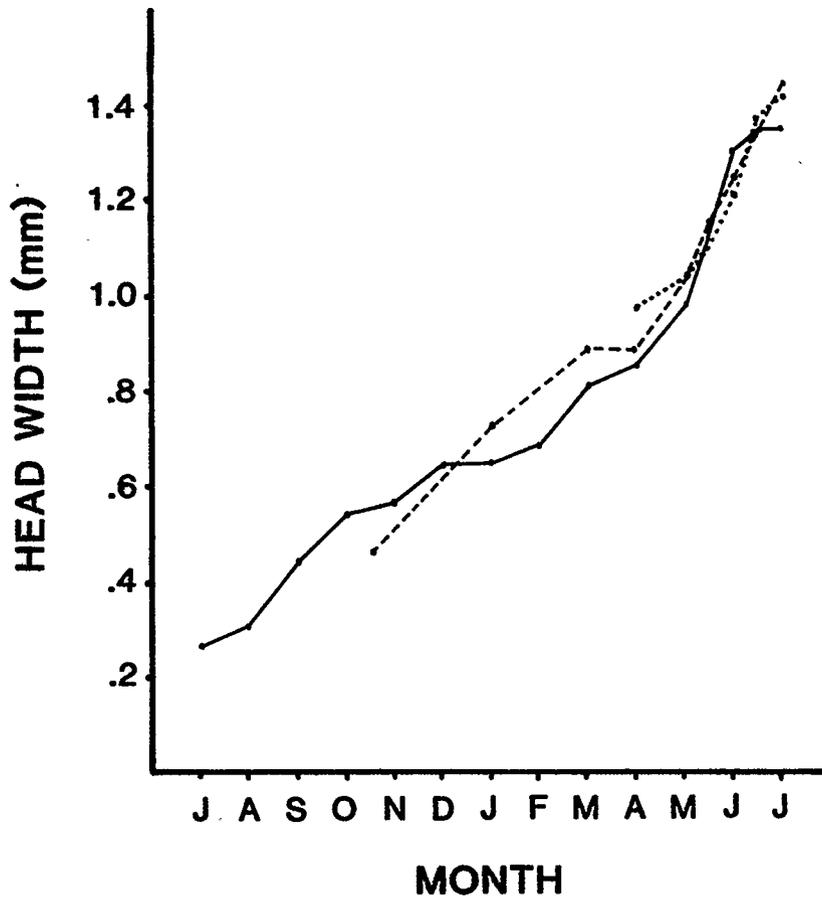


Fig. 2.7. Average head width of *Kogotus* collected from Site 3 (—), Site 2 (---) and Site 1 (···) (1981-1982).

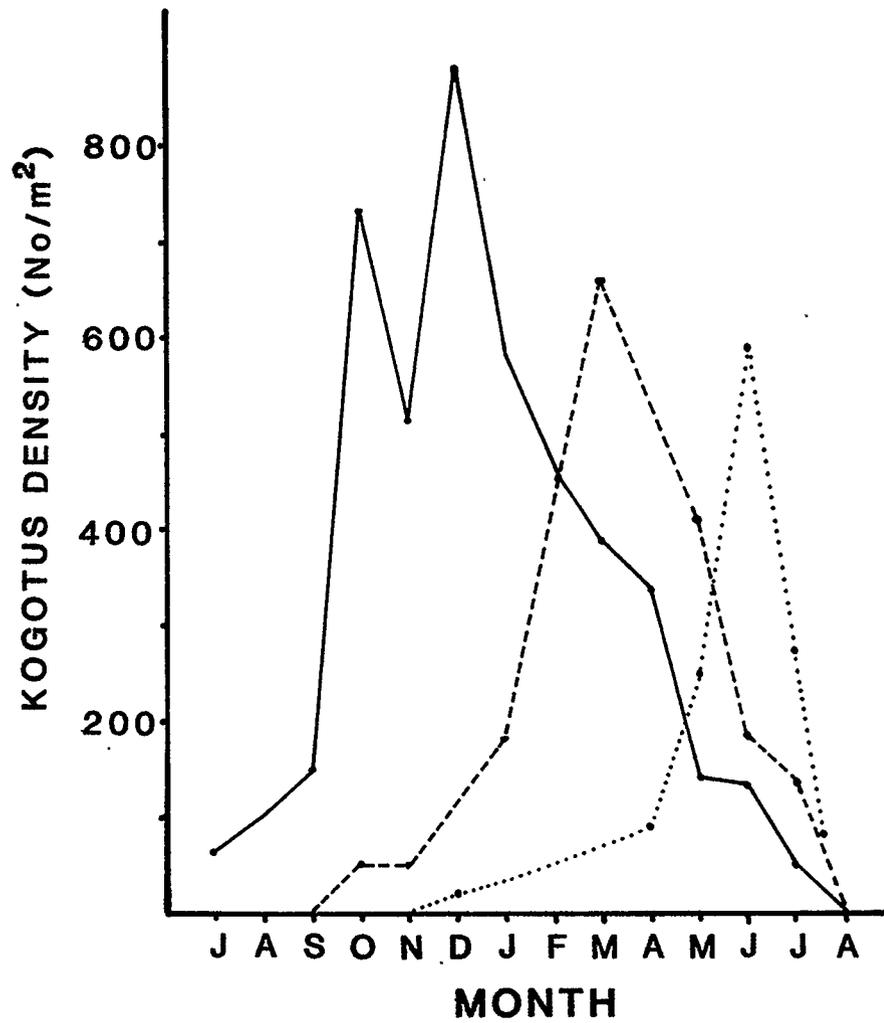


Fig. 2.8. Seasonal (1981-1982) change in Kogotus density at Site 1 (···), Site 2 (---) and Site 3 (—).

#### 2.4. Seasonal Variation in the Diet of Kogotus

To determine seasonal changes in the diet of Kogotus, the foreguts of animals collected in the sampling program (minimum of 20 per date) were dissected out, mounted on slides and the contents identified under 40X magnification. As Kogotus is an engulfer and only the foregut was examined, the consumed prey were frequently whole and could almost always be easily identified to family.

The prey consumed by Kogotus consisted almost entirely of two taxa, Baetis tricaudatus (Ephemeroptera) and the chironomid subfamily, Orthoclaadiinae. All other taxa combined occurred in only 1.5% of the guts examined (Table 2.3). The diet of a closely related species, Kogotus modestus (Banks), has also been shown to consist primarily of Ephemeroptera and Chironomidae (Allan 1982).

Table 2.3. Occurrence of prey other than Baetis or Orthocladiinae in the 1655 Kogotus guts analyzed for seasonal changes in diet.

TAXON	NO. OCCURENCES	% OF TOTAL GUTS EXAMINED
Nemouridae	12	0.73
Tanytarsini	5	0.30
<u>Kogotus</u>	3	0.18
Ostracoda	2	0.12
Oligochaeta	1	0.06
Tricladidae	1	0.06
Tanypodinae	1	0.06
	-----	-----
Total	25	1.51

The proportion of Kogotus individuals feeding on each of the two prey types varied both with season and with sampling site (Fig. 2.9). At all sites, small instars (August - November) fed almost exclusively on Orthoclaadiinae, even though in late fall (October - November), there were two to four times as many Baetis as orthoclads at the upstream site. In mid-winter (December - February) Baetis began to be utilized, although to a much greater extent at the most upstream site than at Sites 1 and 2. Consumption patterns were similar at all sites in spring (March - May), with the two prey types found in nearly equal numbers of Kogotus guts. In summer (May - July), a greater proportion of the guts of the upstream Kogotus larvae contained Baetis, while at the downstream sites, more Kogotus utilized Orthoclaadiinae.

The site to site differences in gut contents can be explained by differences in prey densities. Site 3 showed a marked increase in Baetis density in mid-winter, reaching densities eight times greater than that seen at Site 2 (Fig. 2.10). The December - February increase in Baetis consumption at the upstream site was probably just a response to a suddenly very abundant food supply. Likewise, in summer, the downstream sites experienced very high orthoclad densities, and this prey formed the major component of the diet of Kogotus (Fig. 2.11).

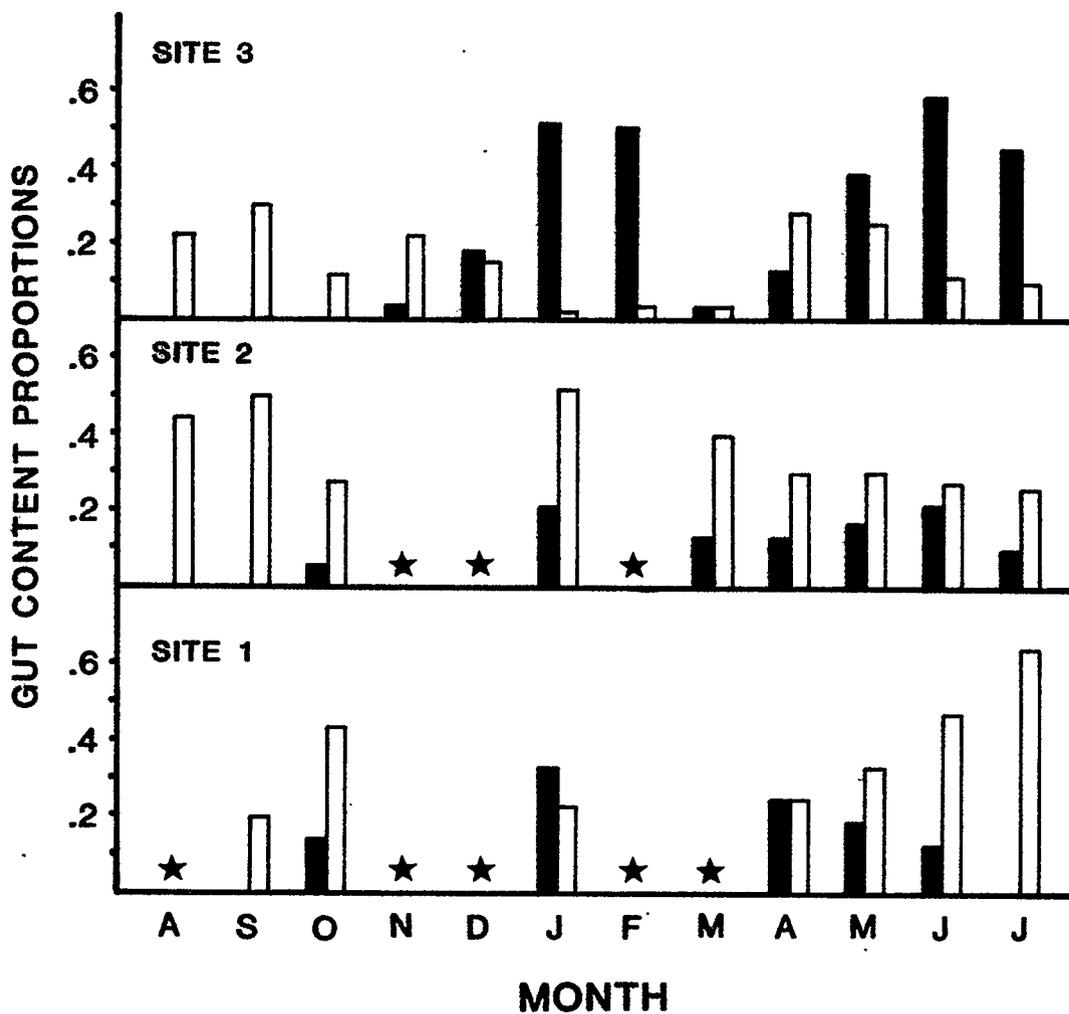


Fig. 2.9. Proportion of *Kogotus* guts containing *Baetis* (shaded bars) and Orthoclaudiinae (clear bars). Months for which no data was obtained are indicated by stars.

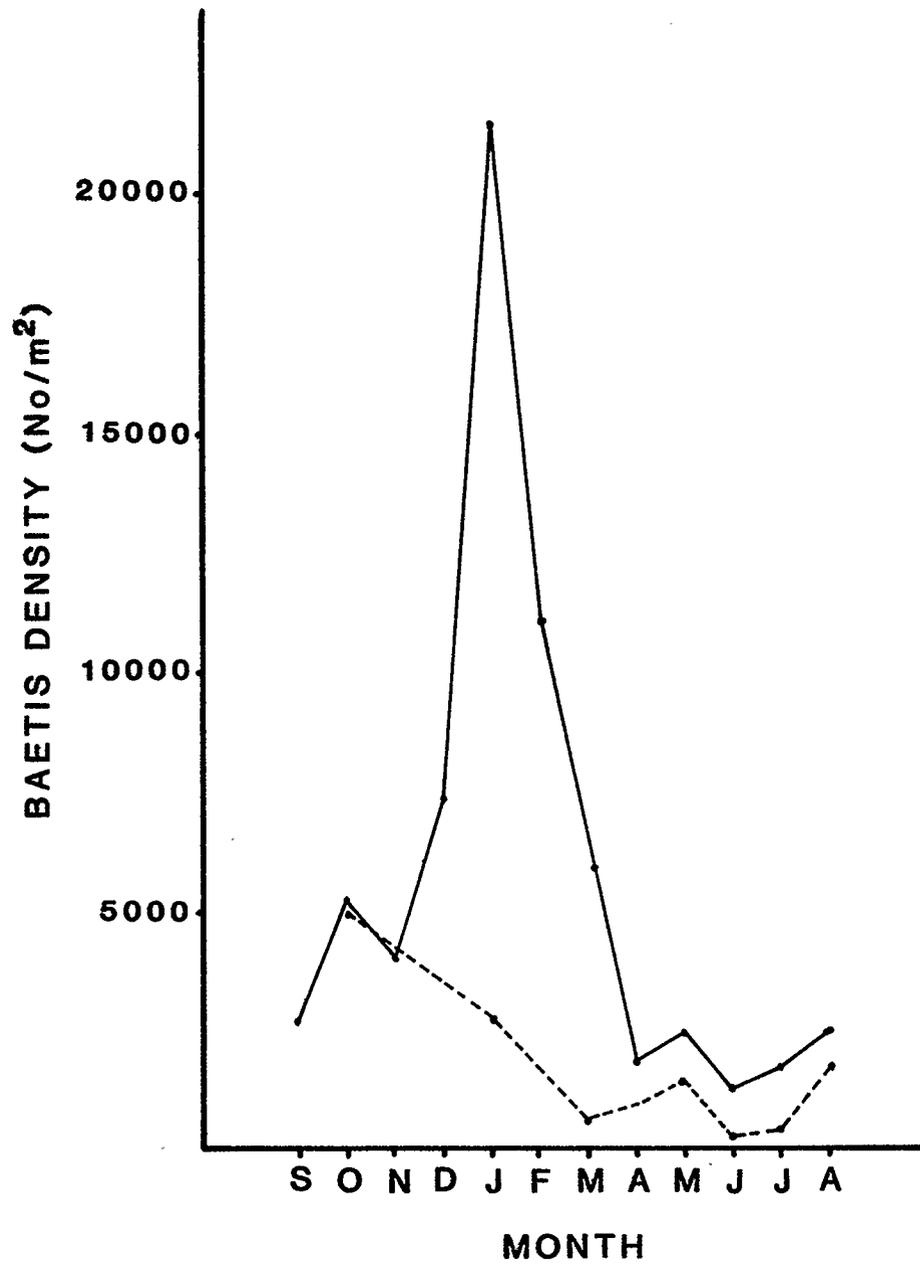


Fig. 2.10. Seasonal change (1981-1982) in Baetis density at Site 2 (---) and Site 3 (—).

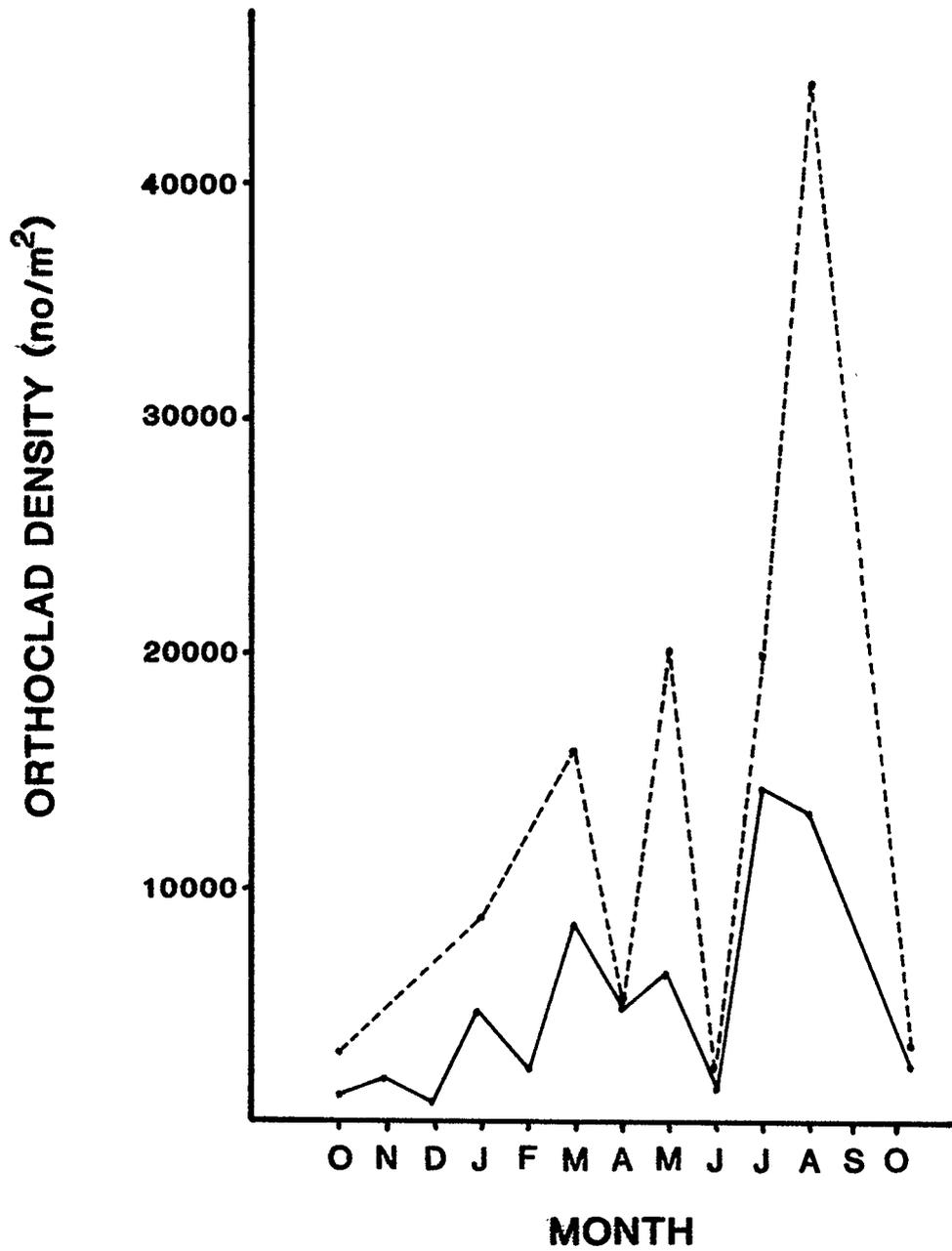


Fig. 2.11. Seasonal change (1981-1982) in Orthocladiinae density at Site 2 (---) and Site 3 (—).

To determine if the relative abundance of the two food types in the diet of Kogotus was a simple reflection of measured benthic abundances, an electivity index, Chesson's (1978) alpha, was calculated for Sites 2 and 3. This index was selected since it is unaffected by the changes in the relative abundance of food types, making comparisons between different dates possible (Lechowicz 1982). Proportions of the two prey types in the guts of Kogotus and in the benthic samples were compared statistically using a chi-square test (Lechowicz). As expected, early instar Kogotus were shown to feed disproportionately on Orthoclaadiinae (Fig. 2.12). This may indicate that small Kogotus are likely unable to capture or subdue the very active Baetis. At the downstream site, feeding throughout the rest of the year was approximately in proportion to background densities. At Site 3, however, Kogotus fed more heavily on Baetis than would be predicted from benthic densities alone.

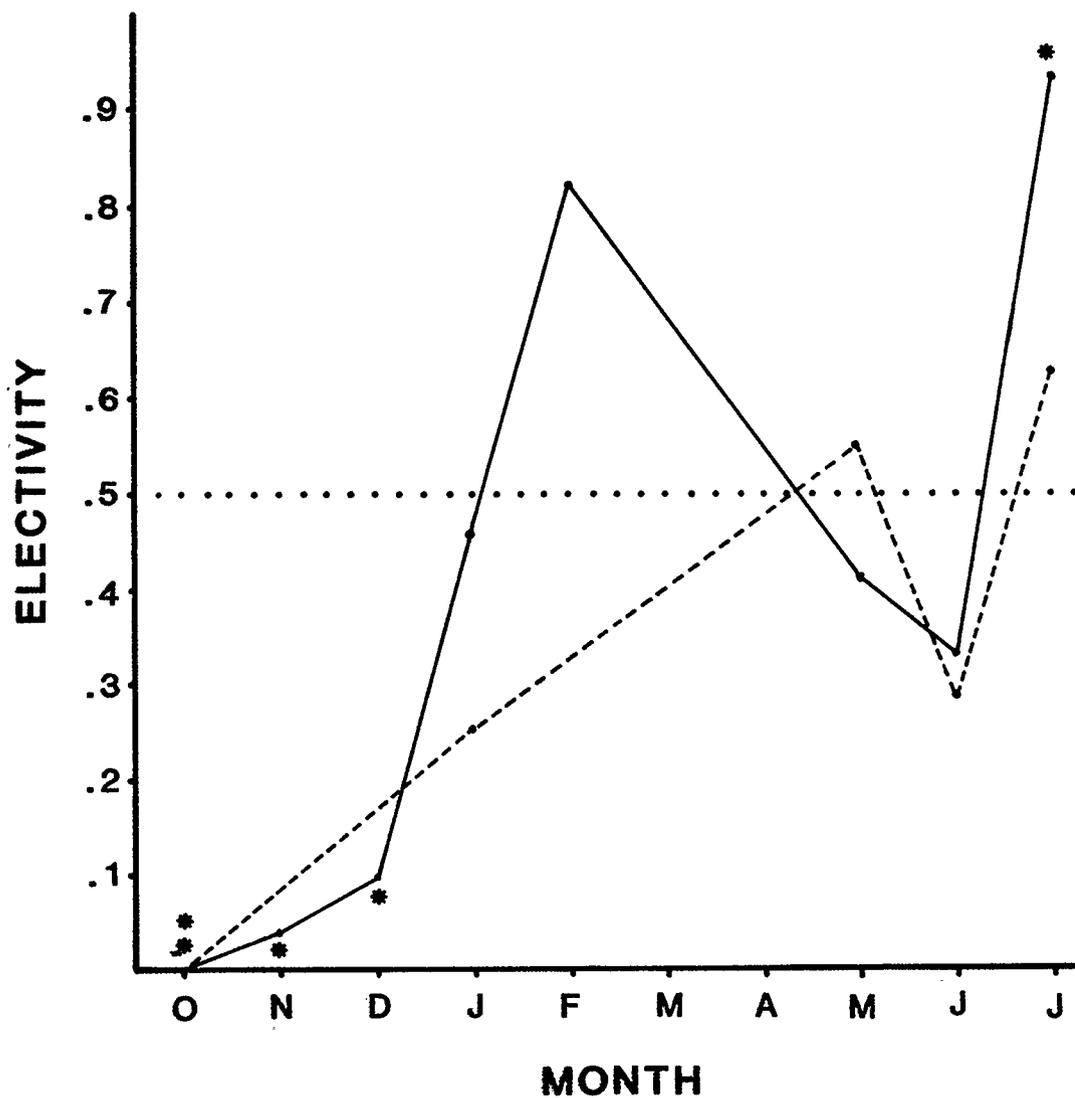


Fig. 2.12. Seasonal variation (1981-1982) in prey electivity by *Kogotus* at Site 3 (—) and Site 2 (---). Values greater than 0.5 indicate that *Baetis* was taken more frequently than predicted by its abundance and values less than 0.5 indicate that Orthocladiinae were taken disproportionately. Asterisks indicate points that are significantly different from the 0.5 line.

A possible explanation is that the high Baetis densities caused Kogotus to key in on the microhabitat occupied by Baetis (tops of stones) as opposed to that of the orthoclads (under stones). If Kogotus are largely occupying one microhabitat or the other, the frequency of occurrence of both Baetis and Orthoclaadiinae in the same gut should be lower than if encounters were random. This hypothesis was tested by a chi-squared test (Table 2.4), and it was found that at Site 3, Baetis and Orthoclaadiinae did co-occur in the guts significantly less frequently than would be expected on the basis of random encounters. This result lends indirect evidence to the suggestion that at Site 3, where Baetis was very abundant, Kogotus was actually altering some aspect of its foraging behavior. At the other sites, however, where orthoclads predominate, the co-occurrence patterns cannot be differentiated from a random-search hypothesis.

Table 2.4. Chi-squared tests (with Yates correction) for co-occurrence of Baetis and Orthocladiinae (Orth.) in Kogotus guts.

SITE	ORTH.	<u>BAETIS</u>	NEITHER PREY	BOTH PREY	EXPECTED BOTH PREY	CHI SQUARE	p
3	94	160	428	11	25.8	22.30	<.001
2	204	41	365	21	22.1	0.03	>.75
1	137	25	172	12	16.0	1.77	>.10

Gut-through time was measured in the laboratory by starving individual predators for 72 h, allowing them to consume one Baetis, and placing them in chambers at either 5° or 10°C. Individuals of three size classes (5-20 mg, 20-40 mg, and 40-60 gm wet wt) were killed after 4, 8, 16, 24 and 48 h, and the guts examined to determine when the food passed out of the foregut, and when the entire gut was cleared. Time to pass through the foregut was 16 to 24 h, except for small Kogotus at 5°C where the prey was still recognizable in the foreguts of some individuals after 24 h (Table 2.5). Food passed through the entire gut in 48 h at 5°C and in 24 to 48 h at 10°C. Measuring passage time of single prey items likely produced a maximum value for gut-through time, since continued consumption may have speeded up passage. However, as more than one Baetis was infrequently found in the guts of field collected Kogotus, field passage times probably approach this maximum.

A large proportion of the examined guts of Kogotus (15 to 75%) were completely empty, containing no remnants of ingested food (Fig. 2.13). These animals had not eaten, therefore, for at least 24 h prior to capture, indicating that food supply could potentially limit the growth rate of Kogotus individuals, as well as contribute to the population's mortality schedule. Upstream and downstream sites showed similar patterns of numbers of empty guts.

Table 2.5. Time for prey item to pass through foregut and hindgut for three sizes of Kogotus at two temperatures.

TEMP (°C)	KOGOTUS (mg wet wt)	SIZE wt)	GUT THROUGH FOREGUT	TIME (h) HINDGUT
5	5-20		24+	48
	20-40		24	48
	40-60		16	48
10	5-20		16-24	24
	20-40		16-24	24-48
	40-60		16-24	24-48

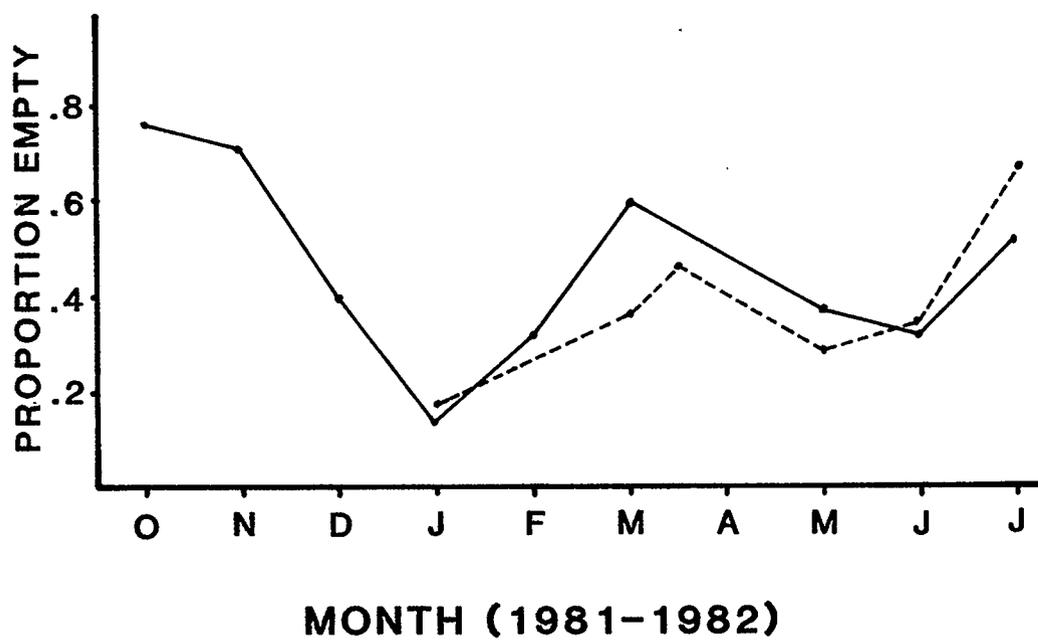


Fig. 2.13. Proportion of *Kogotus* guts that contained no particulate material for Site 3 (—) and Site 2 (---).

## CHAPTER 3

INFLUENCE OF KOGOTUS ON THE PREY COMMUNITY

A predator can alter the structure of a prey community by influencing the density of one or more species or by affecting species distributions. Density effects appear to be most frequently observed, and have been presented in a variety of ways. Mosquito larvae have been shown to reduce the density of protozoans in small rainwater catchments (Maguire et al. 1968), while a turbellarian appears to lower mosquito densities in rice fields (Case and Washino 1979). Fish have been demonstrated to eliminate some species of corixid (Macan 1965; Henrikson and Oscarson 1978) and a species of Chaoborus (von Ende 1979) from ponds. More complex effects resulting from density changes, such as changes in diversity, species composition and size distribution have also been reported. Removal of a starfish predator in the rocky intertidal resulted in a less diverse prey community, as predation pressure on the competitively dominant prey was released (Paine 1966). Rotifers increased in abundance as Chaoborus decreased the density of their microcrustacean competitors (Neill 1984). A shift from large mobile prey to smaller sedentary forms was observed with the addition of fish to experimental

ponds (Hall et al. 1970; Crowder and Cooper 1979), and larger species of zooplankton are present in ponds without Chaoborus or salamanders (Sprules 1972; Dodson 1974).

Shifts in prey microhabitat usage has been observed to occur in the presence of predators. This may occur either by the elimination of prey from certain habitats due to consumption, or by a prey behavioral change in response to the presence of the predator. In the presence of dytiscids, Daphnia were found to be more numerous at the bottom of the water column (Arts et al. 1981), while minnows avoided predatory fish by remaining in structurally more complex habitats (Fraser and Cerri 1982). Mayflies have been shown to avoid areas containing predatory stoneflies even when the predators are not permitted to feed (Peckarsky and Dodson 1980a). Thus many researchers, working in a variety of aquatic habitats have concluded that predators are a significant determinant of community structure. What type of evidence have they used to reach these conclusions?

The first method has been estimation of field consumption rates from gut content analysis or laboratory feeding experiments (Dodson 1972; Federenko 1975; Allan 1983). The potential impact of the predator population on prey density is determined, and the predator categorized as a significant or insignificant factor in determining the prey mortality schedule. While this approach can produce

interesting estimates of the contribution of predation to total prey mortality, no predictions about prey population dynamics in the absence of the predator are possible. The predator may simply be cropping those prey that would otherwise die from other factors, and thus it is impossible to predict from knowledge of feeding rates alone, whether removal of the predator would alter prey density.

A second approach has been to compare the prey communities of similar habitats that naturally occur with or without predators. Much of the work in high altitude zooplankton communities has been of this type (Sprules 1972; Williams 1980). The major shortcoming of this approach is that the abiotic factors determining the presence or absence of predators in particular habitats may also be influencing the distribution of the prey.

A third approach has been the manipulation of predators and/or their prey in the field. If carefully conducted, this method has the potential to less ambiguously demonstrate what role a predator plays in determining community structure. There are still numerous problems with interpretation of these results, particularly with respect to the scale and design of the experimental manipulation. The scope of interpretation possible from this approach will be discussed in more detail later in this chapter.

Most of the examples cited thus far in support of the contention that predators do influence community structure come from work done in lentic freshwater systems. Community structure in streams has traditionally been attributed to abiotic factors such as current (Reice 1977), substrate (Reice 1980), temperature (Sweeney and Vannote 1982), in conjunction with detritus input and distribution (Cummins 1974). Gut content analysis has been used to determine the diet of predators (Siegfried and Knight 1976) and in a few cases feeding rate (Allan 1983). There have been very few attempts to use field manipulative experiments to look at the importance of predation. Allan (1982), Reice (1983), Flecker and Allan (1984) and Culp (pers. comm.) manipulated fish densities, and observed no change in benthic densities or biomass. Flecker (1984) found that sculpins lowered chironomid densities. Invertebrate predators (Plecoptera) have been shown to reduce prey colonization of field enclosures (Peckarsky and Dodson 1980a), and to reduce the density of shredders in leaf packs (Oberndorfer et al. 1984).

Abiotic factors certainly influence stream community structure by eliminating species with physiological requirements not met by the particular environment. However, it is possible that predators further limit the distribution and/or density of some species, thus modifying these abiotically structured communities.

The overall objective of the studies presented in this chapter was to determine if the perlodid stonefly, Kogotus nonus plays a significant role in determining the structure of the benthic community in Big Hill Springs Creek.

Evidence of the importance of Kogotus in this stream will be presented in two sections:

- 1) Field experiments to determine if Kogotus affects within-patch densities of prey.
- 2) Laboratory experiments to determine if Kogotus affects the behavior of Baetis, one of its prey.

### 3.1 INFLUENCE ON PREY DISTRIBUTION

#### Introduction

Field experiments have two advantages over other methods of determining cause and effect relationships in the environment. First the effect can be less ambiguously attributed to the factor in question if this factor is manipulated in an experiment than if relationships are postulated on the basis of observations, correlations or comparisons made in the field. Secondly, field experiments are generally superior to laboratory experiments in the degree to which the results can be applied to natural ecosystems. Field experiments use a protocol that is actually the reverse of that employed in laboratory experiments, where the one factor of interest is varied, while all other aspects of the environment are rigidly controlled. In the field, the factor of interest is controlled, possibly at several levels, while all other factors are allowed to vary naturally (Connell 1974).

Workers conducting manipulative experiments in freshwater habitats have reached different conclusions as to whether predators do significantly affect benthic community structure (Table 3.1). By far the majority of these experiments have been in ponds, and of these, most experiments

Table 3.1. The importance of predation in benthic prey communities as determined by field experiments manipulating predator density.

AUTHOR	PREDATOR	REPS	EXPERIMENT	EFFECTS ON PREY
	INVERTEBRATE		LOTIC	
Peckarsky & Dodson 1980a	Plecoptera	6-25	Cages with free, restricted or no predators (3 d)	Dec prey density with free and restricted predators
Oberndorfer et al. 1984	Plecoptera Trichoptera	?	Cages with/without predators in 3 seasons (2 months)	Dec no. shredders and leaf processing rates
			LENTIC	
Davies 1969	Odonata Newts	1	Prey added to pond, exposed/not exposed to predators (2 wk) (2 exp'ts)	Prey eliminated
Hall et al. 1970	Hemiptera Odonata	5-9	Ponds with/without predators removed (2 yr)	Size distribution shift Dec biomass zooplankton
Benke 1978	Odonata	2	4x4 m pens with/without removal of early and late sp. (6 months)	None Strong cage effects
Benke et al. 1982	Odonata	1	4 predator levels in 21 cages (6 months)	None Treatments not maintained
Thorp & Cothran 1984	Odonata	9-12	4 predator levels in 21 cages (6 wk)	Density and no. species highest at intermediate predator level

Table 3.1. (Continued)

AUTHOR	PREDATOR	REPS	EXPERIMENT	EFFECTS ON PREY
	VERTEBRATE		LOTIC	
Allan 1982	Fish	1	1 fish removal area (1000 m), 2 controls, (4 yr)	None
Reice 1983	Fish Salamanders	5	Baskets (.6m <sup>3</sup> ) allowing/ not allowing vertebrates access (2 months)	None
Flecker & Allan 1984	Fish	8	Fish exclusion cages (.4m <sup>2</sup> ) vs. open controls (18 d)	Little effect
Flecker 1984	Fish	4	4 predator levels in cages (.4m <sup>2</sup> ), plus open controls	Lowered chironomid densities
Culp pers. comm.	Fish	1	4 levels fish in troughs (3 wk)	None

Table 3.1. (Continued)

AUTHOR	PREDATOR	REPS	EXPERIMENT	EFFECTS ON PREY
	VERTEBRATE		LENTIC	
Hayne & Ball 1956	Fish	1	Fish in one pond for 2 mo, transferred to second for 2 mo	Higher benthic productivity Lower standing crop
Hall et al. 1970	Fish	5-9	2 levels of fish in experimental ponds (1yr)	Species shift No biomass change
Kajak 1980	Fish	3	Enclosures (.4m <sup>2</sup> ) excluding fish compared to natural benthos	Lower densities
Menzie 1981	Fish	4	Fish excluded from .5x1 m cages (2 wk)	Lower odonate, higher chironomid densities
Thorp & Ber- gey 1981a,b	Fish	36	Fish & turtles excluded from 2x2 m cages (3 mo)	None
Crowder & Cooper 1982	Fish	2	Fish in 2 of 4 quadrats in each of 3 ponds (2 mo)	Species shifts, inc abundance, dec biomass
Gilinsky 1984	Fish	3	3 fish & macrophyte levels in 2x3 m cages (1 yr)	Fewer species, lower abundances of some sp.
Morin 1984	Fish & turtles	4	1.4 m pens with/without predator access (3 mo)	Inc abundance, especially large odonates

have clearly demonstrated significant effects of fish predation (Hayne and Ball 1956; Hall et al. 1970; Kajak 1980; Menzie 1981; Crowder and Cooper 1982; Morin 1984; Gilinsky 1984) while a few report no effect (Thorp and Bergey 1981a, 1981b). Similarly, invertebrate predators have been reported to significantly influence their prey in some cases (Davies 1969; Thorp and Cothran 1984), to have only minimal impact in others (Hall et al. 1970), or no effect (Benke et al. 1982).

There has been little use of field manipulative experiments in streams to evaluate the importance of predator-prey interactions. This is partly because the importance of factors such as discharge, temperature fluctuations, unstable substrate and patchy substrate and detritus has been thought to largely override the effect of biotic interactions in streams, and partly due to the difficulty of conducting the type of manipulation required to assess biotic interactions in streams. The fact that there is good evidence that physical factors do influence benthic communities does not, of course, rule out the possibility that other significant factors are also operating. Certainly, single factor experiments can only determine whether a given factor has a demonstrable effect, and not the relative importance of different factors.

Of the reported field experiments in streams, four studies report that fish had little or no impact on the

benthic community (Allan 1982; Reice 1983; Flecker and Allan 1984; Culp pers. comm.), and only one that prey densities were significantly reduced (Flecker 1984). Both studies using invertebrate predators reported significant effects, although there were considerable differences between streams and seasons tested (Peckarsky and Dodson 1980a; Oberndorfer et al. 1984). The difference in reported results is probably due to two factors:

- 1) Habitat-related and seasonal variation in the relative importance of abiotic and biotic factors such as predation.
- 2) Differences in experimental design used by the various researchers which may have influenced the experimental outcomes.

The first objective of this study was to establish whether the predator Kogotus nonus exerts any influence on the density of its prey in small patches in the 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 field experimental results were merely a product of the par-

ticular experimental protocol used, or if they could be interpreted more generally as representative of natural processes. If a field experiment is to be considered useful, it must closely mimic the natural environment so that results bear some relationship to natural processes, and it must produce results that can be unambiguously attributed to the treatment. In this study, two aspects of the experimental design were tested, length of experimental period and enclosure size, and the type of control was varied to demonstrate the importance of maintaining identical conditions between treatments and controls.

The experiments reported in this study involve the use of small enclosures in a field situation. Taken conservatively, experiments that manipulate densities within small enclosures, are actually testing the effect of that predator on the prey density within that patch of substrate alone. To interpret this type of result as evidence that the predator actually depresses prey density in the stream as a whole, requires that the enclosures be considered representative of all microhabitats in the stream environment. If this is not the case, the possibility remains that certain parts of the habitat constitute prey refuges and that the prey depression seen in the experiments represents only a very localized depression. The probability of this increases if lowered densities are partly due to prey emigration from the enclosures. I believe,

therefore, that experiments such as those presented here, are more properly considered tests of predator influence on prey distribution. If predators consistently reduce the density of prey patches they encounter, this should ultimately lower prey densities in areas frequented by the predator. This is definitely a change in local distribution, but may or may not produce a change in population density.

## Methods

### Experimental Riffle

All experiments were conducted in a 2 x 5 m riffle located approximately 30 m upstream of Sampling Site 1 (Fig. 2.2). The riffle had a mean water depth of 10 cm, a current velocity of 25 - 35 cm/s, and a substrate composition similar to that of Site 1. The composition of the natural benthic community in this particular riffle was obtained from five benthic samples taken immediately downstream of the experimental containers at the termination of the 1982 and 1983 field experiments (Table 3.2). The abundances of Baetis and Orthocladiinae increased from June to July in both years, but in 1982 densities were considerably higher than in 1983. Summer densities of Kogotus were also lower in 1983.

Table 3.2. Natural benthic densities [no./100cm<sup>2</sup> (SE)]  
in the experimental riffle.

INVERTEBRATES	JUNE	JULY
1982		
Predators		
<u>Kogotus</u>	2.0 (0.5)	1.5 (0.7)
<u>Rhyacophila</u>	0.3 (0.2)	0.5 (0.3)
<u>Polycelis</u>	10.8 (2.8)	14.4 (6.3)
Herbivores		
<u>Baetis</u>	1.8 (0.5)	7.0 (1.7)
Detritivores		
Orthoclaadiinae	251.0 (60.4)	1294.3 (205.3)
<u>Thienemaniella</u>	131.6 (32.2)	443.8 (63.7)
<u>Corynoneura</u>	17.3 (8.5)	43.5 (11.6)
other	79.1 (30.6)	791.5 (193.1)
Tanytarsini		
<u>Stempellinella</u>	74.7 (22.6)	84.0 (18.1)
Large-particle detritivores		
Nemouridae	39.1 (7.8)	43.6 (15.5)
Tipulidae	1.3 (0.5)	1.5 (0.8)
1983		
Predators		
<u>Kogotus</u>	0.5 (0.3)	1.0 (0.2)
<u>Rhyacophila</u>	---	---
<u>Polycelis</u>	3.0 (1.3)	1.0 (0.2)
Herbivores		
<u>Baetis</u>	0.2 (0.2)	2.0 (0.8)
Detritivores		
Orthoclaadiinae	17.6 (4.5)	78.4 (4.4)
<u>Thienemaniella</u>	9.0 (2.9)	20.8 (2.5)
<u>Corynoneura</u>	3.7 (1.4)	2.5 (0.5)
other	5.0 (1.0)	55.1 (4.0)
Tanytarsini		
<u>Stempellinella</u>	84.0 (18.1)	60.1 (20.0)
Large-particle detritivores		
Nemouridae	2.0 (0.3)	3.2 (1.2)
Tipulidae	2.5 (0.9)	1.0 (0.4)

## Experimental Design

### 1) Tests of Predator Effects

The effects of Kogotus on prey populations were determined by varying predator densities in experimental containers (7.5 cm diameter) buried in the stream for 10 d. Container size was selected so that 1 Kogotus per container (45 cm<sup>2</sup>) would be representative of average benthic density at this time of year; local aggregations occasionally produced patch densities of up to 3 Kogotus/45 cm<sup>2</sup>. When the potential prey consisted of relatively high densities of Orthoclaadiinae (July), experiments with zero and two predators per container (1981), zero, one, two and three predators per container (1982), and zero, one and two predators per container (1983) were conducted. When Orthoclaadiinae were relatively less abundant (June 1982 and 1983), experimental treatments were zero, one, and two predators per container.

### 2) Length of Experimental Period

The dependence of the experimental outcome on length of experimental period was tested in July 1981. Additional containers (five per treatment) containing zero and two predators, were randomly interspersed with the 10 d experiments, but were retrieved after 5 d.

### 3) Enclosure Size

In June and July 1983, experiments were conducted using larger containers (11.5 cm diameter) to determine if the predator effects seen were an artifact of the particular enclosure size selected. These containers provided twice the area of the small containers, but were otherwise similarly constructed. Treatments were zero, one, two and three Kogotus per container in June and zero, two and four Kogotus per container in July, and the large containers (five replicates per treatment) were randomly interspersed with the smaller containers.

### 4) Enclosure-only Experiments

Field predation experiments are generally conducted to determine whether benthic communities would be different if predator density was either raised or lowered. When this problem is approached by the use of in situ containers, two different experimental designs are encountered in the literature. Arenas excluding predators are compared with either similar arenas including known densities of predator (enclosure/exclosure experiments) or with unenclosed arenas that permit access by naturally occurring predator populations (exclosure-only experiments). The latter approach, while logistically much simpler in that it avoids direct manipulation of the predator, has the potential to confound

predator effects with container effects since the two containers must be of somewhat different design to allow versus prevent predator access.

To determine if an enclosure-only experimental design would produce the same results as the enclosure/exclosure design, containers excluding 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 each experiment, substrate from a gravel bar was placed in wire baskets in the stream to permit microbial colonization. The experimental enclosures were plastic containers with two side windows (4 x 8 cm, .23 mm mesh) to allow water flow, and with removable top screens (1.5 mm mesh) to allow 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 4.0-9.5 mm; 35% was 9.5-16.0 mm; and

35% 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 a container.

Quantitative benthic samples were taken with the cylinder sampler, all predators removed, and the samples placed in a cone subsampler (Wrona et al. 1982). A subsample was placed in each container so that natural, background quantities of detritus and densities of prey were 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, containers with various densities of Kogotus predators were buried flush with the substrate surface in a uniform portion of the riffle. All treatments were arranged in a completely randomized design (five to eight replicates per treatment). Water depth and current velocity 1 cm above the substrate were measured over every second container at the beginning of each experiment, and water temperature was obtained from the immersible thermograph. To ensure that periphyton growth did not hinder colonization or emigration, the top screens of the containers were scrubbed every second day.

At the termination of each experiment, containers were removed, and animals and detritus were immediately preserved in 10% formaldehyde. Containers in which predators had died or undue sedimentation had occurred (ash wt >15g) were not included in the analysis. Invertebrates of the remaining four to six replicates per treatment were sorted under 12x magnification and identified. Organic and inorganic sediments were sieved into four size-classes (.106-.25 mm, .25-.5 mm, .5-1 mm, 1-2 mm), and were dried at 90°C and ashed at 500°C to determine the ash and ash-free wt of each size-class.

For each experiment, treatments were compared by analysis of variance and Student-Newman-Keuls multiple range test (Zar 1974), after a log (x+1) transformation was performed on the data to stabilize the variance (Elliott 1977).

## Results

## 1) Predator Effects

Physical parameters varied little among the five experimental periods. Deposition of detritus and inorganic sediment (.106-2 mm) ranged from 0.45 to 0.67 g per container, and 6.2 to 9.5 g per container respectively (Table 3.3). 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. Comparison among treatments within each experiment showed no significant differences in detritus and sediment quantities or in size distributions.

Densities of Orthocladiinae were significantly lower in containers with Kogotus in all three July experiments (Fig. 3.1). In 1981 and 1982, a large proportion of this effect was due to one genus, Thienemaniella. In 1982, while one predator lowered Thienemaniella densities by 30% and two predators by 64%, a third predator had little additional effect. A closely related genus, Corynoneura, showed no consistent response to Kogotus. The other Orthocladiinae responded in a manner similar to Thienemaniella, except in 1981, when they were quite rare. Kogotus significantly depressed Baetis densities in only

Table 3.3. Average accumulation [g (SD)] of organic and inorganic sediment (.106-2 mm) in experimental enclosures.

	DETRITUS	SEDIMENT
July 1981	.60 (.03)	8.3 (1.7)
June 1982	.58 (.10)	6.9 (2.7)
July 1982	.45 (.05)	6.2 (2.0)
June 1983	.57 (.22)	7.3 (2.7)
July 1983	.67 (.20)	9.5 (2.4)

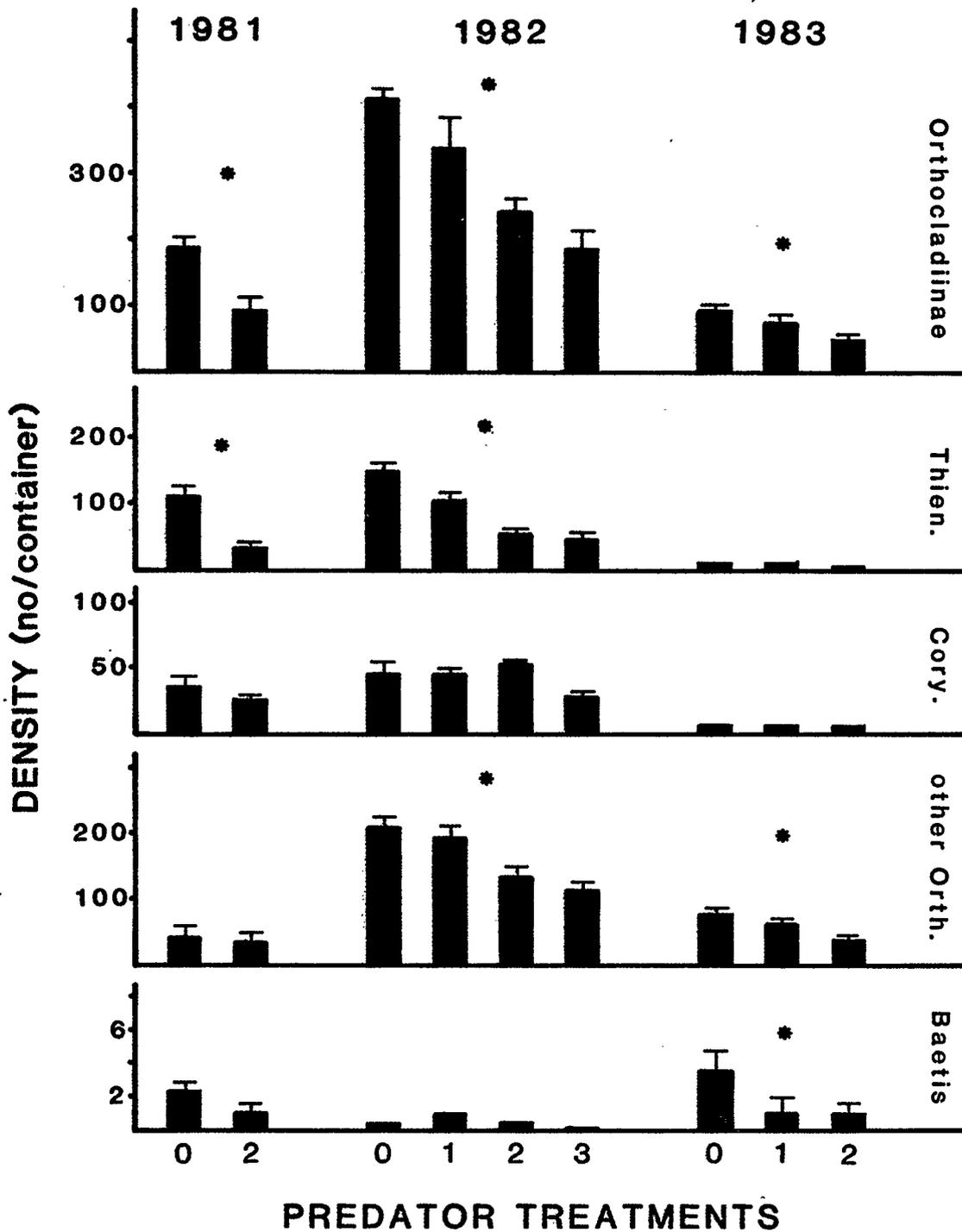


Fig. 3.1. Response of prey density to varying *Kogotus* density within enclosures in July 1981, 1982 and 1983. \* indicates a significant difference. Error bars are 1 SE.

one year out of three (July 1983). Non-prey invertebrates present in the enclosures Stempellinella (Tanytarsini), Nemouridae and Polycelis (Tricladidae) showed no density response to Kogotus (Fig. 3.2).

In the June experiments, Kogotus had no significant effect on Baetis or orthoclads, nor on any other members of the community (Fig. 3.3). Thienemaniella, the dominant orthoclad in 1981 and 1982, was much smaller (24% by weight) in June than in July (Table 3.4). Baetis varied little in average size over the two months, but appears to have presented a slightly more variable range of size in July.

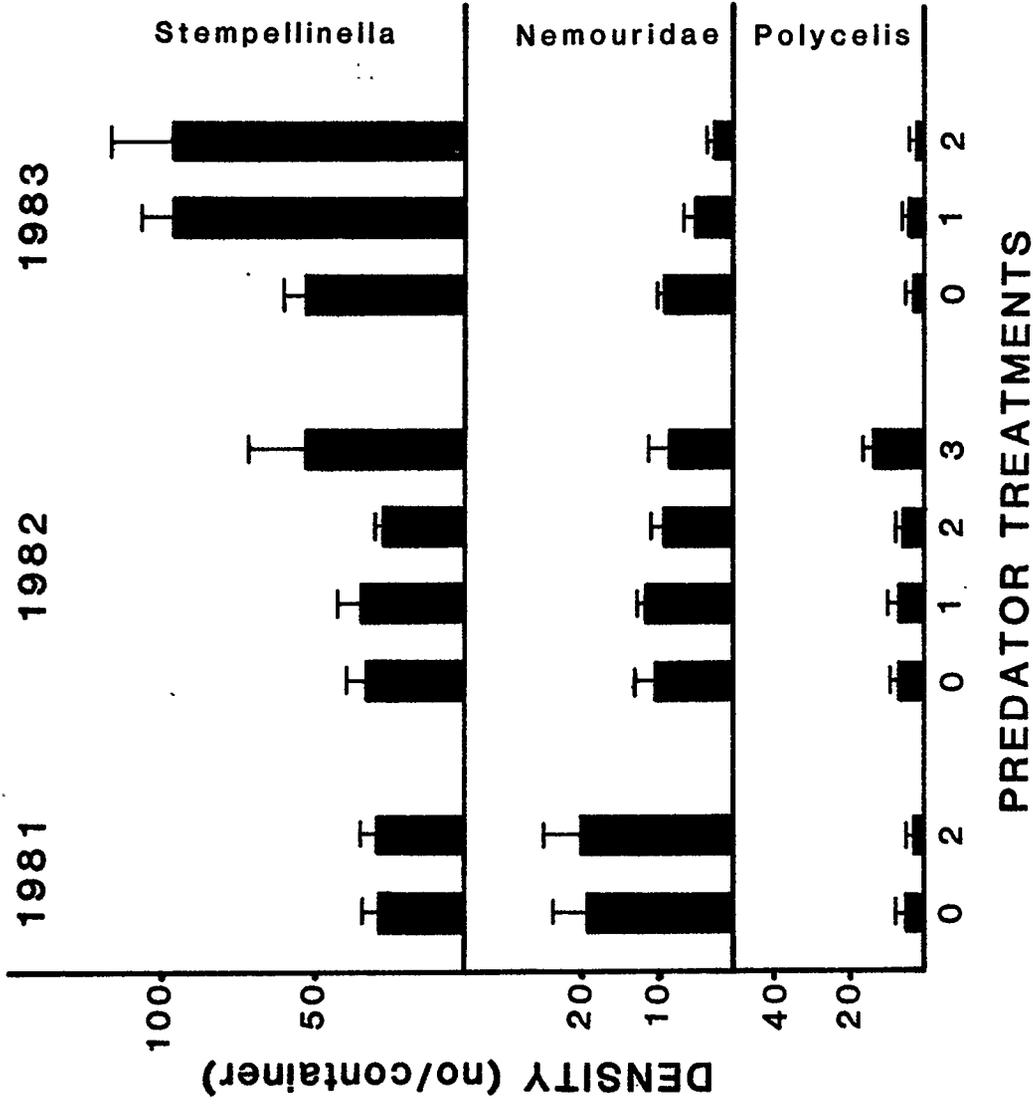


Fig. 3.2. Response of non-prey invertebrates to varying densities of *Kogotus* within enclosures in July 1981, 1982 and 1983. Error bars are 1 SE.

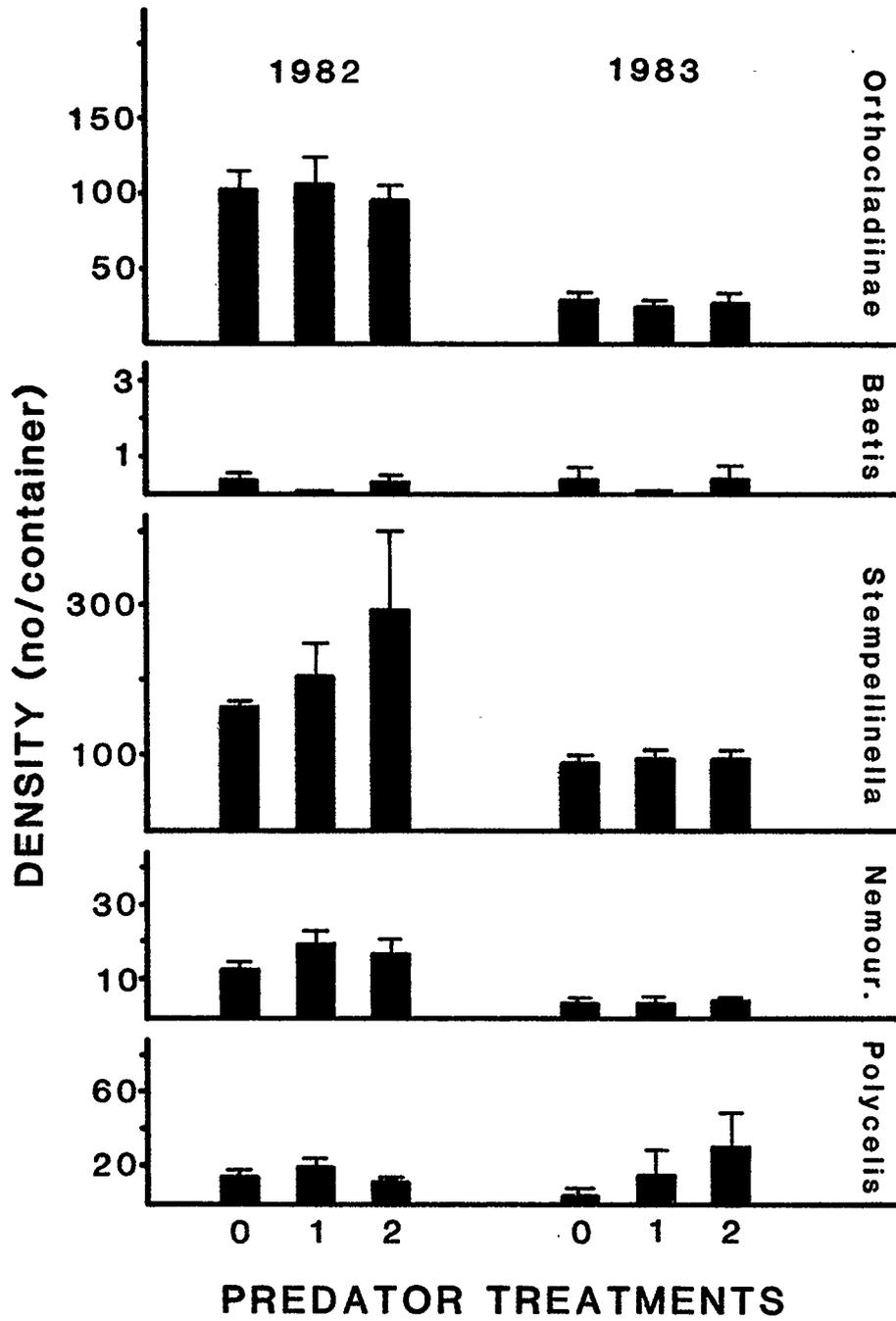


Fig. 3.3. Response of invertebrates to varying *Kogotus* density within enclosures in June 1982 and 1983. Error bars are 1 SE.

Table 3.4. Change in average weight of Thienemaniella (Orthocladiinae) and Baetis from June to July [mg (SD)].

	1981 JULY	JUNE	1982 JULY
<u>Thienemaniella</u>	.012 (.004)	.003 (.001)	.014 (.004)
<u>Baetis</u>	.585 (1.01)	.519 (.636)	.469 (.744)

## 2) Length of Experimental Period

Four replicate sediment traps (identical containers buried in the same riffle without initial detritus and prey) were removed on the third, fifth, seventh and tenth day of the experiment. Although sediment did not accumulate in a regular fashion over the 10 d (peak quantities recorded on the seventh day), the containers did have considerably less detritus and inorganic sediment on the fifth day than on the tenth (Table 3.5).

Despite this, the results of the 5 d experiments were similar to the 10 d July experiments, as Kogotus significantly depressed both orthoclad and Baetis densities (Fig. 3.4). Of the two dominant genera of Orthocladiinae, Corynoneura was strongly affected by Kogotus while the effect on Thienemaniella was significant only at  $p < .10$ . Other taxa present in the enclosures were not affected by the presence of Kogotus.

Table 3.5. Change in quantity of detritus and inorganic sediment [g(SD)] over a 10 d period.

TIME	DETRITUS	SEDIMENT
3 d	.23 (.02)	5.2 (1.1)
5 d	.29 (.05)	5.8 (3.6)
7 d	.75 (.24)	12.2 (5.9)
10 d	.60 (.03)	8.3 (1.7)

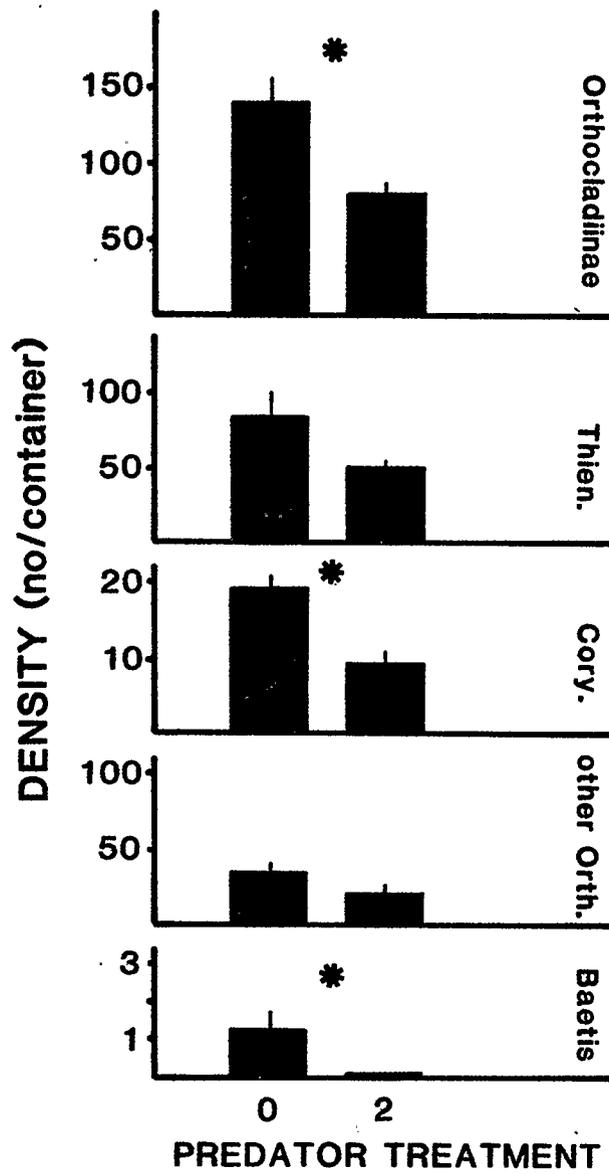


Fig. 3.4. Response of prey to *Kogotus* in 5 d experiments. \* indicates a significant difference. Error bars are 1 SE.

### 3) Container Size

Deposition of detritus and inorganic sediment (.106-2 mm) did not differ on a per unit area basis between small and large containers (Table 3.6). As had been observed in the small container experiments, Kogotus did not significantly affect prey densities in June (Fig. 3.5). (The significant difference in Baetis densities did not show a directional trend with predator density.) In July, Kogotus significantly depressed both orthoclad and Baetis densities (Fig. 3.5), again the same result as obtained from the corresponding small containers (Fig. 3.1).

Table 3.6. Deposition ( $\text{g}/100\text{cm}^2$  (SD) of detritus and inorganic sediment (.106-2 mm) in small (S) and large (L) enclosures.

	JUNE		JULY	
	S	L	S	L
DETRITUS	1.32 (.45)	1.12 (.48)	1.51 (.42)	1.73 (.28)
SEDIMENT	16.2 (7.7)	15.4 (5.9)	19.2 (7.6)	22.9 (5.8)

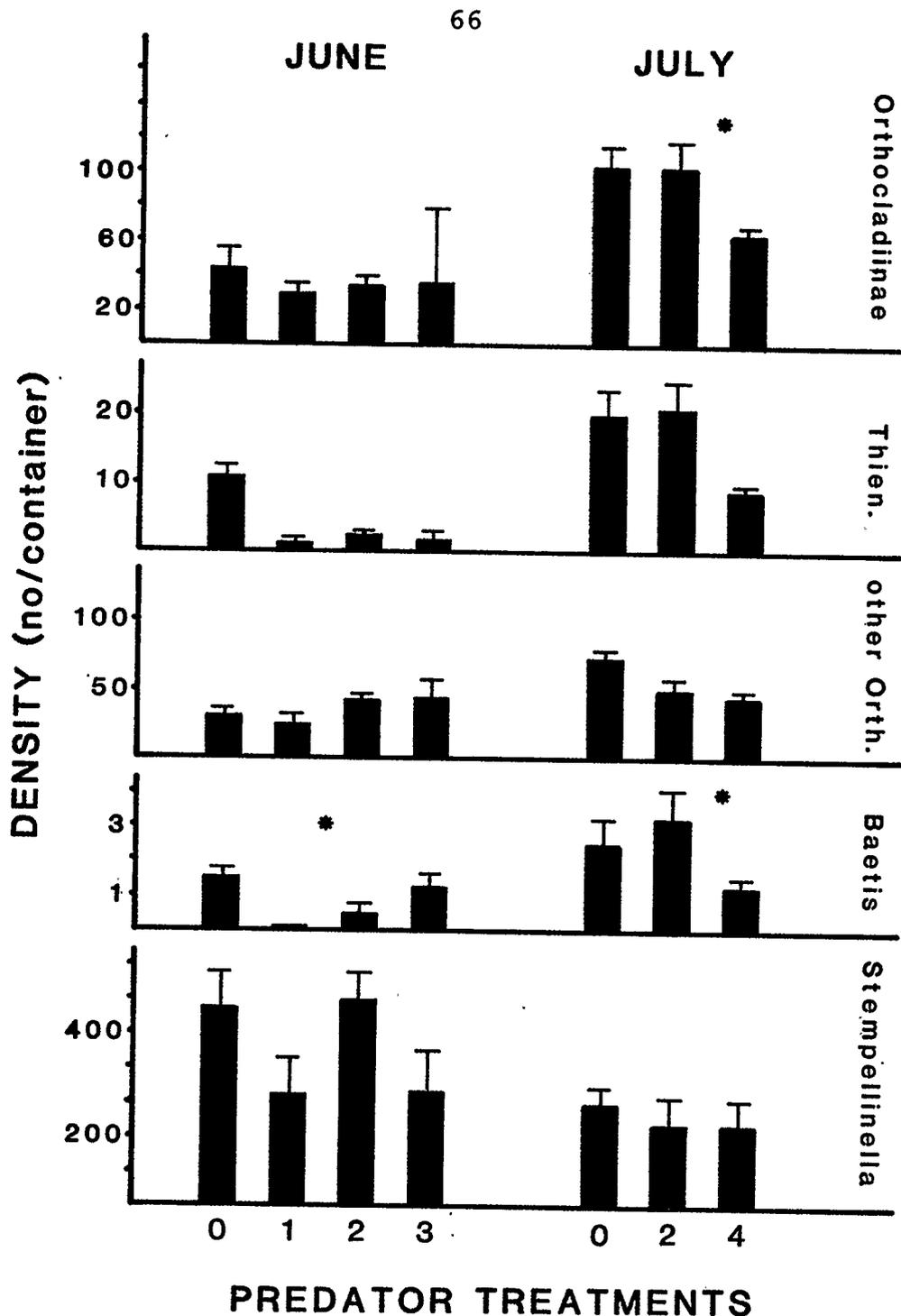


Fig. 3.5. Response of invertebrates to varying *Kogotus* density within large (11.5 cm diameter) enclosures. \* indicates a significant difference. Error bars are 1 SE.

#### 4) Enclosure/Exclosure Experiments

Containers that allowed immigration/emigration of free predators (no screened tops) accumulated approximately the same total amount of sediment and detritus as did containers excluding predators (screened tops), but unscreened containers had more coarse and less fine material present (Table 3.7). 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 (Table 3.8).

When containers that excluded Kogotus were compared with control containers that permitted Kogotus to enter and exit at will (July 1981), no significant differences were found in Thienemaniella or Baetis densities, but there was a decrease in Corynoneura, a fourfold increase in other Orthocladiinae, and a ninefold increase in Stempellinella density (Fig. 3.6). Secondly, 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, while no significant differences were observed for Thienemaniella, other Orthocladiinae, or Baetis (Fig. 3.6).

Table 3.7. Detritus and inorganic sediment quantities (g) in enclosures with and without top screens (July 1981).

	DETRITUS SIZE (mm)				Total [g (SD)]
	1-2	.5-1	.25-.5	.106-.25	
SCREEN	.051	.026	.157	.344	.60 (.03)
NO SCREEN	.096	.087	.096	.234	.51 (.14)

	SEDIMENT SIZE (mm)				Total [g (SD)]
	1-2	.5-1	.25-.5	.106-.25	
SCREEN	2.3	0.3	1.4	4.3	8.3 (1.7)
NO SCREEN	4.1	2.3	1.6	2.8	10.8 (3.8)

Table 3.8. Detritus quantities (g) within enclosures and in the benthos (June and July 1982).

	DETRITUS SIZE (mm)			Total [g (SD)]
	1-2	.5-1	.25-.5	
<u>JUNE</u>				
ENCLOSURES	.02	.09	.16	.26 (.06)
BENTHOS	.04	.01	.01	.06 (.03)
<u>JULY</u>				
ENCLOSURES	.01	.07	.14	.22 (.03)
BENTHOS	.03	.02	.03	.07 (.02)

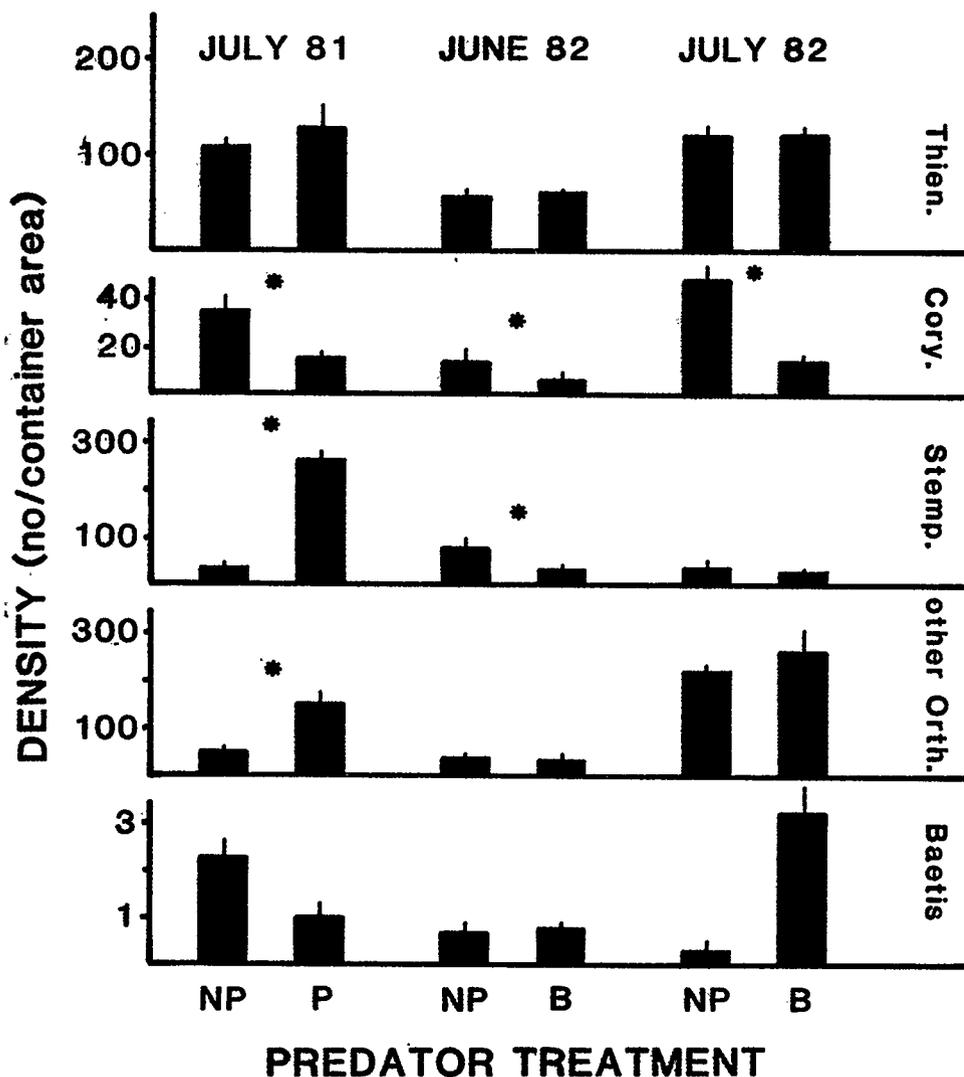


Fig. 3.6. Response of prey in predator exclusion-only experiments. Predator treatments were: no predator in container (NP), predator allowed access to container (P), and the benthos (B). \* indicates a significant difference. Error bars are 1 SE.

## Discussion

In any experiments comparing treatments such as predator densities it is critical 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 of high levels of fine sediment. Testing for differences in physical parameters among treatments is imperative, and random placement of containers in an apparently homogeneous riffle does not guarantee consistency.

The consistent depression of Orthoclaadiinae densities in July 1981, 1982 and 1983 suggests that Kogotus is likely to influence orthoclad 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 (July 1982) 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 refugia in the containers 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 laboratory observation (Chapter 5) and higher mortality of predators in treatments of high predator density suggest that interference may be an important factor with respect to this species.

Kogotus did not affect Stempellinella densities in any of the experimental periods, even when Stempellinella densities were relatively high. It appears that Kogotus either does not recognize the Stempellinella tube as containing an animal or is unable to extract the animal. The absence of any effect also indicates that Stempellinella does not move out of a patch in response to disturbance by this predator.

Kogotus had a significant influence on Baetis densities in only one experiment out of five (July 1983). This may have simply been due to the fact that significant differences are difficult to obtain at the extremely low densities observed. On the other hand, Kogotus may have a less consistent effect on Baetis either due to this prey's ability to rapidly move in and out of patches or to the importance of other factors in determining Baetis distribution.

The objective of most field manipulative experiments is to identify processes that naturally occur in the ecosystem under consideration. Because it is rarely possible to manipulate replicate ecosystems (certainly impossible for large lakes, oceans and most streams), experimental manipulations are generally restricted to small areas within the ecosystem. Although processes are readily identified and quantified within such subsystems, it is not immediately clear whether such results can automatically be extended to whole streams, lakes or marine ecosystems.

The critical first step is to ensure that the observed results are actually due to the predator treatment, not to some correlated factor such as design of the experimental containers. 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 from an enclosure-only design to the absence of predators or to the effects of the container. This has been suggested by marine researchers (Virnstein 1977; Hulberg and Oliver 1980), and it appears that the criticism is equally valid for freshwater ecosystems. In the enclosure-only experiments of this study, 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 rarely 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 containers themselves. The similarity of Baetis densities inside and outside the containers indicated that the containers had little or no effect on this species.

In general, exclosure-only experiments produced very different results from the enclosure/exclosure experiments. Potential prey were either not significantly different

inside and outside the containers, possibly indicating a low level of visitation by the predator, or showed effects attributable to the presence or absence of the enclosure.

Once it has been ascertained that the observed results are indeed predator effects, it becomes necessary to consider whether these predator effects are likely only seen under this particular experimental regime or if they probably occur more generally. Two aspects of the design of these experiments were varied to determine if the predator effects remained consistent. Results were very similar in experiments conducted for only half the length of time (5 d), and thus the predator effects were not specific to the arbitrarily chosen experimental period (10 d). The robustness of these experiments with respect to time was likely due to the fact that an initial prey community was established in the containers at the onset of the experiments. Time is probably much more critical in experiments that rely solely on prey colonization through the course of the experiment. Secondly, it was thought that the small container size might be producing aberrant behavior on the part of the predator and/or prey. Since similar results were obtained with containers of double the size, this also seemed less likely.

Much caution needs to be exercised when interpreting the results of field experiments in which predators have

been manipulated. Negative results do not necessarily mean that the predator in question plays no significant role in determining community structure, but merely that an effect could not be observed under a particular set of experimental conditions. Effects could easily be masked if physical conditions are not standardized between containers. Positive results must also be viewed critically in an attempt to discern systematic biases which could have produced the results. The scale of the experiment, both temporal and spatial, also determines to what extent the result can be interpreted as a general occurrence. In these experiments containers were small, representing an area equivalent to a prey patch. Conclusions are thus limited to the effect Kogotus has on a patch of prey, and cannot be directly extended to include effects on the total prey population density. Similarly, these experiments were conducted only with mature larvae in the summer, and thus the effect Kogotus has in the fall and winter remains open to conjecture.

In conclusion, then, these tests of experimental design show that the conclusions reached from the field experiments are reasonably robust. The effects of Kogotus were consistent across three years, two experimental periods and two sizes of experimental container. The importance of maintaining controls with exactly the same

physical conditions as the treatments was demonstrated, indicating the necessity of carefully taking abiotic conditions into consideration.

### 3.2. INFLUENCE ON PREY BEHAVIOR

#### Introduction

Many aquatic invertebrates have been shown to alter their behavior in the presence of predators. In ponds, gerrids escape from predatory birds by skating away or by feigning death (Bronmark et al. 1984), and juvenile notonectids avoid areas frequented by conspecific adults (Murdoch and Sih 1978). An attacking trout induces a defensive posture with raised cerci in a perlid stonefly (Otto and Sjostrom 1983), while stream dwelling mayflies have a variety of behavioral responses to predatory stoneflies that include entering the drift (Baetidae), crawling away (Heptageniidae) and assuming a scorpion-like posture (Ephemerellidae) (Peckarsky 1980).

Baetis shows a marked diel periodicity in drift rates, and these cycles have been attributed to an endogenous rhythm (Harker 1953; Elliott 1968), a nocturnal feeding pattern (Elliott 1968; Ploskey and Brown 1980), a direct response to light (Holt and Waters 1967; Muller 1974), temperature (Pearson and Franklin 1968), oxygen levels (Wiley and Kohler 1980), and an evolved response to day-active predators such as fish (Allan 1982). Drift rates have also been linked to current velocity and substrate type (Corkum et al. 1977). Predator-induced

drift has been demonstrated to occur for one detritivorous stonefly, but was not evident in the heptageniid mayfly tested (Walton 1980). A stonefly predator did significantly increase the drifting of Baetis vagans during dark periods (Corkum and Pointing 1979).

Since Baetis responds to predators by swimming up into the current and drifting downstream (Peckarsky 1980; pers. obs.), foraging on the part of Kogotus could potentially increase Baetis drift rates. A significant increase in behavioral drift could affect the Baetis population in terms of distribution, available foraging time and vulnerability to drift-feeding predators. Furthermore, if the predator effect is limited to the night, predator foraging could be enhancing the nocturnal drift pattern. The objective of this set of experiments was to determine:

- 1) if the drift rate of Baetis is increased by the presence of Kogotus in the same patch.
- 2) if the drift response of Baetis to Kogotus is similar with moving and stationary predators.
- 3) if the drift response of Baetis to Kogotus is dependent on light regime.

## Methods

All drift experiments were conducted in replicate circular laboratory streams (8.8 cm diameter, 50 cm<sup>2</sup> area) containing a gravel substrate (1-2 cm) (Fig. 3.7). Temperature was maintained at 8°C, current at 10 cm/s. Baetis and Kogotus were collected from the field site, transported to the laboratory in coolers (0.5 h), and maintained in incubators at 5°C. Field temperatures at this time of year (May) ranged from 4°C at night to 11°C during the day. Twenty Baetis (0.5-1 mm head width) were placed in each stream and allowed to acclimate for 1 h. (Previous trials showed that drift rates stabilized after 30 min.) Drift rate was determined by counting the number of Baetis drifting past an imaginary vertical line in the stream during ten replicate 1 min intervals. To minimize variation due to season or to any endogenous rhythm that might exist, all experimental runs were conducted in early June between 1400 and 1800 h.

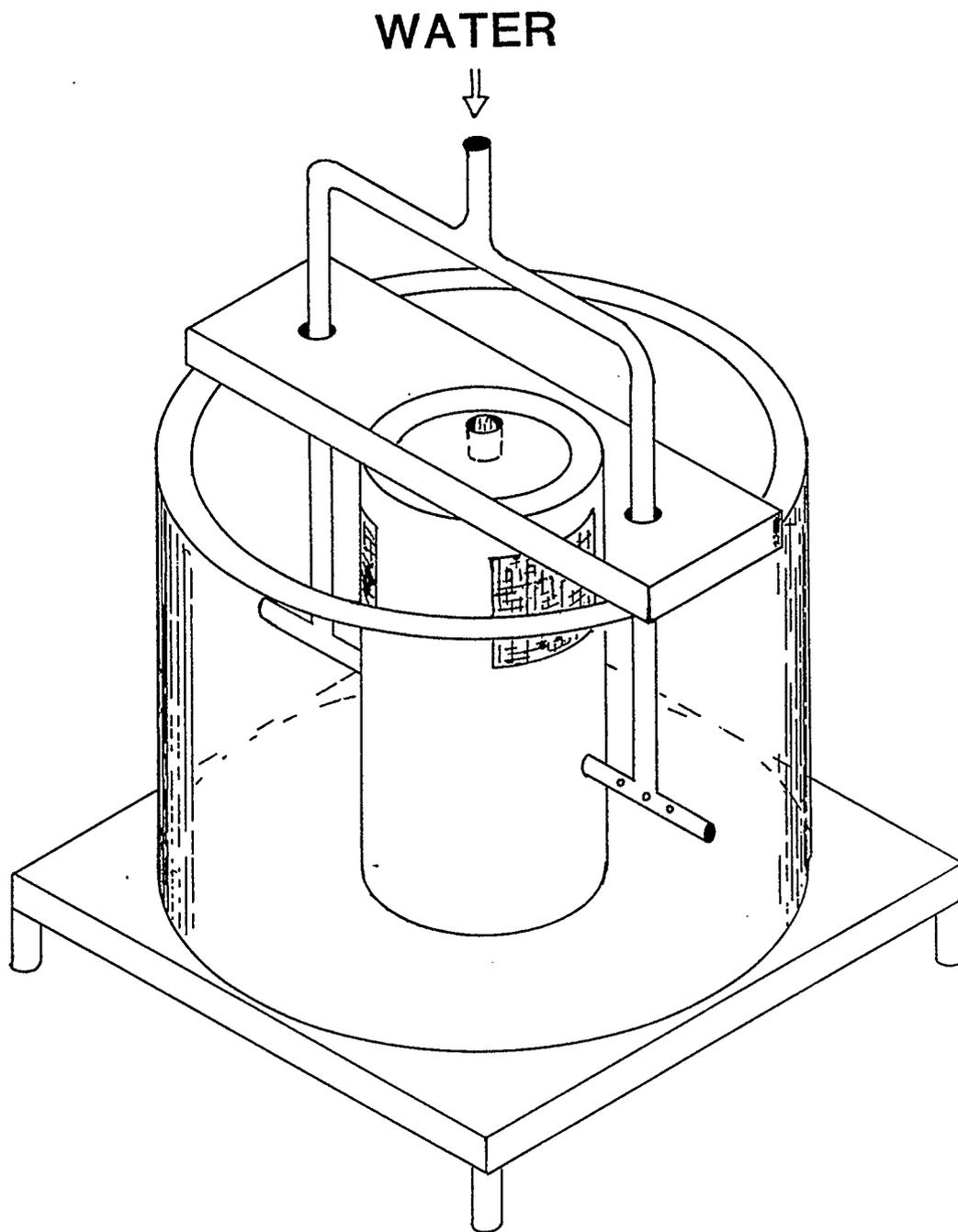


Fig. 3.7. Design of artificial streams. Current was produced by forcing water through the dual tee drive system with a Little Giant pump. Water flowed out through the 0.23 mm mesh windows in the centre standpipe.

To determine if Baetis drift could be directly affected by light regime, drift was measured first under a dull red light (15 lx) and then 5 min after exposure to flourescent light (1000 lx). The effect of Kogotus on drift rates was determined by comparing drift rates before and after the addition of a single starved predator (20-25 mg wet wt) under both red and white light. The activity of the predator in terms of movement was recorded. All comparisons were made using the Mann-Whitney U test.

## Results

Baetis drift rate was significantly depressed by light in six out of seven trials (Table 3.9). Average drift rate in white light was 3.8/min, with a low variance, while under a red light the drift rate was considerably higher, 16.1/min, with a very high associated variance.

When moving on the substrate, predators significantly increased the drift rate of Baetis, both under white and red light regimes in all but one trial (Table 3.10). Inactive predators, however, produced no change in Baetis drift rates.

Table 3.9. Drift response of Baetis to light regime. Significant differences are indicated by \* ( $p < .05$ ), \*\* ( $p < .01$ ), \*\*\* ( $p < .001$ ), NS ( $p > .05$ ).

	DRIFT RATE [no/min (SE)]		
	RED LIGHT	WHITE LIGHT	
	10.1 (1.1)	4.9 (1.3)	*
	5.2 (0.6)	0.3 (0.2)	***
	27.9 (2.1)	5.5 (1.1)	***
	30.0 (2.5)	4.6 (0.9)	***
	1.3 (0.5)	1.5 (0.5)	NS
	6.0 (0.8)	3.4 (0.9)	*
	31.9 (2.2)	6.7 (1.0)	***
Trial mean	16.1	3.8	
Variance	176.3	5.1	

Table 3.10. Drift rate of Baetis in the presence/absence of Kogotus. Significant differences are indicated by \* (p<.05), \*\* (p<.01), \*\*\* (p<.001), NS (p>.05).

RED LIGHT	DRIFT RATE [no/min (SE)]		PREDATOR MOVING	
	Absent	Present		
	3.7 (1.0)	5.6 (1.0)	NS	yes
	7.1 (1.6)	13.2 (1.2)	*	yes
	13.1 (1.3)	21.2 (1.0)	***	yes
	1.4 (0.6)	6.4 (1.4)	**	yes
	0.0 --	5.4 (1.4)	***	yes
	22.1 (1.6)	23.0 (1.5)	NS	no
	34.8 (1.4)	39.0 (3.2)	NS	no
WHITE LIGHT				
	0.6 (0.3)	9.3 (1.6)	***	yes
	1.8 (0.7)	16.2 (1.0)	***	yes
	10.9 (1.8)	14.9 (2.2)	NS	intermittent
	0.6 (0.3)	0.2 (0.1)	NS	no
	0.6 (0.3)	1.7 (0.4)	NS	no

## Discussion

These experiments have demonstrated that behavioral drift by Baetis tricaudatus is strongly inhibited by high light intensities, which is in agreement with that observed for B. rhodani (Elliott 1968; Muller 1974) and for B. vagans (Holt and Waters 1967). Unlike B. rhodani (Elliott 1968) but like B. harrisoni (Hughes 1966b), B. tricaudatus did not show a negative phototaxis, remaining on the upper surface of the stones in lighted conditions. Higher drift in the dark was not, therefore, a passive result of moving to the surface to forage, but was an active phenomenon. The reason for such drift is not clear, but it could be a behavior directed at searching for periphyton patches (Kohler 1984). Although light uniformly inhibited drift, the absence of light did not necessarily produce high drift rates (Table 3.9). The high variance associated with drift under red light suggests that other factors were involved in determining drift rates. A multiple-peaked endogenous rhythm might be present, as shown for B. rhodani (Harker 1953), or the B. tricaudatus used in these experiments may have varied in some physiological factor such as hunger level.

Differential predator effects during dark and light periods was not, therefore, required as a proximal causal factor inducing higher drift rates at night, although

predation has certainly not been eliminated as the ultimate factor selecting for the Baetis light response. Predator foraging could, however, increase Baetis drift rate over and above its intrinsic rate, and this was observed for predators moving about on the substrate under both red and white light conditions. The increased drift rate appeared to be a disturbance effect; drift was produced by the Baetis escape response which was induced by contact with a predator. Stationary predators did not significantly increase prey drift rates, indicating that long-range chemo-sensory or visual cues were either absent or ineffective.

These results suggest that patches of Baetis in the stream environment would be quickly depleted by the arrival of a foraging stonefly. This depletion would be largely due to Kogotus acting as a localized disturbance increasing drift from the patch, with only a small portion of the effect due to predation. These experiments add further evidence that Kogotus can affect the distribution of its prey on a microscale level. Increased drift from profitable patches could also increase Baetis mortality by reducing feeding rate, increasing energy expenditure, or increasing the probability of drifting to an unfavorable

area of the stream. A detailed energetics study would be required, however, to assess the magnitude of these effects.

## CHAPTER 4

EFFECT OF AN ABIOTIC DISTURBANCE ON THE  
PREDATOR-PREY INTERACTION

## Introduction

Both biotic factors, (competition (McAuliffe 1984), predation (Peckarsky and Dodson 1980a), detritus (Rabeni and Minshall 1977)) and abiotic factors (current (Reice 1977), spates (Scullion and Sinton 1983), temperature (Sweeney and Vannote 1978), substrate (Reice 1980)) have been shown to significantly affect stream benthic communities. There has been at least one attempt to integrate these two types of factors conceptually in order to assess their relative importance (Peckarsky 1983). Her model can be paraphrased as follows:

In the absence of disturbance (biotic or abiotic), stream community structure is determined by competition. If the abiotic regime is harsh, abiotic disturbances cause the observed community structure to deviate from that expected on the basis of competition. If the environment is very benign, on the other hand, predation disturbs the community, resulting in yet a different structure.

This model was originally proposed by researchers working in the marine ecosystem, where gradients of harshness were related to shore height and wave exposure (Dayton 1971; Menge 1976). There is good evidence from the marine ecosystem that abiotic disturbances do alter competitive outcomes (Dayton 1971; Levin and Paine 1974). There is also evidence that predators have a similar disturbing effect on some communities (Paine 1966; Dayton and Hessler 1972; Menge and Sutherland 1976), and it was observed that these predator-dominated communities tended to occur in areas where environmental conditions were relatively benign.

The alteration of a competitive outcome by an abiotic disturbance has also been demonstrated in streams (Hemphill and Cooper 1983) where frequent scouring of the substrate by floods allowed the coexistence of an opportunistic colonizer with its competitive superior. There are few examples in the literature of stream communities that are structured by predators, and thus there is even less evidence that such communities tend to occur more frequently in benign habitats. Fox (1977) suggested that the higher species diversity found in tropical as compared to temperate streams is produced by higher numbers of predatory species in tropical streams, but this proposal has yet to be tested. In a comparison of two streams, Peckarsky (1983) found that predation exerted a greater influence in

a temperate woodland stream than in a mountain stream. She suggested that harsh conditions such as considerable seasonal and diel fluctuation in temperature, habitable space and current resulted in lower densities of predators, and thus reduced their impact on community structure.

Increasing the level of fine sediment in a foothills stream such as Big Hill Springs Creek is likely to produce a relatively harsh abiotic regime, since high levels of fine sediment tend to have deleterious effects on many benthic organisms, resulting in marked changes in community structure. In general, Ephemeroptera, Plecoptera and filter-feeding Trichoptera and Diptera are reduced in numbers or eliminated by high sediment levels, while Tubificidae, Naiadae and some Diptera are little affected or may actually increase in abundance (Matter and Ney 1981; Lemly 1982). Sediment deposition tends to fill in the substrate interstices, and thus the major impact on benthic invertebrates seems to be reduction of available habitat, resulting in increased drift or movement out of the affected area (Rosenberg and Wiens 1978; McClelland and Brusven 1980; Walton et al. 1977). Elimination of shelter may also increase susceptibility of some invertebrates to predation (Hildrew and Townsend 1977; Brusven and Rose 1981). A secondary effect of sediment deposition, reduced

oxygen levels in the substrate, may eliminate some species (Erikson 1964) and these respiratory problems may be compounded by gill injury (Griffiths and Walton 1978).

The objective of this set of experiments, then, was to determine if imposition of a harsher abiotic regime in terms of increased levels of fine sediment would alter the impact that Kogotus has on its prey community in Big Hill Springs Creek.

## Methods

Sediment manipulations were conducted three times, in July 1981, June 1982 and July 1983. These were two factor experimental designs with two levels of sediment (high, low) in each case, and two predator levels (0, 2 Kogotus per enclosure) in 1981 and 1982, and three predator levels (0, 1 and 2 per enclosure) in 1983.

Using the procedure described in Chapter 3, experimental containers were prepared with natural substrate, detritus, and background densities of prey. In 1981, a plywood board was buried 10 cm into the substrate, dividing the experimental riffle into two longitudinal sections. Predator treatments were buried in a randomized design on either side of this divider. Fine sediment (.106-1 mm) was obtained from deposits downstream and swirled to remove most of the organics, resulting in a 95% inorganic sediment. Every second day throughout the course of the 10 d experiment, this sediment was released from a screened box for 10 min at three stations along the length of one side of the riffle. To ensure a fairly even distribution of sediment along the length of the riffle, the number and location of these stations had been determined in preliminary trials in another riffle. As a control for inadvertant substrate disturbance during this procedure,

the box was placed at the corresponding locations on the unsedimented half of the riffle for similar periods of time, but without release of sediment.

In the following two years, 1982 and 1983, the sediment treatments were prepared by adding 50 g of ashed fine sediment (0.5-1.0 mm) to the enclosures before placing them in the stream. While this did not mimic the natural process as closely as did the first method, it had the advantage of allowing the high and low sediment treatments to be interspersed throughout the riffle.

All enclosures were retrieved after 10 d, the invertebrates identified and counted, and ash and ash-free wt of sediment (.106-2 mm) determined for each container. Prey densities in predator treatments (4 to 6 replicates per treatment) containing high levels of sediment were compared using analysis of variance after a  $\log(x+1)$  transformation. The results of these manipulations were then compared to the results obtained under low sediment conditions (Chapter 3).

## Results

### Sediment Levels

Sediment levels were significantly increased in the high sediment treatments. High sediment treatments contained twice the amount of fine inorganic sediment (.106-2 mm) found in the low sediment controls in 1983, and were four to five times higher in 1981 and 1982 (Table 4.1). Detritus levels did not vary significantly between the high and low sediment treatments. The size distribution of sediment did vary somewhat between the three experimental periods, with the July 1981 and July 1983 experiments having a larger proportion of very fine inorganic and organic sediments than the June 1982 experiment (Table 4.2). Predator treatments did not vary significantly in detritus or inorganic sediment quantities within sediment levels during each experimental period.

Table 4.1. Total detritus and inorganic sediment (0.106-2.0 mm) in high (H) and low (L) sediment treatments [g (SD)].

	DETRITUS		SEDIMENT	
	H	L	H	L
July 1981	.82 (.12)	.60 (.03)	46.4 (11.7)	8.3 (1.7)
June 1982	.43 (.12)	.57 (.10)	43.1 (7.9)	7.1 (3.2)
July 1983	.83 (.17)	.68 (.20)	18.3 (2.2)	9.3 (2.4)

Table 4.2. Size distribution of inorganic sediment and detritus in high sediment treatments (g/enclosure).

	SEDIMENT SIZE (mm)			
	1-2	.5-1	.25-.5	.106-.25
July 1981	5.5	6.9	21.0	12.9
June 1982	1.5	16.2	12.7	3.7
July 1983	0.2	3.3	5.6	9.3

	DETRITUS SIZE (mm)			
	1-2	.5-1	.25-.5	.106-.25
July 1981	.051	.026	.157	.344
June 1982	.019	.099	.117	.191
July 1983	.012	.170	.252	.392

### Predator Effects

Under natural sediment conditions, Kogotus significantly lowered the density of Orthocladiinae in July 1981 and 1983, and the density of Baetis in July 1983. The addition of fine sediment eliminated both the impact of Kogotus on Orthocladiinae densities (Fig. 4.1), and the effect on Baetis densities (Fig. 4.2). In June 1982, however, the addition of sediment resulted in a predator effect where none had existed before (Fig. 4.1).

The direct effect of the sediment on the prey was investigated by comparing densities in containers without predators under high and natural sediment regimes. High sediment levels reduced orthoclad densities in both 1981 and 1983, and Baetis densities in 1983 (Fig. 4.3). One indication of the impact of the sediment on Kogotus is the percent of predators not surviving through the experiment. Mortality of Kogotus for low and high sediment treatments respectively, was 8 and 50% in July 1981, 50 and 43% in June 1982, and 20 and 40% in July 1983.

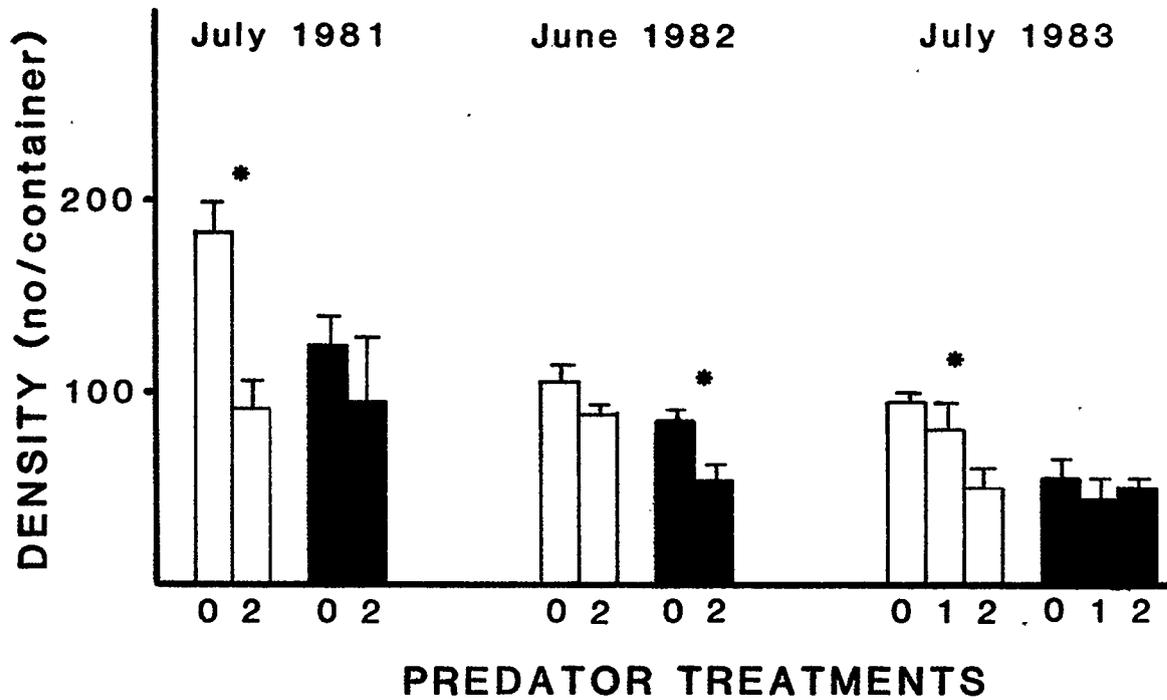


Fig. 4.1. Response of Orthocladinae to various *Kogotus* densities within enclosures under high (shaded) and low (unshaded) levels of sediment. \* indicates a significant difference. Error bars are 1 SE.

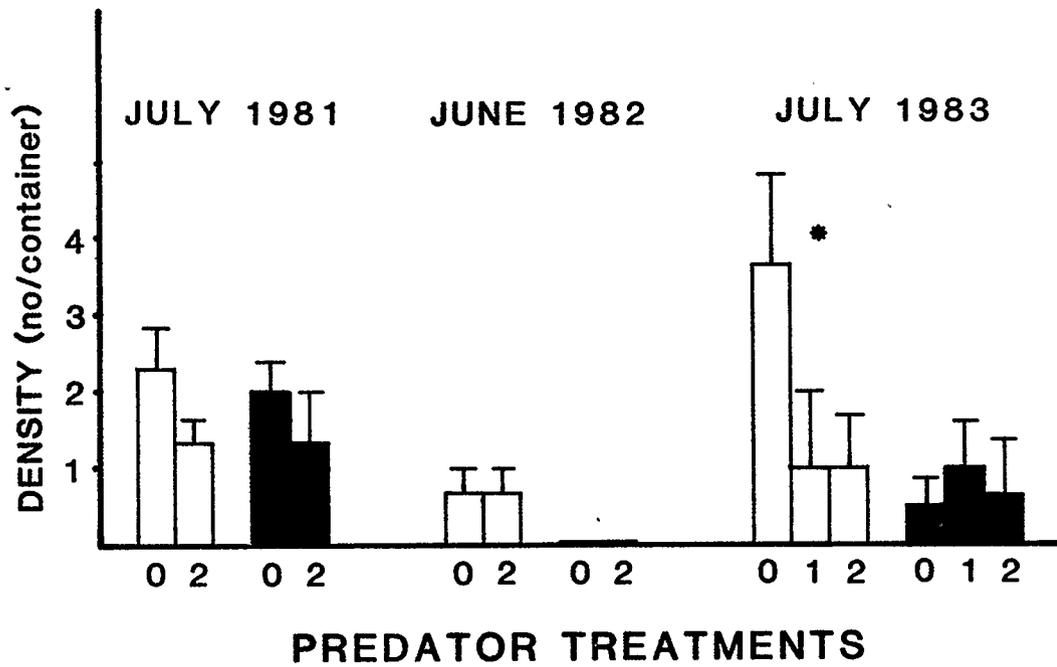


Fig. 4.2. Response of *Baetis* to various *Kogotus* densities within enclosures under high (shaded) and low (unshaded) levels of sediment. \* indicates a significant difference. Error bars are 1 SE.

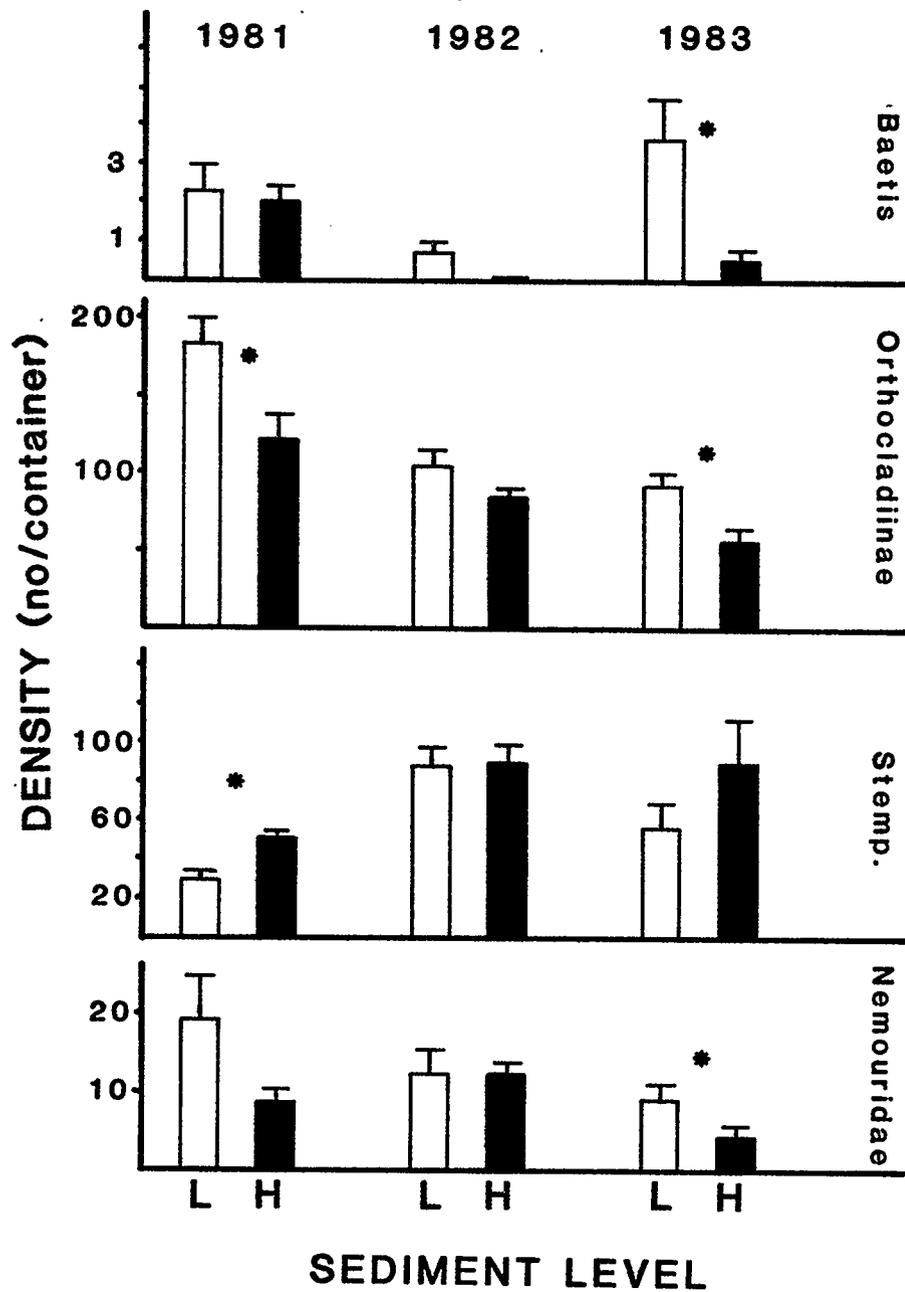


Fig. 4.3. Response of invertebrates to high (H) and low (L) levels of sediment in enclosures without *Kogotus*. \* indicates a significant difference. Error bars are 1 SE.

## Discussion

Two requirements must be met by any attempt, experimental or otherwise, to test the proposition that predation is more important in structuring communities in benign environments. There must be 1) a method of correctly assessing the impact or importance of predation in a given environment, and 2) a method of correctly assessing each habitat with respect to the harshness of its abiotic regime.

As discussed earlier (Chapter 3), field experiments tend to produce the most direct evidence that predators are influencing prey density or distribution. However, such manipulations tend to show only whether predator impact is discernible or not in a particular system, rather than the extent to which it is important. Thus, we are limited to concluding either that predators are having a significant effect or that they are not having a measurable impact.

Before a habitat can be placed on the continuum from harsh to benign, it is necessary to define what is meant by these terms. Use of the word 'harsh' to describe an environment usually implies that animals living there are physiologically stressed either because conditions are perpetually close to their tolerance limits or because fluctuations in the abiotic regime periodically produce such conditions. The unpredictability of these fluctua-

tions further contributes to harshness, since the stress cannot be as easily alleviated by physiological adaptations to the conditions or by timing of life cycle events so as to minimize impact. A harsh regime, therefore, is one in which an animal is less fit than it would be in another, where this reduction in fitness is caused by abiotic factors. What are these abiotic factors that lead either to decreased survivorship or decreased fecundity? Any factor that has an optimum when plotted against fitness will be a candidate. In streams these will likely include temperature, current, substrate size, frequency of flooding, sediment load, oxygen content, various aspects of water chemistry and so on. Ideally, then, if two distinct habitats are to be compared, the relative importance of all these factors would have to be estimated, so that a single value could be calculated as a measurement of harshness.

Clearly, this is no straightforward task. However, assuming that the harshness of the environment could be measured for a given species, a second problem must be faced. When the model refers to a harsh environment, it is not clear which species are supposed to be perceiving the environment as stressful. Three possibilities exist within the framework of the model: 1) the environment may be perceived as harsh by the predator but have little or no impact on the prey, 2) the environment may be stressful for both predator and prey or 3) the environment may harsh with

respect to the prey, while the predator is unaffected. Intuitively, different outcomes in terms of predator importance in the community would be anticipated, given the three situations. If the predator is more susceptible a decrease in the predator's impact is expected as the regime becomes harsher. If the prey is affected while the predator is not, the predator's impact could increase if the prey becomes more vulnerable (eg. Hildrew and Townsend 1977), or decrease if prey densities are lowered to the point where few prey are available. If both predator and prey are affected, the outcome will depend both on how severely the predator is affected, and on the manner in which the prey is affected, that is, whether it is made more or less available to the predator. It follows, then, that if the model predicts that increased harshness consistently decreases predator impact, it must assume that the predator is negatively affected by the abiotic factor, while the prey is either unaffected or made less available. The importance of this will become evident as the results of this particular set of experiments are discussed.

By manipulating only one abiotic factor within a single habitat, the need to integrate the large number of factors that contribute to environmental harshness was avoided in these experiments. Two lines of evidence suggested that the increased levels of fine sediment

constituted a harsher regime than did natural levels. First, numerous sedimentation studies have shown that Plecoptera and Ephemeroptera are found in reduced densities under high sediment levels (Nuttall 1972; Scullion and Sinton 1983; Matter and Ney 1981; Lemly 1982). Secondly, it was evident from a comparison of sedimented and unsedimented containers without predators, that the addition of sediment had a negative effect on both the predator and prey in the July experiments. Containers with high sediment levels had lower densities of orthoclads and Baetis. Survivorship of Kogotus was also lower in the sedimented containers than in the unsedimented containers.

The results of the two July experiments are in agreement with the proposition that the importance of predation in structuring prey communities decreases with harsher abiotic conditions. A strong and consistent depression of orthoclad densities by Kogotus was eliminated by the addition of fine sediment, as was the impact of Kogotus on Baetis densities in 1983. The mechanism underlying these results cannot be determined from these experiments, but a number of possibilities exist. Sediment may have reduced the effectiveness of Kogotus by filling in the interstices, eliminating access to the prey, or it may have affected the behavior of the predator, causing it to remain stationary, reducing both predation rate and disturbance effects. Alternatively, the effect on the prey

may have produced this result. At lower densities the prey may have been either unavailable or insufficient in numbers to stimulate foraging activity on the part of the predator.

The results of the June experiment, however, are exactly opposite to that predicted by the model under consideration. Addition of sediment produced a significant predator effect where none had existed before. Several differences exist between the June and July experiments. In July, the relatively finer sediment caused a decline in orthoclad densities; in June with predominantly coarser sediment, no such effect was seen. In July, high sediment levels increased predator mortality, while in June this was not the case. It is likely, then, that in July the addition of fine sediment constituted an increase in the harshness of the environment for both predator and prey. The impact of the predator was eliminated and the final prey density was determined by the sediment. In June, the sediment did not seem to be as detrimental to either Kogotus or the prey; its only effect appeared to be to make the orthoclads more available, thus enhancing the predator's effect. This could have been accomplished by the sediment settling into the substrate, reducing available interstitial habitat and forcing the orthoclads nearer the surface of the substrate.

Peckarsky's (1983) model, as presented, makes the prediction that increasing the harshness of the abiotic regime should reduce the importance of predators in determining community structure. Given that this prediction is robust only if particular conditions with respect to the effect of the harsh regime on the predator are met, it is not surprising that more than one type of result was obtained in the present experiments. While two of the results (July 1981 and 1983) were consistent with the model, violation of these assumptions probably caused the contradictory outcome (enhancement of predator effect) in June 1982. Similar criticisms are now being leveled at the application of this model to marine systems (Underwood and Denley 1984). It is concluded, therefore, that any predictions with respect to the relationship between harshness of abiotic regime and the importance of predation require, minimally, that the species affected by the harshness of the environment be identified, and the way in which they are influenced by the abiotic regime be specified.

## CHAPTER 5

INFLUENCE OF THE PREY COMMUNITY ON KOGOTUS

The previous two chapters were concerned with one aspect of the predator-prey interaction, the potential influence of Kogotus on the distribution of its prey, Baetis and Orthoclaadiinae. This chapter will deal with the complementary aspect of this interaction, the influence of the prey community on Kogotus. There are basically two ways in which predators can be influenced by their prey, 1) a limiting food supply may control predator density and 2) predator distribution may be affected. The objective of this chapter was to look at the second of these two possibilities, that is, to determine if the distribution of Kogotus is influenced by its prey. There is a possibility that density effects may also be present, as shown by gut content data (Chapter 2). To confirm this possibility, however, would involve demonstrating that competition for prey is actually limiting the population size of the predator. This would require much information outside the scope of this study, including determination of feeding and growth rates throughout the life cycle of Kogotus, and investigation of other factors potentially decreasing survivorship and reproduction, such as predation on larvae

and adults, cannibalism, abiotic disturbances, probability of finding mates and failure to oviposit in suitable locations.

The first section of this chapter will establish that field distributional patterns from Big Hill Springs Creek do not support the view that Kogotus is responding to the distribution of its prey, in particular, Baetis. In the following two sections, two possible explanations for this finding will be explored, the first based on the occurrence of mutual interference between Kogotus larvae, and the second incorporating the factor of prey mobility.

## 5.1. THE RELATIVE DISTRIBUTION OF PREDATOR AND PREY

### Introduction

Ecological theory rests on the assumption that natural selection tends to maximize the relative fitness of individuals. Foraging theory, and in particular, optimal foraging theory, makes an additional assumption, that foraging efficiency is linked to fitness, that is, if an organism can either obtain more food (energy maximizer) or can obtain its food requirements faster (time minimizer) than others of the same species, it will have a higher fitness than its conspecifics (Schoener 1971). Natural selection should, therefore, tend to produce efficient foragers.

Optimal foraging theory has explored three areas in which predators can make choices which potentially increase or decrease foraging efficiency, response to a range of prey types, response to patchily distributed prey and selection of search paths (Krebs and Davies 1978). The second area is particularly relevant to the study of stream predators since almost all benthic macroinvertebrates show aggregated distributions (Elliott 1977). Optimal foraging theory predicts that predators should maximize gain by foraging in high density prey patches, leaving a patch when the return rate is below that of the habitat average. This

foraging strategy should result in non-random distributions of predators which correspond to the spatial variation in prey densities, an aggregative response (Hassell 1966).

There is evidence in the literature that some stream predators are positively associated with their prey while others do not appear to aggregate in response to prey. Using bivariate comparisons, Hildrew and Townsend (1976) found that the association of two lotic invertebrate predators with prey biomass was higher than with any abiotic variable. Adding prey biomass as a factor to a multivariate model incorporating abiotic variables increased the fit of the model to the observed distribution of one of the predators, Plectrocnemia (Trichoptera), six times out of seven, but prey biomass was a significant factor for Sialis (Megaloptera) only two times out of seven (Hildrew and Townsend 1982). Significant correlations were also found between Dinocras (Plecoptera) and prey abundance, and discriminant analysis produced groups that were correlated with both prey abundance and some abiotic factors (Malmqvist and Sjoström 1984). A principle components analysis suggested that the habitat of Calineuria (Plecoptera) coincided with that of its prey (Sheldon 1980). In a set of experiments manipulating habitat type, Reice (1981) found some predator-prey associations that were independent of substrate, but these constituted only a small proportion of the total number of possible

predator-prey associations. Stonefly predators did not preferentially colonize areas in which prey density had been increased (Peckarsky and Dodson 1980b). Thus, the large-scale, non-experimental approaches which looked at a range of habitats within a stream tended to find significant associations between predator and prey (Hildrew and Townsend 1976, 1982; Sheldon 1980; Malmqvist and Sjostrom 1984), while smaller scale manipulations within a riffle report less association (Peckarsky and Dodson 1980b; Reice 1981).

The objective of this section was to determine whether a significant association between the predator, Kogotus, and its prey was present in Big Hill Springs Creek, both when considering samples taken within fairly uniform riffles, and when samples incorporating a larger range of habitat variables were used. Four questions were asked:

- 1) Do Kogotus and its prey show significant levels of aggregation?
- 2) Are Kogotus densities correlated with those of either of its prey, Baetis or Orthocladiinae?
- 3) Are the patch sizes of predator and prey the same?
- 4) Are other factors (biotic and abiotic) correlated with the distribution of Kogotus?

## Methods

The data collected for Kogotus, Baetis and Orthocladiinae from the relatively homogeneous sampling sites (Chapter 2) were used to compute variance to mean ratios ( $I$ ) for each sampling date. This ratio, corrected for the number of samples [ $I(n-1)$ ], approximates a chi-square distribution and can thus be used to determine if distributions are significantly different from random (Elliott 1977). Nonparametric correlations of predator and prey density were performed on the same sampling data to determine if there were significant associations between Kogotus and its prey.

To determine patch size, six replicates of four sample sizes (areas of 50 cm<sup>2</sup>, 120 cm<sup>2</sup>, 300 cm<sup>2</sup>, and 900 cm<sup>2</sup>) were taken in May 1984 in a previously unsampled reach of the stream. Invertebrates were sorted and identified, and ash-free dry wt of detritus determined. An estimate of patch size for the various taxa found in the samples was obtained by plotting ratios of Morisita's index of dispersion against size of sample (Elliott 1977).

In addition, a curved reach of the stream was selected so that it contained a range of depths, current velocities and substrate sizes. At each of 20 sample locations, current 1 cm above the substrate and water depth were measured. At each location, the invertebrates, detritus

and inorganic substrate were collected to a depth of approximately 8 cm. The dry weight of the inorganic substrate was determined for each of the phi classes, -6 through 2, and mean phi was calculated as in Chapter 2. Invertebrates from each sample were sorted and identified and ash-free dry wt of the sediment determined. A series of bivariate non-parametric correlations were performed on the various taxa and abiotic measurements.

## Results

The sampling data were divided into three periods, July to October (small larvae, rapid growth), November to March (small to medium-sized larvae, slow growth), April to July (large larvae, rapid growth). In all three periods, the majority of sampling dates indicated significantly aggregated distributions for both prey types, greater than 90% for Orthoclaadiinae and 70% for Baetis (Table 5.1). Kogotus, however, had a distribution that was significantly different from random less than 25% of the time. There was also little evidence of association between the distributions of Kogotus and Baetis (Table 5.2). The frequency of significant positive correlations was low for all periods, and the co-occurrence of several negative correlations suggests that the few observed associations were likely produced by chance. There was a little more evidence of association between Kogotus and Orthoclaadiinae for the larger larvae (April to July), as a significant positive correlation was observed on nearly 25% of the sampling dates.

Table 5.1. Proportion of sampling dates in which a significant level of aggregation occurred for Kogotus, Baetis and Orthocladiinae as determined by the variance to mean ratio.

Period	PROPORTION		
	<u>Kogotus</u>	<u>Baetis</u>	<u>Orthocladiinae</u>
July - October	0.25	0.79	0.93
November - March	0.07	0.92	0.92
April - July	0.24	0.69	0.94

Table 5.2. Correlation of Kogotus with that of its prey. Number of significant positive and negative correlations obtained from within-riffle sampling.

Months	<u>Baetis</u>		Total
	+ Corr	- Corr	
July - October	2	2	12
November - March	2	0	11
April - July	2	1	33

Months	<u>Orthocladiinae</u>		Total
	+ Corr	- Corr	
July - October	1	0	12
November - March	0	2	11
April - July	8	0	33

Morisita's index of dispersion ( $I_s$ ) was calculated for each sample size, and the ratio ( $I_s/I_{s+1}$ ) plotted against sample size (Fig. 5.1). Peaks in the graph indicate patch size for that taxon. Baetis, Rhyacophila, and cased Trichoptera had patch sizes of less than or equal to 120  $\text{cm}^2$ . No peak was observed for Kogotus, indicating that its patch size was outside the range tested. A patch size of 300  $\text{cm}^2$  was seen for Stempellinella, Oligochaeta and Acari, corresponding to that for fine detritus, and a weak peak at 300  $\text{cm}^2$  was also observed for Orthocladiinae.

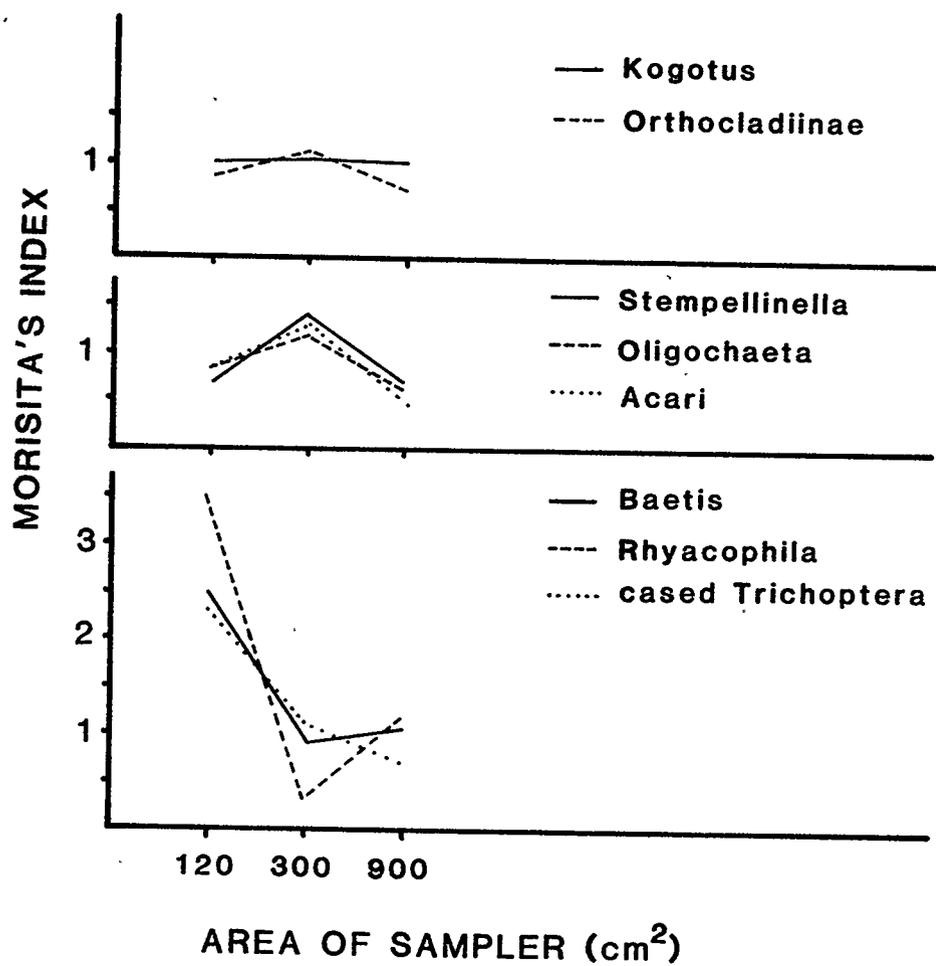


Fig. 5.1. Plot of Morisita's index versus area of sampler. Peaks indicate patch size.

In the samples taken over a larger range of abiotic variables (May 1984), Kogotus densities were strongly correlated with current, depth, both prey types, and the non-prey taxa, Rhyacophila, Stempellinella, cased Trichoptera and Acari (Table 5.3). Of the abiotic variables, depth and current were strongly correlated, and both were weakly correlated with fine detritus (0.25-0.5 mm). Substrate size was negatively correlated with coarse detritus (1-2 mm), but unrelated to any other measured factors. There appeared to be one group of taxa associated with deep, fast areas of the stream, including Kogotus, Rhyacophila, Orthocladiinae, Baetis, Stempellinella, Acari and cased Trichoptera. A second, smaller group, Tipula and Oligochaeta, showed little relationship to current and depth, but were more strongly correlated with detritus. Other detritivorous taxa were weakly associated with fine detritus only (Baetis, Orthocladiinae, Stempellinella, cased Trichoptera, Acari).

Table 5.3. Nonparametric correlation matrix indicating significant ( $p < .05$ ) associations between taxa and abiotic parameters. Correlations with coefficients  $> 0.7$  are indicated by ●,  $> 0.6$  by ⊙,  $> 0.5$  by ⊖, and  $> 0.4$  by ○.

	Kogotus	Baetis	Orthoclaadiinae	Stempellinella	Rhyacophila	cased Trichop.	Nemouridae	Tipula	Oligochaeta	Acari	current	depth	substrate	c. detritus	m. detritus	f. detritus
Baetis	●															
Orthoclaadiinae	●	●														
Stempellinella	●	●	●													
Rhyacophila	●	⊖	●	⊖												
cased Trichop.	⊖	●	●	⊖	⊖											
Nemouridae		⊖	⊖	⊖	⊖											
Tipula	⊖	⊖	⊖		⊖	⊖										
Oligochaeta		○		○		○										
Acari	●	⊖	●	●	●	⊖	⊖									
current	●	●	●	⊖	●	⊖		⊖								
depth	●	●	●	⊖	⊖	●		⊖	●	●						
substrate																
c. detritus								⊖				⊖				
m. detritus								⊖	●			○				
f. detritus		○	⊖		○	⊖	●	●	⊖		⊖					

## Discussion

This investigation offers three lines of evidence that Kogotus does not aggregate in prey patches. First, the data obtained on a seasonal basis from the three sampling sites showed little sign of an aggregative response to the patchy distributions of the prey. Both prey types tended to be significantly clumped within the riffles under study, while on the majority of sampling dates the distribution of Kogotus was not significantly different from random.

Secondly, the contention that Kogotus was not aggregating in Baetis patches was supported by the observation that Kogotus density was infrequently correlated with Baetis density, and the fact that some of the correlations were negative. The absence of a response to Baetis is consistent with the results of Peckarsky and Dodson (1980b), who seeded cages with mayfly prey and observed no numerical response on the part of the stonefly predators. There was a little more evidence for association between Kogotus and Orthocladiinae in the spring period, but the occurrence of positive correlations 25% of the time does not constitute a very consistent response. These results are also in agreement with those of Reice (1981), who in conducting experiments on standardized substrate, found only a few significant interactions.

Thirdly, calculation of patch size showed that Kogotus patches are of a markedly different area than those of Baetis. Baetis has been shown to aggregate in periphyton patches (Kohler 1984) and the small patch size observed ( $<120 \text{ cm}^2$ ) is likely related to the size of rocks containing high densities of algae. Kogotus, on the other hand, had a patch size outside the range of 120 to  $900 \text{ cm}^2$ . Since the lower end of the range already approaches substrate size, Kogotus is likely responding to some factor that occurs on a scale larger than  $900 \text{ cm}^2$ . The peak at  $300 \text{ cm}^2$  for Orthoclaadiinae may be the result of a response to fine detritus. The poorer definition of this peak may be due to the inclusion of a number of species in one analysis, or it may indicate a concurrent and stronger response of Orthoclaadiinae to other larger or smaller scale phenomena. The different patch sizes indicate that Kogotus is either not recognizing or not responding to individual prey patches in the classical optimal foraging theory sense. However, this set of samples has only identified aggregation within a limited range of potential patch sizes. It remains possible that Baetis and Orthoclaadiinae are also aggregated on a larger scale and that Kogotus is responding to prey aggregations on this level.

Although Kogotus tends to be randomly distributed within particular riffles, this is not the case for the

stream as a whole, as evidenced by the results of sampling on a larger scale. When microhabitats varying in current, substrate and depth were included, the distribution of Kogotus was found to be strongly correlated with current and depth, as well as with the majority of the taxa present in the stream. While a correlation analysis such as this cannot demonstrate cause and effect relationships, it does point out associations that occur in the stream ecosystem. The high degree of intercorrelation in this analysis suggests that many of the taxa could be responding to common cues. These taxa (Kogotus, Rhyacophila, Baetis, Orthocladiinae, Stempellinella, cased Trichoptera, Acari) were all most abundant in fast, deep water, making velocity and depth appear likely proximal cues. If, indeed, Kogotus is responding directly to these cues, this has the beneficial effect of placing the predator in the same general habitat as both of its major prey. However, this cue would not be sufficient to produce aggregation in more localized prey patches.

Tipula and Oligochaeta appeared to form a second group, strongly correlated with detritus and less associated with the deep, fast water habitat. Occupation of a different habitat type may be the reason that these taxa are rarely consumed by Kogotus.

In conclusion, these results emphasize the importance of considering scale when comparing the distributions of

various taxa. Correlations present at one level may not be present at another. The data from the larger-scale investigation showed that the distribution of Kogotus was strongly correlated with that of its prey, as well as with that of most other invertebrates present in the stream. Similar predator-prey associations were seen in the studies cited in the introduction. Strong correlations between Kogotus and its prey were not observed in the smaller scale (within-riffle) study, indicating that the mechanisms producing whole stream distributions are likely different from those within riffles.

A plausible scenario arising from these results is that Kogotus is responding to the abiotic cues of water depth and/or current velocity (or to some correlate of these factors), with the result that its distribution forms a large scale mosaic over the stream bottom. This response incidentally puts Kogotus into the general habitat type of both its major prey, Baetis and Orthocladiinae, and this overlap in distribution could be the primary reason that these prey types make up most of the diet of Kogotus. Within a particular current/depth regime, however, Kogotus generally shows a random distribution, not responding in an aggregative manner to the smaller Baetis and Orthocladiinae

patches. Possible explanations for the absence of such an aggregative response will be explored in the remainder of this chapter.

5.2. MUTUAL INTERFERENCE AND KOGOTUS FORAGING BEHAVIOR

## Introduction

As previously discussed, optimal foraging theory predicts that when prey distribution is clumped, predators should aggregate in patches of high prey density, leaving a patch when its density is reduced to that of the habitat average (Krebs and Davies 1978). If, however, there is a cost to foraging in high density prey patches, namely, close association with other predators, the benefit derived from being in a high density patch will be reduced. Mutual interference between predators, therefore, is one mechanism which may alter the optimal distribution of a predator; if there is considerable interference between predators the optimal distribution for a predator population will be less aggregated than that predicted by response to prey density alone.

A number of studies have demonstrated mutual interference between aquatic invertebrate predators. Net-spinning Trichoptera have been shown to be somewhat territorial, defending their nets against intruders (Hildrew and Townsend 1980), which results in a regularly spaced pattern at high densities (Glass and Bovbjerg 1969). Zygopteran nymphs also space themselves out, competing for preferred sites near food sources (Baker 1980), and the

feeding rate and distribution of notonectid larvae is influenced by the presence of conspecific adults (Murdoch and Sih 1978). Aggressive behavior leading to lowered feeding rates has been observed both within and between two species of perlotid stonefly (Peckarsky and Penton 1985), and similar aggression was observed for perlid stoneflies competing for preferred retreats (Sjostrom 1983).

Behavioral interference can reduce capture rates when time is 'wasted' interacting with other predators and thus is unavailable for searching for prey (modelled by Rogers and Hassell 1974; Beddington 1975). Alternatively, a predator may make the prey in a patch less available to other predators, by causing either a redistribution of the prey or by producing some change in the prey behavior pattern (Sih 1979). Finally, the presence of other predators may change the behavior of the predator itself, altering its time allocation to various activities, its probability of encountering, attacking and eating a prey item, or its tendency to leave or remain in a particular prey patch.

Given that mutual interference has been demonstrated to occur for a number of aquatic predators, and the potential it has for altering the optimal distribution of a predator, experiments were designed to determine if interference influences the foraging behavior of Kogotus. The overall objective of these experiments was to measure

the trade-off between benefits accrued from hunting in a high density prey patch, and the cost of sharing such a patch with conspecific predators. From these cost/benefit estimates, predictions about predator distribution and foraging will be made, and compared with distributional data from the field. Specifically, the objectives of this study were to determine:

- (1) the benefit of feeding in high density prey patches, in terms of capture rate.
- (2) the cost attributable to behavioral interference resulting from predator aggregation within a patch.
- (3) the optimal predator distribution, given the experimentally derived costs and benefits.

#### Methods

Benefit accruing from foraging in high density patches was determined by constructing a functional response curve using solitary Kogotus and prey densities of 5, 10, 20, 30, 40 and 50 Baetis per artificial stream. Behavioral observations were carried out in order to quantify changes in encounter and attack rates, as well as any changes in time allocated to the activities of moving, resting and swimming.

The cost of behavioral interference was determined by increasing predator density in the artificial stream and

measuring the per-predator capture rate. Behavioral observations were carried out during the experiments to elucidate the cause of any change in capture rate. Predator densities ranged from one through four per stream, and experiments were conducted at densities of 10, 30 and 50 Baetis per stream. One Kogotus per artificial stream was equivalent to the average field density, with higher densities representing local patch densities occasionally encountered in the field. Average Baetis density in the field was approximately equal to ten per artificial stream.

Experiments were conducted in circular plexiglass streams (Fig. 3.7), with current maintained at 5-7 cm/s, temperature at 8°C, and photoperiod at 16 h light (0600-2200h) and 8 h dark, similar to the natural photoperiod. A layer of sand (1-2 mm) was used as substrate for the animal to grasp.

Kogotus and Baetis were collected in May and June 1982 from Big Hill Springs Creek, transported in coolers to the laboratory (0.5 h) and kept in aerated containers at 5°C. Kogotus weighing between 20 and 25 mg wet wt were used experimentally within 48 h of collection, and medium-sized Baetis (head capsule width 0.5-1.0 mm) within 5 d.

Hunger state was standardized by placing predators in individual streams for 48 h of acclimation and starvation prior to experimental trials. Each 24 h experimental run was initiated at 1400 h by combining starved Kogotus to

produce densities of one to four per stream, and then placing the various densities of Baetis in each stream. Fifteen minute observations were made between 1500 and 1600 h, 1700 and 1800 h, 700 and 800 h, and 1100 and 1200 h, and then combined to give 1 h of observation per replicate. The observed behavioral repertoire is given in Table 5.4. Prey were counted, and missing or dead animals replaced every 4-8 h, so that prey depletion never exceeded 20% at any time. Five replicates measuring capture rate and four replicates including behavioral observations were conducted for each of the treatment combinations.

Interference coefficients were calculated from the slope of regression of  $\log(\text{predator density})$  versus  $\log(\text{area of discovery})$  (Hassell 1971). Slopes were compared using an F-test for multiple-slope comparison (Zar 1974). Behavioral data were normalized using a  $\log(x+1)$  transformation, and the effects of increasing prey and predator density analyzed using regression and partial regression analysis.

Table 5.4. Behavioral repertoire exhibited by Kogotus during functional response and interference experiments.

BEHAVIOR	DESCRIPTION
Moving	Crawling on substrate
Resting	Stationary on substrate
Swimming	In water column, swimming or drifting
Encounter	Contact prey with head or antennae
Attack	Lunge toward encountered prey
Capture	Prey grasped, followed by at least partial consumption
Handling time	Time from capture to total consumption or discarding of prey
Predator encounter	Contact with another predator

## Results

### Benefit/Cost Estimates

#### 1) Functional Response

The functional response shown by Kogotus over a 24 h period (one complete light/dark cycle) was a typical Type II (sensu Holling 1959) curve (Fig. 5.2). After the initial 8 h period when the predators fed avidly, the numbers of prey taken did not vary between the periods of light and dark (Table 5.5). Due to the absence of diurnal periodicity (see also Chapter 6), the behaviors observed during the light periods were taken to be representative of overall feeding behavior.

Time spent moving, resting or swimming was not significantly correlated with prey density. However, significantly more time was spent moving at intermediate prey densities (20) than at high (40, 50) or low (10) prey densities ( $F=3.73$ , ANOVA on log-transformed data). Encounter rate while moving (number of encounters per minute moving) was seven times higher than while resting (Fig. 5.3a), although actual number of encounters was only about 2.5 times higher, since Kogotus spent about 75% of its time stationary. Kogotus attacked the same percentage of encountered prey (30%) while moving as while resting.

Encounter rate when moving or resting increased significantly with increases in Baetis density (partial regression analysis correcting for time moving ( $r=.60$ ) or resting ( $r=.72$ )) (Fig. 5.3a). The actual number of moving Kogotus-Baetis encounters increased as Baetis density increased to 20 per stream, and then decreased steadily with further increases in Baetis density (Fig. 5.3c). This appeared to be related to the amount of time Kogotus spent moving on the substrate (Fig. 5.3b). When encounters while resting were included, the number of Kogotus-Baetis encounters tended to level off at high prey densities (Fig. 5.3c). Tendency to attack an encountered prey did not change as function of Baetis density. Thus, increased capture rates with increased Baetis density appeared to be simply a function of increased encounter rate and changes in time spent moving.

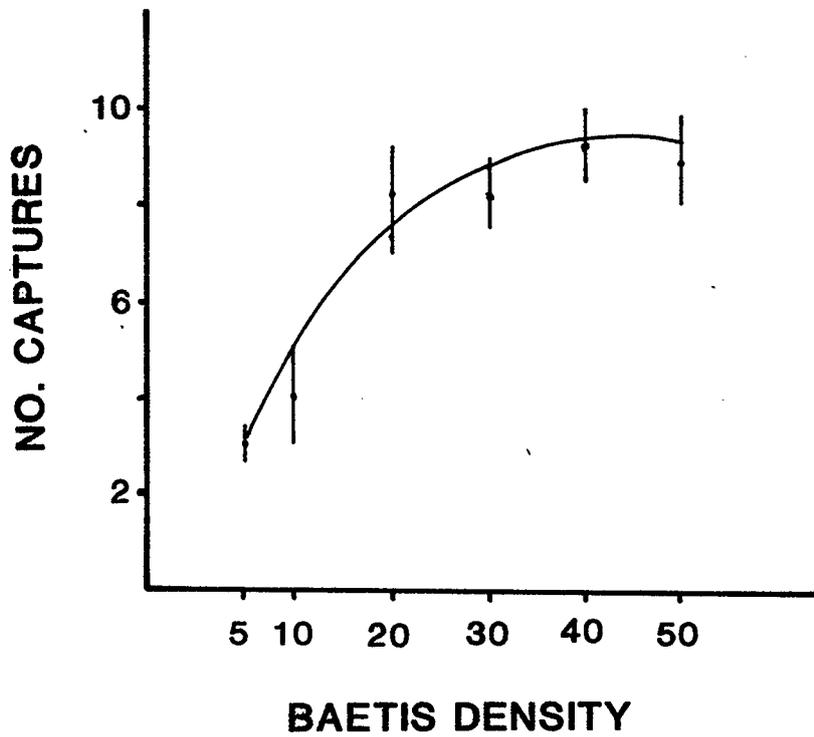


Fig. 5.2. The functional response of Kogotus determined over a period of 24 h. Error bars are 1 SE.

Table 5.5. Comparison of number of captures during light and dark 8 h intervals, excluding the first 8 h period. Standard errors are in parentheses.

<u>BAETIS</u> DENSITY	CAPTURES	
	LIGHT	DARK
5	0.8 (0.3)	1.4 (0.6)
10	1.1 (0.2)	1.3 (0.4)
20	0.9 (0.3)	1.4 (0.4)
30	1.8 (0.3)	1.4 (0.3)
40	1.3 (0.3)	1.4 (0.4)
50	1.7 (0.3)	0.8 (0.3)

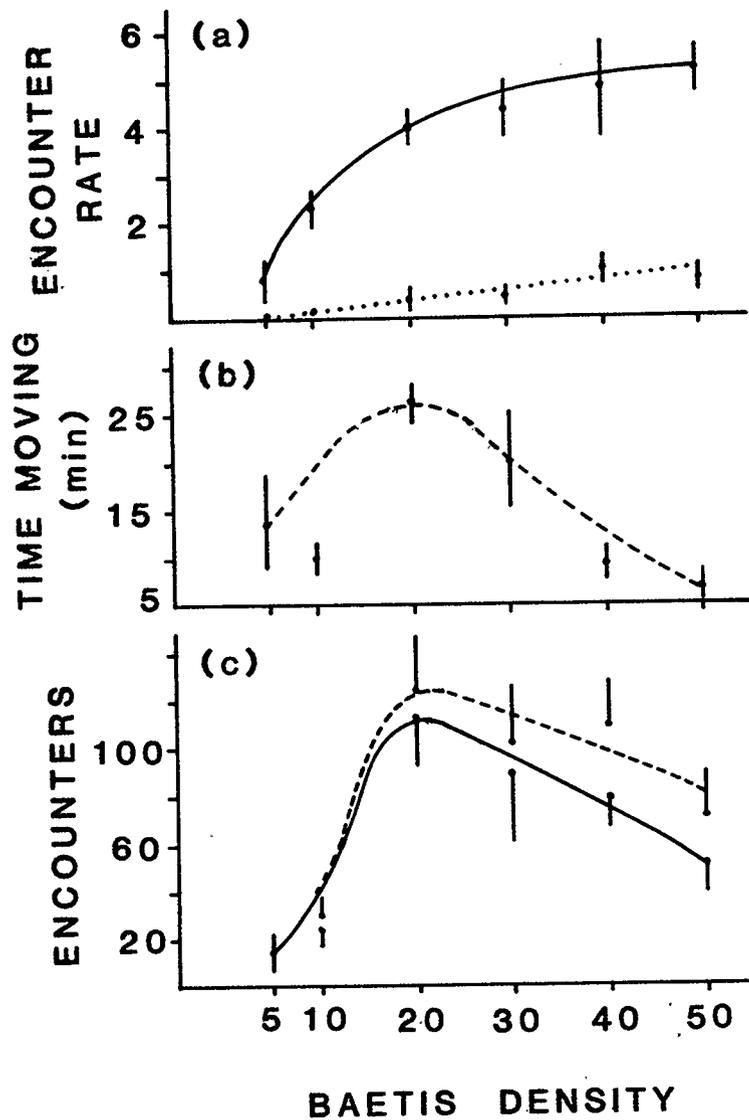


Fig. 5.3. The effects of Baetis density on (a) encounter rate (encounters/min) while moving (—) and resting (···), (b) the time spent moving by Kogotus and (c) the total number of Baetis-Kogotus encounters (---) and the number of encounters while Kogotus was moving (—). Error bars are 1 SE.

## 2) Interference

Increasing the predator density within the streams caused a significant decrease in the number of captures per Kogotus at each prey density ( $r = -.53, -.65$  and  $-.56$  for 10, 30 and 50 Baetis) (Fig. 5.4). Interference coefficients did not differ significantly between prey densities (0.77, 0.62, and 0.55 for 10, 30 and 50 Baetis per stream, respectively).

At a density of ten Baetis, capture rates were positively correlated with number of encounters ( $r = .52$ ) and attacks ( $r = .70$ ) by Kogotus while moving. As predator density increased, Kogotus tended to spend less time moving ( $r = .35$ ), and thus the number of encounters while moving also decreased ( $r = -.63$ ) (Fig. 5.5). Encounter rates while moving ( $r = -.60$ ) and while resting ( $r = -.46$ ) were also lower at high Kogotus densities. No significant increase in encounters with other predators was observed, due to the reduced time spent moving, and the probability of attack did not change with predator density.

At higher Baetis densities, despite a similar decrease in number of captures per predator, there was no significant correlation between encounter or attack rates and number of Kogotus present. Predator-predator encounters while resting, however, were significantly higher at high predator density (ANOVA,  $F = 12.5, 8.0$  for 30 and 50 Baetis).

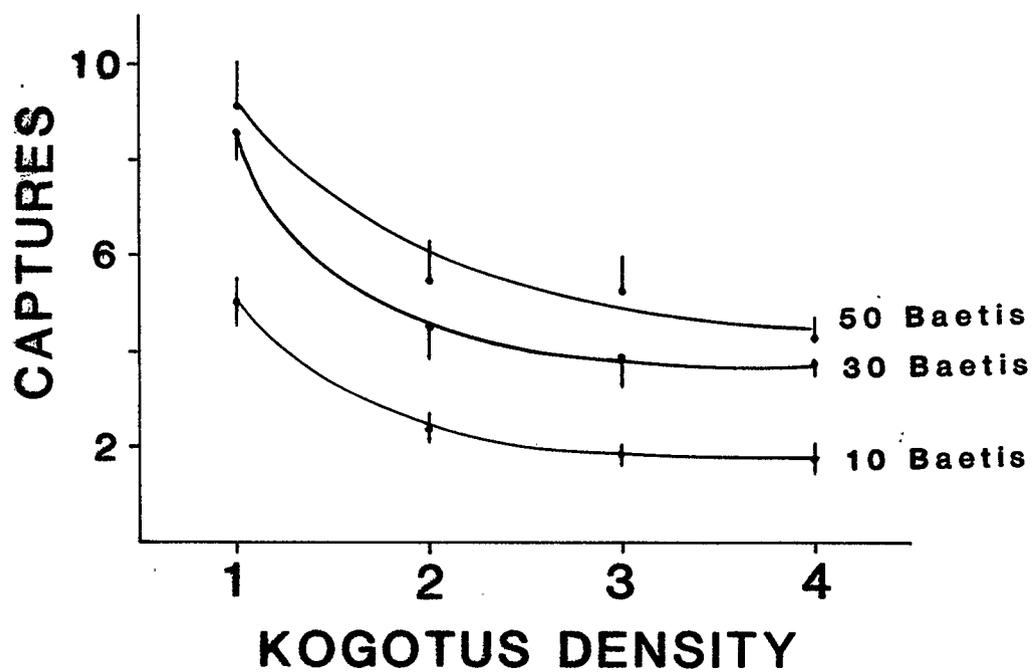


Fig. 5.4. The effect of increasing Kogotus density on per predator capture rate at prey densities of 10, 30 and 50 Baetis per stream. Error bars are 1 SE.

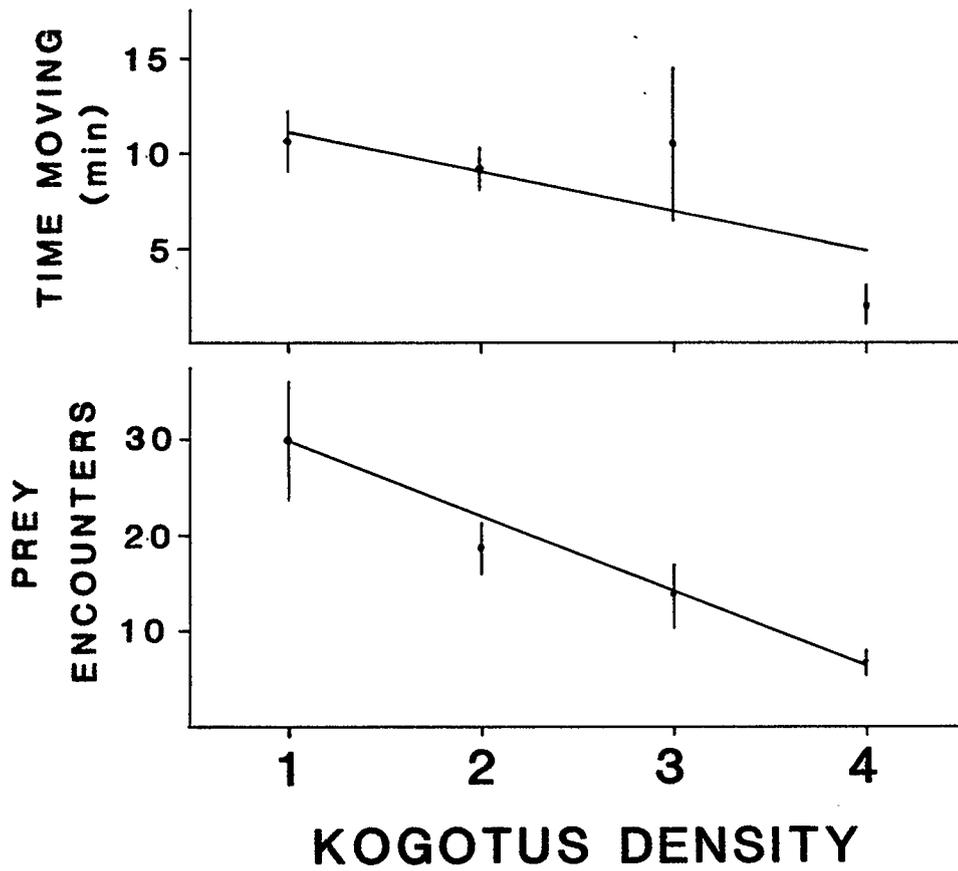


Fig. 5.5. The change in time spent moving and the number of prey encounters as Kogotus density (number per stream) increased for the prey density of 10/stream. Error bars are 1 SE.

### Optimal Predator Distribution

The laboratory experiments provided data on per predator capture rates in a single patch, from which the following relationships between prey and predator density, and capture rates were derived. Capture rates ( $f$ ) as a function of prey density ( $x$ ) for a solitary predator are given by an approximation to a Michaelis-Menten function:

$$f = 11x/(x+12)$$

where 11 is the maximum attainable feeding rate, and 12 is the prey density at which a feeding rate of one-half the maximum occurs. A Michaelis-Menten function is mathematically equivalent to Holling's disc equation, but does not require the estimation of handling time or area of discovery (Williams and Juliano 1985). Capture success ( $c$ ) when interference from other predators is considered is given by the linear approximation of the interference curves:

$$c = p(f-1.8(p-1))$$

where  $p$  is predator density in a patch, and 1.8 is the average slope of the interference curves. (Captures were not permitted to be negative.)

Using these equations, it was possible to predict the optimal distribution of predators for various levels of prey contagion. Assuming a particular distribution of prey in ten patches, capture rates were calculated for predator

distributions ranging from uniform to contagious. The increasingly aggregated distribution of the predator was arranged to correspond with the distribution of the prey, that is, predators aggregated in good (high prey density) patches rather than poor ones. The variance ( $s^2$ ) to mean ( $x$ ) ratio was used as a measure of contagion, where a distribution is uniform for  $s^2/x < 1$ , random for  $s^2/x = 1$  and contagious for  $s^2/x > 1$  (Elliott 1977). The effect of increasing predator contagion was examined at three levels of prey aggregation, a uniform distribution, and degrees of contagion corresponding to the average ( $s^2/x = 1.7$ ) and double the average ( $s^2/x = 1.5$ ) level observed in the field.

The optimal predator distribution was determined by plotting the degree of predator aggregation against number of captures, assuming, first, no interference and then the measured level of interference. Without interference, increasing predator aggregation had no effect when prey were uniformly distributed, but increased capture rates when prey were clumped (Fig. 5.6a). When interference effects were included, the exact location of the optimum shifted slightly with differing levels of prey contagion, but the highest capture rates were always produced by a uniform to random predator distribution (Fig. 5.6b).

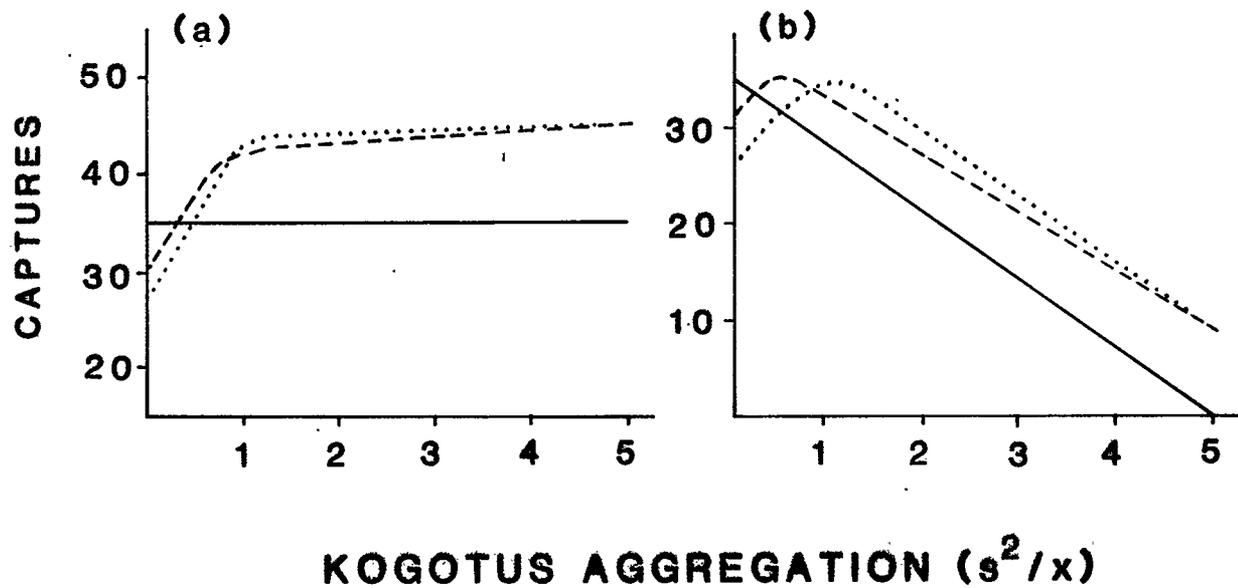


Fig. 5.6. Changes in the calculated predator capture rate with increasing predator aggregation using (a) experimentally derived benefits only and (b) including costs owing to interference. Prey distributions were assumed to be uniform (—), moderately clumped (---), and highly clumped (···).

## Discussion

## Assessment of Cost and Benefits

## 1) Functional Response

Although every effort was made to present the animals with as natural an environment as was possible in a laboratory, certain artificial conditions could not be avoided. The environment was necessarily simplified over that in the field, with a constant temperature rather than diel fluctuations, constant current, and a substrate of homogeneous coarse sand rather than a heterogeneous mixture. Circular streams, which allowed the animals unlimited movement upstream and downstream minimized the effects of using a relatively small area. This was particularly important for Baetis which escapes by swimming downstream. In order to fully predict behavior in the natural environment, each of these factors would have to be analyzed both in isolation and in conjunction with the other factors. These experiments were conducted in standardized conditions which simulated the mean but not the variance of natural conditions, and thus must be considered only a first approximation to elucidating the behavior of Kogotus in the field.

The functional response shown by Kogotus was similar to that shown by a variety of other aquatic invertebrate predators without alternative food available (Thompson

1975; Fox and Murdoch 1978; Giller 1980; Porter et al. 1983). It is unlikely that the asymptote of the curve was produced by increased handling time limiting the available search time (Holling 1959), as handling time averaged 1.5 min per prey, and even at the highest capture rate, total handling time would be less than 15 min, or about 1% of the total 24 h available. In addition, at higher prey densities some prey were often left partially consumed, and thus satiation would appear to be a more plausible explanation.

Increase in capture rate with higher prey density appeared to be primarily a function of encounter rate. As prey density increased, Kogotus tended to spend, first more time, then less time moving on the substrate, and thus total number of encounters levelled off at the higher prey densities. In addition to being energetically advantageous, this strategy could minimize prey disturbance and dispersal, and reduce the vulnerability of Kogotus to predation. It has been postulated that damselflies also decrease movement at high prey densities (Akre and Johnson 1979), and dytiscid larvae have been shown to switch tactics from active search to ambush as prey density increased (Förmanowicz 1983). There was no change in the tendency of Kogotus to attack an encountered prey as prey density increased, indicating no tendency for attack rate

to be either stimulated or depressed by encounter frequency. The functional response curve, therefore, appears to be produced solely by increased encounter rate as a passive result of increased prey density, modified behaviorally by changes in time spent moving.

## 2) Interference

The interference experiments were conducted to test whether the predators negatively affected each other's foraging efficiency when present in the same patch. The calculated interference coefficients ranging from 0.55 to 0.77 are at the upper end of the range of recorded laboratory results (Hassell 1978). As the present experiments were designed to measure only behavioral interference, eliminating effects of prey exploitation and aggregation, the coefficients are especially high. If patch densities had been allowed to deplete as prey were taken, measured interference effects would have been even higher, particularly at low prey densities.

Since, with a high level of interference, the impact each predator has on the prey population decreases sharply as predator density goes up, a stabilizing effect on the predator-prey interaction would be expected (Hassell 1978). If the interference coefficients had decreased as prey density increased, this would have further contributed to stability (Sih 1981), but despite a five-fold difference in

prey density, no significant difference in interference coefficients was observed. It was predicted, therefore, that the mechanisms leading to reduced foraging efficiency would be independent of prey density.

From behavioral observations, however, there appeared to be a difference in the factors leading to reduced capture rates at high and low prey densities. At low prey densities, factors influencing encounter rate seemed to be of primary importance. The decrease in number of prey encounters was largely, but not entirely, due to decreased time spent moving, since encounters, when corrected for time spent moving and resting, also decreased. Possible explanations include changes in predator speed and increased prey avoidance. Since Baetis reacts to contact with Kogotus by rising into the water column and swimming away (Peckarksy 1980; pers. obs.), it is likely that Baetis spends more of its time swimming and drifting when predator densities are high. As probability of attack was not increased or decreased by prey density, reduction in capture rate appears to be primarily a result of decreased encounter rates attributable to change in predator behavior (decreased time moving) and prey behavior (increased swimming).

At high prey densities, on the other hand, reduced capture rates were neither related to encounter rate nor to

probability of attack, but were negatively correlated with numbers of encounters with other predators. At low prey densities predator encounter rate remained low, as predators reduced the amount of time spent moving. At higher prey densities, however, predators did not modify their behavior, and predator encounter rates were high. As a result, interference mechanisms likely to be produced by high predator encounter frequencies, such as interruption of attacking predators, mis-direction of attack due to distraction, or other factors leading to an increase in prey escape success, probably took on greater importance.

#### Interference and Optimal Distribution

A particular distribution of animals in a lotic ecosystem is the end product of many processes, including predator foraging strategies, prey response and physical constraints. However, a calculation of optimal distribution ignores the processes and constraints affecting its production and maintenance, and simply determines the most advantageous endpoint. It is clearly possible for a particular distribution pattern to be produced by quite dissimilar mechanisms, which this determination of optimal distribution did not attempt to address.

The calculated optimal predator distribution was dramatically affected by including mutual interference

between predators. When interference between predators was excluded, traditional optimal foraging theory correctly predicts that aggregating in high density prey patches will increase capture rates (Fig. 5.6a). At the level of interference measured for Kogotus, however, distributions that were uniform or random produced higher capture rates than aggregation in prey patches. This implies little advantage for developing the ability to accurately assess prey density or for foraging in high density patches. In addition, this result is consistent with the earlier observation (Section 5.1) that in the field Kogotus is usually randomly distributed despite the contagious distribution of its prey. This study has demonstrated that, given the measured level of interference between Kogotus larvae, there is no advantage in terms of capture rate, to aggregating in high density prey patches. Two mechanisms which have the potential to produce a random predator distribution, avoidance of other predators and ephemeral prey patches, will be discussed in the next section.

### 5.3. A COMPARISON OF ALTERNATIVE FEEDING STRATEGIES

#### Introduction

The preceding analysis demonstrated that given the level of mutual interference between Kogotus larvae, a random distribution produced higher rates of food intake than a highly aggregated distribution. It did not, however, attempt to identify mechanisms by which such a distribution might be attained and maintained. There are at least three mechanisms which could potentially produce a predator distribution which is uniform to random in spite of patchily distributed prey. The first is a predator strategy in which areas containing other predators are avoided. The spacing effect of between predator aggression has already been demonstrated for Trichoptera (Glass and Bovbjerg 1969; Hildrew and Townsend 1980), a zygopteran (Baker 1980), and a perlid (Sjostrom 1983). The circumstances under which such a strategy is advantageous are not completely obvious, however. Presumably a high cost associated with sharing prey patches is a necessary prerequisite, but particular prey distributions and densities, predator densities and costs of movement between patches could either reduce or enhance this advantage. A second possible mechanism involves the behavior of the prey. Patch use models associated with optimal foraging

theory have assumed a sedentary rather than active prey, and therefore assume that prey density in the immediate future will be similar to that presently assessed, subject only to exploitation by the predator. A prey such as Baetis that actively avoids its predators by swimming away does not easily fit this pattern. Patches become very short-lived, probably too ephemeral for predator aggregation to be observed, and perhaps even too ephemeral for attempts to respond to prey density to be beneficial for the predator. A third possibility is that of no strategy at all; the predator could be simply moving at random within a given habitat.

This study determines, by means of a computer simulation, what types of circumstances favor a strategy of responding to prey distributions, as opposed to responding to the presence of conspecific competitors. The following questions were posed:

- 1) Does a strategy of responding to prey patches produce, on average, a higher feeding rate than a strategy of avoiding other predators?
- 2) How do these results vary with prey density, predator density, degree of prey mobility, and cost of travelling between patches?
- 3) Which strategy produces the lower between predator variance in food gain?

- 4) What predator distributions are produced by the two strategies?

#### Methods

The movement of predators and prey in an arena of 100 discrete patches (Fig. 5.7) was simulated using a Honeywell 6880 computer. Initially, prey were placed in the patches in an aggregated distribution and the predators randomly assigned to the patches. Predators fed at a rate dependent on prey and predator density within the patch, using the relationship determined in Section 5.2, and moved between patches according to the rules of one of two strategies. Predators attempting to aggregate in prey patches (Aggregative Strategy AS) remained in a patch if prey density was above the habitat average. Probability of moving out of a patch increased as prey density dropped below this level. Predators avoiding conspecifics (Spacing Strategy SS) remained in a patch if alone, and the probability of leaving a patch increased as predator density in that patch increased. In both cases probabilities of moving were used to allow likelihood of encounter with, and thus response to, prey or other predators to be an increasing but stochastic function of density. Predators electing to move out of a patch selected the next patch at random. To simulate a prey

escape response such as that seen for Baetis, prey moved out of patches that contained predators. Preliminary simulations showed that feeding rates and distributions usually stabilized in 20 to 25 cycles of feeding and movement, and thus all calculations were performed after 30 cycles.

Levels of the critical input variables, prey and predator density, initial prey aggregation, fraction of prey moving out of a patch, and predator travel costs were varied in the simulation (Table 5.6). Five replicate runs were made for each combination of variable levels and the food gains of predators using the two strategies were compared using analysis of variance. Between predator variation in food intake, the final levels of predator and prey aggregation and the final correlation between predator and prey distributions were also calculated for each strategy.

To determine if the differences between the two strategies were simply the result of differential rates of movement rather than a particular pattern of movement, each strategy was also compared to a control which mimicked the rate of movement between patches, but imposed these movements randomly rather than in response to prey or predators.

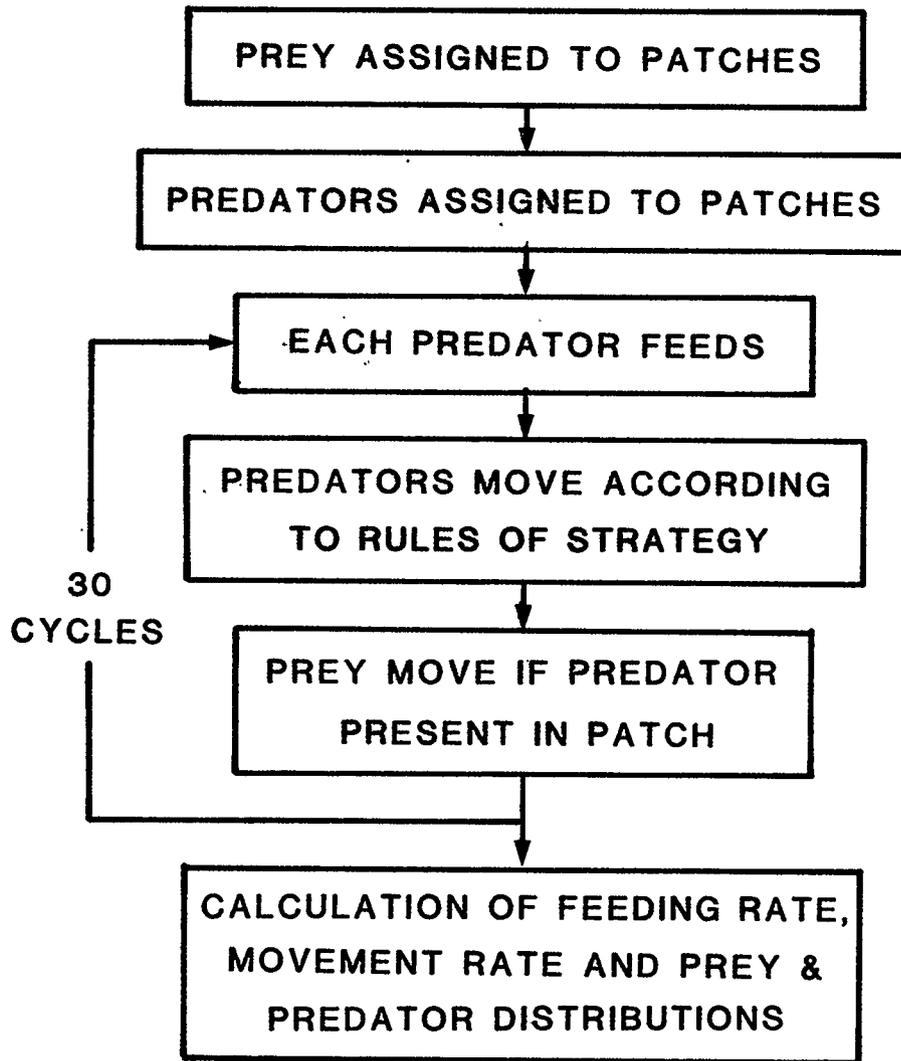


Fig. 5.7. Flowchart of the computer program simulating predator feeding strategies.

Table 5.6. Levels of variables included in the comparison of feeding strategies by simulation.

FACTOR -----	LEVELS -----
Prey density (per patch)	5, 10, 20, 30
Initial prey aggregation (variance to mean ratio)	5.0, 20.0, 75.0
Fraction of prey moving in response to predator	0, 0.2, 0.4, 0.6
Predator density (per patch)	0.5, 1.0, 2.0, 3.0
Cost of moving between patches (prey equivalents)	0, 0.5, 1.0, 1.5, 2.0

## Results

## Predator Distribution

An aggregative strategy (AS) produced a positive correlation between predator and prey only when the prey were sedentary (Table 5.7). The correlation between predator and prey increased as prey clumping increased. When prey were allowed to move between patches, the aggregative strategy resulted in uncorrelated distributions. The spacing strategy (SS) resulted in uncorrelated distributions as well, except when predator densities were very low and prey were allowed to move. In this case the prey 'escaped' into patches without predators, producing negative correlations.

Table 5.7. Correlation of the final distributions of prey and predator obtained under aggregative (AS) and spacing (SS) strategies for the lowest level of prey aggregation. Coefficients greater than .17 indicate a significantly positive correlation.

PREY MOVES	PREDATOR DENSITY	CORRELATION COEFFICIENT (r)			
		LOW PREY		HIGH PREY	
		AS	SS	AS	SS
0%	0.5	.30	.00	.12	.00
	1.0	.32	.00	.13	.00
	2.0	.15	.00	.12	.00
	3.0	.09	.00	.05	.00
20%	0.5	-.04	-.36	-.09	-.45
	1.0	-.11	-.08	-.12	-.08
	2.0	.01	.00	-.08	-.01
	3.0	.01	.00	.01	.00
40%	0.5	-.04	-.40	-.11	-.47
	1.0	.02	-.13	-.11	-.13
	2.0	.03	-.01	-.03	-.01
	3.0	.02	.00	.02	.00
60%	0.5	-.08	-.44	-.10	-.47
	1.0	-.06	-.15	-.10	-.15
	2.0	.01	-.02	-.04	-.03
	3.0	.02	.00	.02	.01

When prey were sedentary, an aggregative strategy resulted in a significantly clumped predator distribution at the higher levels of prey aggregation (Table 5.8). When level of prey aggregation was low, significant predator clumping was restricted to the lower predator densities (Table 5.8). When prey were allowed to move, however, AS predator distributions were not significantly different from random, irrespective of prey contagion or predator density. A spacing strategy (SS) always resulted in a distribution that was significantly uniform at the lowest predator density, and not different from random at higher predator densities (Table 5.8).

Table 5.8. Final predator distributions with sedentary prey as determined by the variance to mean ratio test. Distributions are significantly clumped (+), or uniform (-), or not significantly different from random (0).

		DISTRIBUTION							
		PREY				DENSITY			
		5		10		20		30	
PREY AGG.	PRED DENSITY	AS	SS	AS	SS	AS	SS	AS	SS
5.0	0.5	0	-	+	-	+	-	+	-
	1.0	0	0	+	0	+	0	+	0
	2.0	0	0	0	0	0	0	0	0
	3.0	0	0	0	0	0	0	0	0
20.0	0.5	+	-	+	-	+	-	+	-
	1.0	+	0	+	0	+	0	+	0
	2.0	+	0	+	0	+	0	+	0
	3.0	0	0	+	0	+	0	+	0
75.0	0.5	+	-	+	-	+	-	+	-
	1.0	+	0	+	0	+	0	+	0
	2.0	0	0	+	0	+	0	+	0
	3.0	0	0	0	0	+	0	+	0

### Average Food Intake

As the initial level of prey aggregation and prey density had little effect on the pattern of strategy success, these levels were combined for graphical analysis. An aggregative strategy (AS) was always superior in terms of average food gain at low predator densities (<1 per patch) while at high predator densities either the spacing strategy (SS) was superior or there was no difference between the strategies (Fig. 5.8). At high predator densities, spacing tended to be superior when prey were either completely sedentary ( $F=0$ ), or when movement rate was high ( $F=0.6$ ). As travel cost increased there was less difference between the strategies.

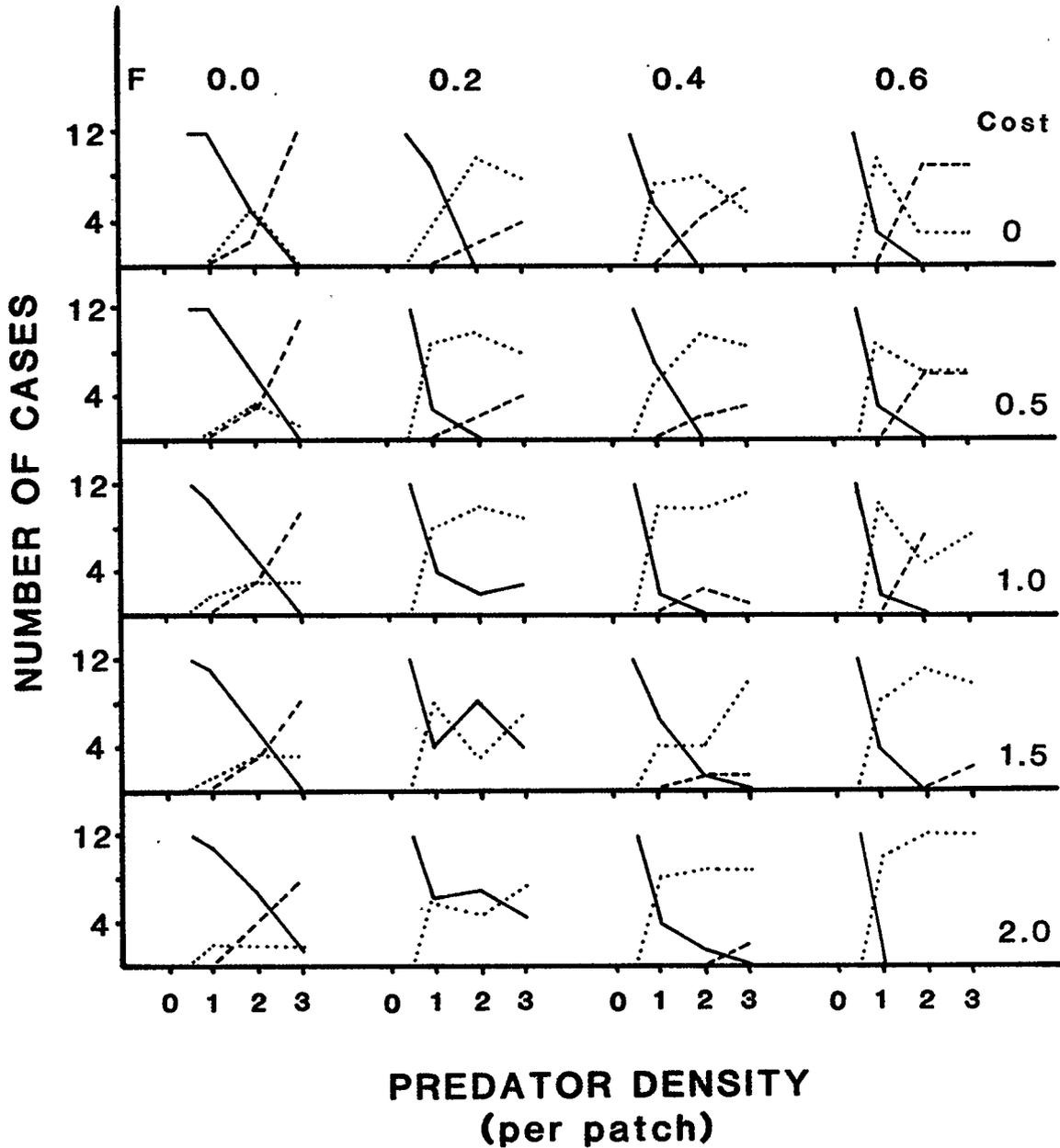


Fig. 5.8. Number of treatment combinations resulting in higher food gain for predators aggregating (—) versus spacing (---), as the fraction of prey moving (F) and predator travel cost increases. The number of cases in which the two strategies did not differ significantly is indicated by (···).

### Predator Movement

In general, AS predators moved more frequently than SS predators at low predator densities, while the reverse was true at high predator densities (Fig. 5.9). For AS predators, movement rates were both lower and less influenced by predator density at high prey levels. SS predator movement, of course, was not affected by prey density at all.

Since higher rates of movement corresponded to higher feeding rates, each strategy was then compared with a control run in which predators moved randomly at the appropriate frequency for each prey density/predator density combination. Aggregating predators did much better than the randomly moving controls at low predator densities, indicating that the movement pattern and not just the rate were responsible for the high feeding success of this strategy (Fig. 5.10). At high predator densities, randomly moving predators actually did better than aggregating predators, demonstrating again that this movement pattern itself was responsible for the feeding rates observed. Spacing predators were more successful than randomly moving predators in about half the cases at low predator densities (Fig. 5.10); random movement was superior a few times, and there was no difference in food

intake the rest of the time. At high predator densities, there was no difference between a spacing strategy and random movement.

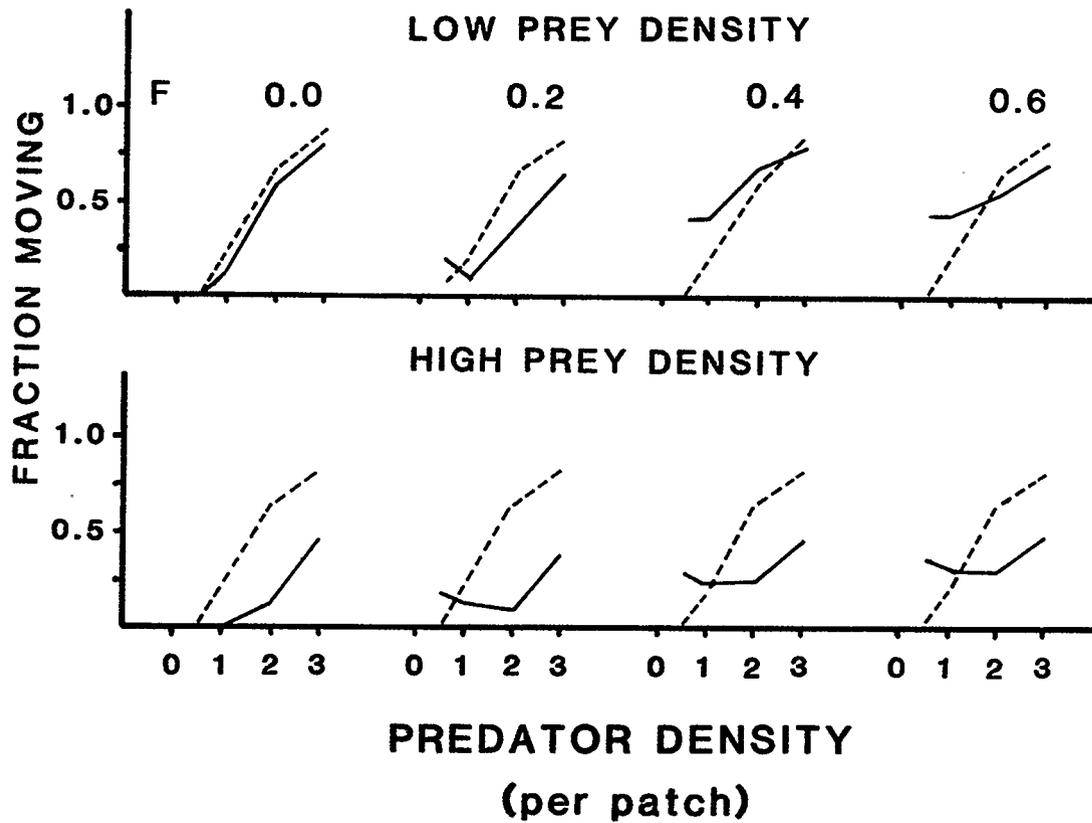


Fig. 5.9. Change in fraction of predators moving between patches each cycle under aggregation (—) versus spacing (---) strategies. Low prey includes densities of 5 and 10 per patch, and high prey includes 20 and 30 per patch.

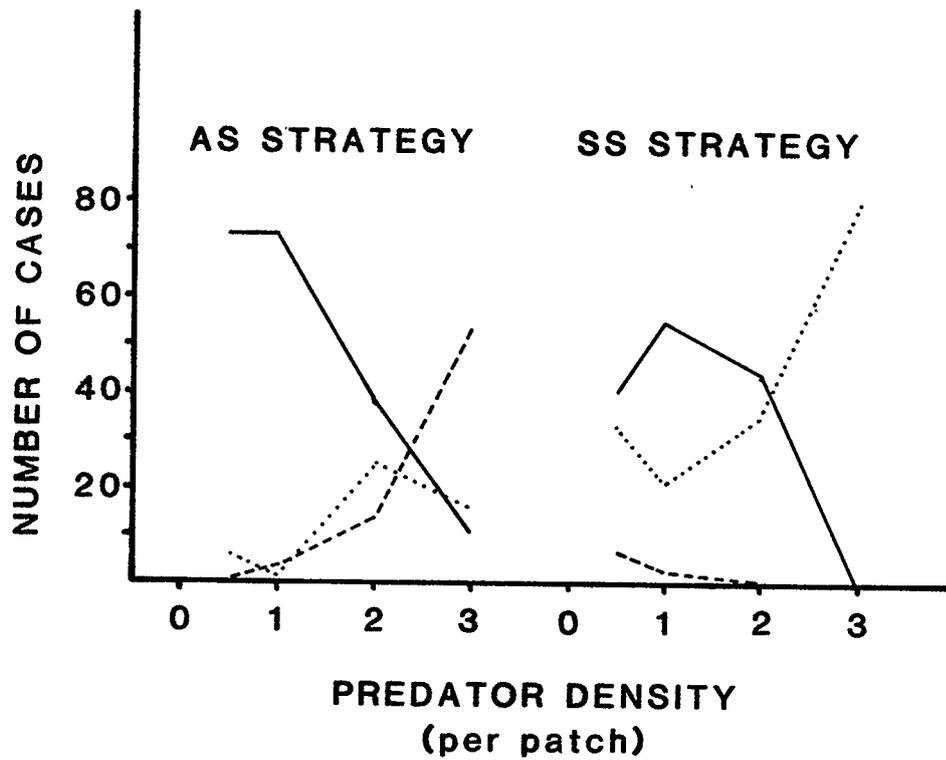


Fig. 5.10. Number of cases resulting in higher food gain for predators using aggregative (AS) or spacing (SS) strategies (—) versus randomly moving predators (---). The number of cases in which the strategy did not differ significantly from the random control is indicated by (···).

### Variation in Food Intake

Low prey and predator densities tended to result in lower variation in food gain for aggregating predators than for spacing predators when prey were sedentary (Table 5.9). When prey were allowed to move, spacing predators generally had a less variable food intake at the lowest predator density (0.5 per patch), but at higher predator densities similar variation was seen for both strategies. These trends were consistent across the various travel costs.

Table 5.9. Comparison of aggregative (AS) and spacing (SS) feeding strategies with respect to variation in food gain.

PREY MOVES	PRED DENSITY	COEFFICIENT OF VARIATION							
		AS	SS	AS	SS	AS	SS	AS	SS
0%	0.5	.38	.91	.22	.47	.21	.24	.20	.14
	1.0	.47	.68	.24	.42	.20	.23	.20	.18
	2.0	.62	.61	.40	.40	.28	.23	.19	.15
	3.0	.84	.79	.53	.49	.34	.31	.27	.24
20%	0.5	.23	.19	.17	.00	.18	.17	.16	.22
	1.0	.18	.40	.19	.17	.18	.14	.16	.16
	2.0	.28	.26	.26	.23	.19	.15	.16	.12
	3.0	.41	.43	.36	.38	.26	.25	.23	.21
40%	0.5	.26	.11	.21	.06	.20	.00	.15	.00
	1.0	.28	.38	.22	.25	.19	.19	.18	.17
	2.0	.43	.46	.30	.31	.24	.20	.17	.16
	3.0	.64	.67	.46	.45	.30	.29	.25	.23
60%	0.5	.26	.00	.23	.00	.21	.00	.17	.00
	1.0	.27	.31	.24	.28	.23	.21	.20	.20
	2.0	.38	.36	.29	.28	.27	.21	.21	.17
	3.0	.51	.54	.40	.42	.30	.29	.27	.25

## Discussion

## Predator Distribution

This simulation demonstrates that either a spacing strategy or an aggregative strategy coupled with prey movement has the potential to produce a random predator distribution. Significant clumping of predators attempting to aggregate in prey patches occurs only when prey are completely sedentary, and a significantly uniform predator distribution occurs only when predators attempting to avoid each other are very rare. Similarly, positive correlations between aggregating predators and their prey only occur when the prey are completely sedentary. In view of these results, the random predator distributions observed within natural riffles in the field and the absence of significant correlations with the mobile prey, Baetis (Section 5.1), are not surprising. Random predator distributions are expected in all except the unrealistic category of completely sedentary prey, and even within this category, low prey/high predator combinations produce random distributions. The higher degree of correlation with Orthocladiinae may reflect the lower mobility of this group.

### Relative Food Intake

At low predator densities superiority of the aggregative strategy occurs for two reasons. First, predator density was low enough that any one patch did not often attain high predator densities and thus there was only a small interference effect countering the advantage of being in good prey patches. Secondly, SS predators are actually disadvantaged at low predator densities, since once the predators have spaced themselves, a large number of patches without predators remained as refugia for the prey. At low predator densities, an effective spacing strategy would have to include some movement in response to the absence of prey for a period of time, a giving-up time as was seen for a net-spinning trichopteran (Hildrew and Townsend 1980). At low predator densities, the advantage of aggregating over spacing was not solely due to the higher movement rate of AS predators, since an aggregating predator did much better than a predator moving randomly at the same rate. Spacing behavior was marginally better than the corresponding random movement, but this pattern of movement was clearly less beneficial than aggregating in prey patches.

At high predator densities, the interference effect took on a greater significance, eliminating the advantage of the aggregative strategy. The higher movement rate of

SS predators in this case was again likely a partial but not a total explanation. At high predator densities spacing was indistinguishable from random movement, and the movement rates were likely particularly effective with the highly mobile prey. An aggregating strategy, however, was actually poorer than random movement. In the case of sedentary prey, this result appeared to be due solely to interference effects, particularly since the aggregative strategy was least effective at low prey densities. When prey were mobile, moving out of patches with predators, the falseness of the prey density cue used by the predators probably also reduced food gain. As travel costs increased, the high movement rates of SS predators became a liability, and the two strategies produced similar final food gains.

There was no evidence that the disadvantage of a slightly lower average food gain was countered by lower between-predator variation in food intake. In most cases either there was little difference in feeding variability between the strategies, or the strategy with the higher food intake was also less variable. The only exceptions were the cases when prey were mobile and predator density was 0.5 per patch. In this case, however, the poorer strategy (SS) had such a low variance because food intake was at or near 0.

#### 5.4. CONCLUSION

From the distributional data, it seems clear that Kogotus is not effectively aggregating in prey patches. Within riffles, i.e., under relatively uniform substrate, current and depth, the distribution of Kogotus was uncorrelated with that of Baetis, and was significantly correlated with Orthoclaadiinae on only 25% of the sampling dates (April to July). The very different patch sizes observed for Kogotus ( $>900 \text{ cm}^2$ ) and its prey Baetis ( $<120 \text{ cm}^2$ ) and Orthoclaadiinae ( $=300 \text{ cm}^2$ ) provided further evidence that Kogotus was not directly responding to high density prey patches. In addition, Kogotus was usually randomly distributed within riffles, despite a significantly clumped prey distribution. This pattern was shown to be advantageous when predator-predator interactions were taken into consideration. The feeding rate of Kogotus was substantially lower when conspecifics were in close proximity, rendering the gain derived from a particular prey patch dependent on both prey and predator density. As a result of this mutual interference, highly aggregated predator distributions produced lower capture rates than random distributions.

Assuming that increased foraging efficiency increases fitness, it is expected that natural selection will have

favored mechanisms ensuring these favorable distributions. Two possible mechanisms were considered, 1) predators may be spacing themselves behaviorally or 2) prey mobility may be eradicating any distributional evidence of attempted aggregation on the part of the predator. Simulation showed that either spacing behavior or aggregative behavior coupled with a prey escape response was sufficient to produce random predator distributions. Furthermore, while aggregating produced higher feeding rates at low predator densities and spacing tended to be more beneficial at high predator densities, at intermediate densities there is no clear advantage to either strategy. These intermediate densities (1 and 2 per 50 cm<sup>2</sup> patch) are the most frequently encountered densities in the natural benthos from April through June (Fig. 5.11).

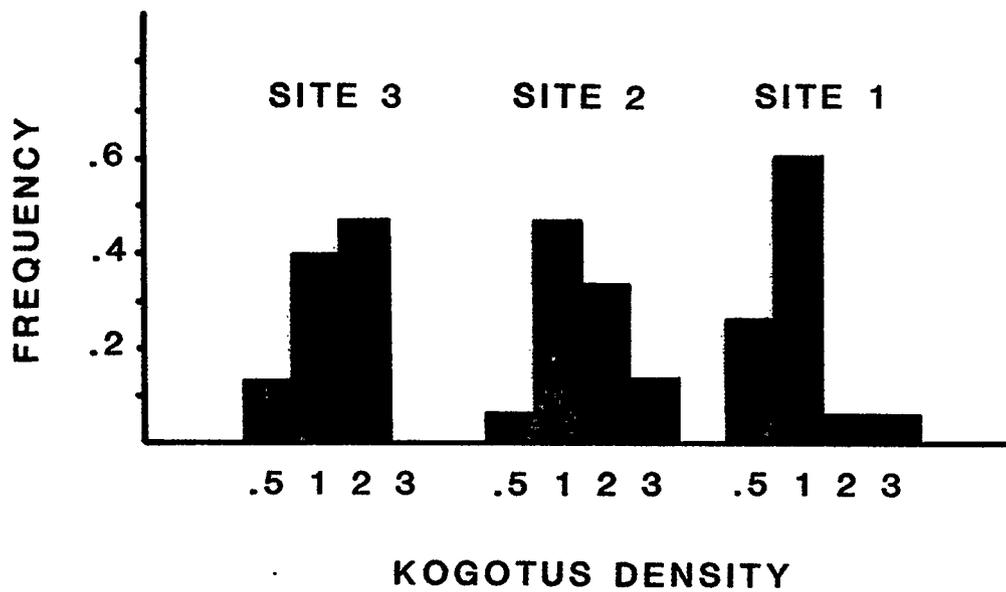


Fig. 5.11. Frequency of occurrences of four categories of natural Kogotus densities (per 50 cm<sup>2</sup> area) from April through June (1982-1984).

Behavioral observations also lead to somewhat ambivalent conclusions. Laboratory observations indicate that there is some response on the part of Kogotus to prey density, although it cannot be interpreted as clearly leading to aggregation in prey patches. Decreased movement rates in high prey density patches would tend to keep predators in such high quality patches. The same tendency at very low prey densities, however, would have exactly the opposite effect. Similarly, the observed aggressive behavior of Kogotus does lead to predators avoiding each other and occupying spaces out of touching distance of one another. At low prey densities predators avoided each other by reducing movement rates as predator density increased. At higher prey densities, however, movement rates were unrelated to predator density, indicating that other factors were influencing predator behavior.

It seems probable, therefore, that the foraging behavior and distribution of Kogotus is the end result of the interaction of several factors. The primary distribution pattern seems to be set by current and depth, or some unmeasured correlate of these factors. Within favorable ranges of these factors, Kogotus movement rates may be influenced by prey density or encounter rate. No aggregative pattern is seen, however, for at least three reasons. First, the instability of prey patches produced by even a relatively low rate of prey mobility makes

effective aggregation impossible. Secondly, movement patterns are affected by predator-predator encounters, and such spacing, even on a small scale, would tend to disrupt aggregative patterns. Thirdly, although a large number of predators are feeding on Baetis at this time of year, some are feeding on the alternative prey, Orthocladiinae, further obscuring any observable pattern.

In conclusion, although Kogotus does show some response to prey density in the laboratory, this response does not result in a distribution correlated with that of its prey in the field, probably due to predator-predator interactions and prey mobility. The fact that several mechanisms have been shown to have the potential to produce similar final distributions, re-emphasizes the dangers inherent in attempts to infer process from observed patterns.

## CHAPTER 6

THE EFFECT OF HUNGER LEVEL AND SUBSTRATE TYPE ON  
THE FUNCTIONAL REPOSE OF KOGOTUS

## Introduction

Functional response curves, which are simply a measure of how a predator responds to increases in prey density, have been divided into three categories (Holling 1959) (Fig. 6.1). Type I curves are characteristic of some filter feeders, Type II curves are observed for most invertebrate predators, and Type III curves are usually seen when an alternative prey is available or in heterogeneous environments (Hassell 1978). Predator response, and thus the shape and height of these curves varies with experimental conditions such as predator hunger level and heterogeneity of the experimental arena.

Some invertebrate predators have been shown to be more selective when satiated than when starved (Molles and Pietruska 1983; Pastorak 1980; Akre and Johnson 1979), and two distinct mechanisms have been reported to produce this shift in relative capture rates. In two species of Plecoptera as well as for Chaoborus (Diptera), change in the pattern of captures was effected by a change in attack frequency on particular prey (Molles and Pietruska 1983;

Pastorak 1980). The zygopterans, however, switched from a walking to ambush mode of search when satiated, thus altering the frequency of encounter (Akre and Johnson 1979).

A change in substrate type from sand, an essentially two dimensional surface, to gravel, results in a three dimensional and thus more heterogeneous arena. An increase in heterogeneity has been associated with reduced capture rates on the part of some predators. Trichoptera captured fewer plecopteran prey on stones and leaves than on sand (Hildrew and Townsend 1977), and predation by sculpins was reduced by the addition of pebbles and cobbles to a sand substrate (Brusven and Rose 1981). In both cases the mechanism thought to be producing the lower capture rates was the provision of prey refugia. It was not made clear, however, whether a fixed number of refuges were supposed to have produced these results or if reduced predator searching efficiency (equivalent to refuges for a fixed proportion of prey) was thought to be the causal factor. These two alternatives can be separated by construction of functional response curves. If prey captures are lower because some of the prey are in refugia (areas inaccessible to the predator), there should be a range of low prey densities (corresponding to the number of refugia) over which capture rate does not increase, producing a Type III

curve. (This result is functionally equivalent to reduced predator efficiency at low prey density only.) The two curves should ultimately reach the same plateau, although the asymptote obtained with refugia present will be delayed (Fig. 6.2a). If, on the other hand, the difference between capture rates is caused solely by lowered predator efficiency on one substrate type, the curves will differ as in Fig. 6.2b. Capture rates will be lower at all prey densities, but a sigmoid curve produced by low capture rates through a range of prey densities is not expected. Nor are the curves expected to necessarily reach the same final plateau.

The first objective of this section was to measure the effect that Kogotus hunger level has on prey capture rates, and to determine whether this change was produced by a change in movement pattern and thus encounter rate, or by a reduced tendency to attack encountered prey. The second objective was to compare functional response curves obtained on two substrate types, sand and gravel, with respect to shape and height of the curves.

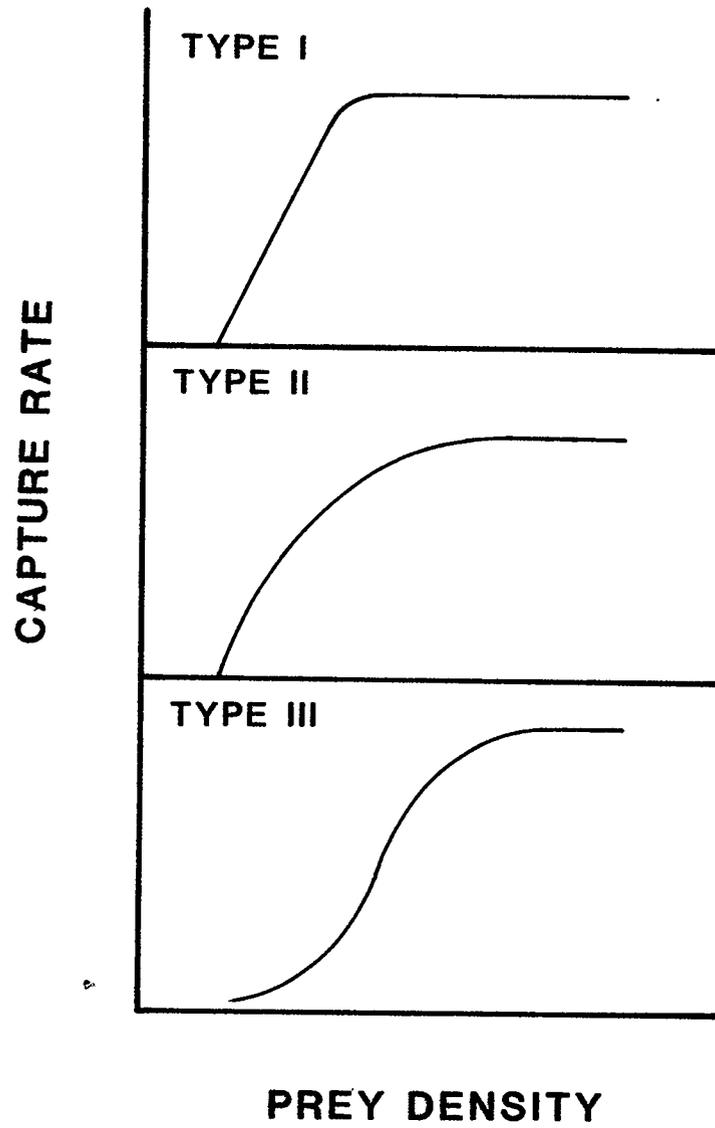


Fig. 6.1. Type I, Type II and Type II functional response curves.

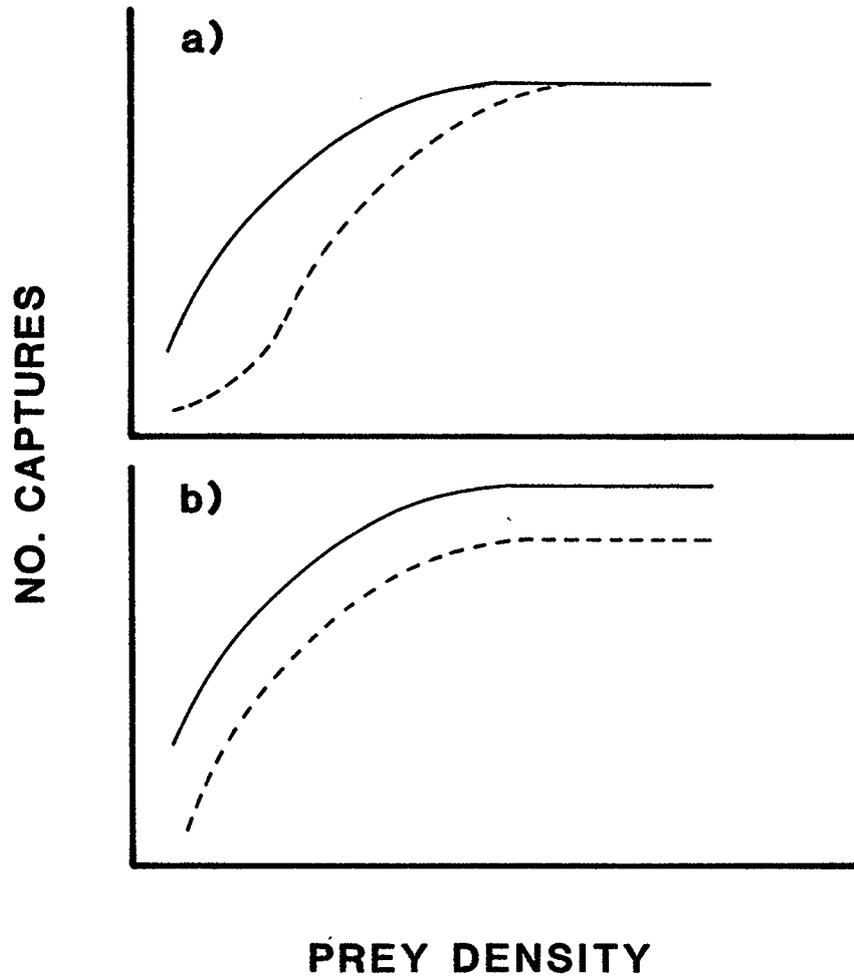


Fig. 6.2. Idealized functional response curves on homogeneous (—) versus heterogeneous (---) substrate. a) response when refugia are created and b) response when capture efficiency is lowered.

## Methods

All feeding trials testing for the effects of hunger level were conducted in small circular artificial streams (Fig. 3.7) at 8°C, with a sand substrate (1-2 mm) and a current of 5-7 cm/s. Predators of 20 to 25 mg wet wt were placed in individual streams where they were either starved for 48 h or fed ad libitum (50 Baetis available) for 24 h. Predators were used for the 'fed' treatment if they had consumed at least four Baetis over the 24 h feeding period. All experimental runs (8 h) were initiated at 1400 h by placing 5, 10, 20, 30, 40 or 50 Baetis (0.5-1.0 mm head width) in the streams (five replicates per treatment). Captured prey were replaced every 4 h to minimize exploitation effects. Behavioral observations (15 min) were conducted between 1500 and 1600 h, and between 1700 and 1800 h, as described for the interference experiments (Section 5.2).

Functional response curves were also constructed for predators foraging on a gravel (1 cm) versus sand (1-2 mm) substrate. Experimental runs (48 h) were conducted as above, with number of captures recorded every 8 h. Missing prey were replaced every 4 to 8 h. Captures at each prey density (five replicates per treatment) were compared using a Mann-Whitney-U test.

Functional response curve type was initially determined by comparing regressions corresponding to Type I, Type II and Type III curves. Type I involved a simple regression of captures (N) on prey density (D). Type II involved a regression of D/N on D/t, derived from:

$$D/N = 1/at + H(D/t), \quad (1)$$

a rearrangement of Holling's (1959) disc equation where 'H' is handling time, 'a' is search efficiency and 't' is time. Equation (1) produces a sigmoid (Type III) curve when:

$$a = bD/(1+cD) \quad (2)$$

where 'b' and 'c' are constants. This can be rearranged to produce the following straight line relationship:

$$D^2(1/N - H) = 1/b + c/b(D) \quad (3)$$

where  $D^2(1/N-H)$  can be regressed on D. The handling time obtained from the Type II regression was used for 'H' in this calculation.

A second method of distinguishing Types I, II and III curves, plotting the proportion captured versus the number of prey available, was also employed. In a decelerating (Type II) response, a negative slope should emerge, that is, the proportion captured will decrease with increasing prey density. In a Type I response, the slope should be 0, and portions of a Type III response should show a positive slope.

## Results

### Hunger Level

Starved Kogotus showed significantly higher capture rates than fed Kogotus at all experimental prey densities (Fig. 6.3). Hunger level did not affect time spent moving on the substrate, nor the number of encounters with the prey (Fig. 6.3). Starved predators, however, attacked a higher proportion of encountered prey than did fed predators (Table 6.1). In addition, fed Kogotus left a larger percentage of successfully captured prey partially unconsumed, particularly at high prey densities (Fig. 6.4).

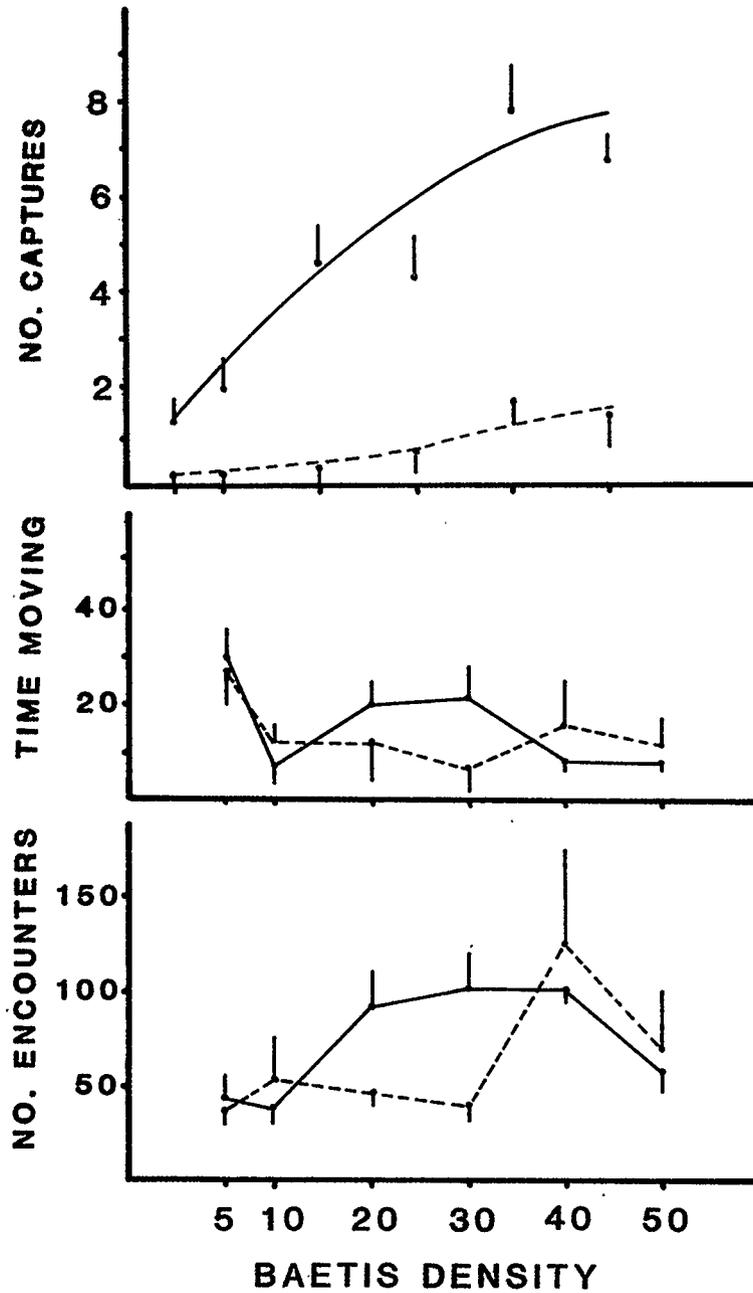


Fig. 6.3. Comparison of starved (—) and fed (---) Kogotus with respect to number of captures, time spent moving and number of encounters with the prey. Error bars are 1 SE.

Table 6.1. Proportion of encountered Baetis that were attacked by starved and fed Kogotus. Standard errors are in parentheses.

<u>BAETIS</u> DENSITY	PROPORTION	
	STARVED	FED
5	0.39 (0.11)	0.09 (0.06)
10	0.49 (0.18)	0.08 (0.03)
20	0.47 (0.18)	0.13 (0.02)
30	0.19 (0.03)	0.14 (0.11)
40	0.43 (0.10)	0.30 (0.08)
50	0.45 (0.08)	0.26 (0.14)

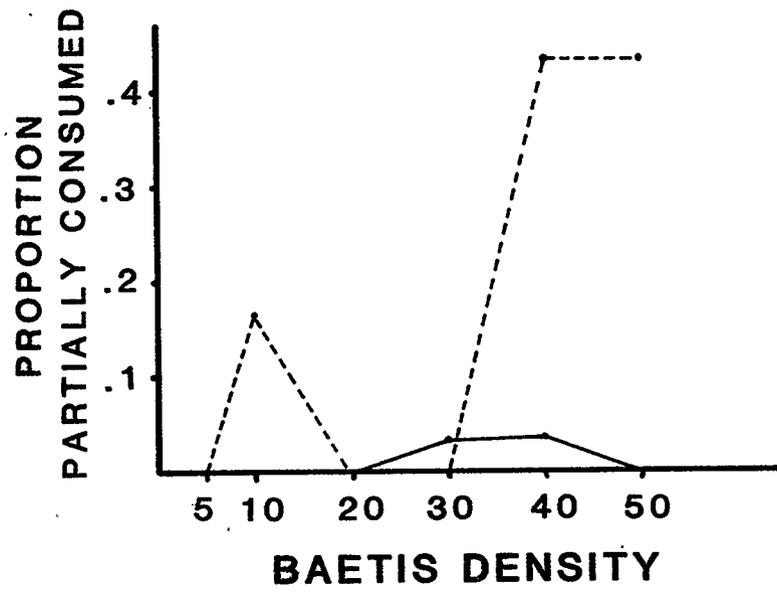


Fig. 6.4. Comparison of starved (—) and fed (---) Kogotus with respect to proportion of Baetis partially consumed.

### Substrate Type

Prey capture rates were lower for Kogotus foraging on a gravel as opposed to sand substrate (Fig 6.5). On sand over an 8 h period, the curve was best described by a straight line (Type I), while over the longer periods of 24 and 48 h the curves fit a Type II functional response (Table 6.2). On gravel, the 8, 24 and 48 h curves all showed the best fit to a Type I response curve.

Plots of proportion captured versus prey density also indicated that the 24 and 48 h responses on sand were Type II (Fig. 6.6). The overall slopes of the response on gravel as well as the 8 h response on sand were not significantly different from 0, coinciding again with the results of the regression analysis. The increase in proportion captured between densities of 5 and 10 Baetis for the 24 and 48 h responses on gravel, however, indicated that these curves are tending toward Type III.

As Baetis density increased, an increasing proportion of total captures took place in the first 8 h period (Table 6.3). Predators foraging on gravel tended to have a lower proportion of total captures in the first 8 h than did predators on sand (Table 6.3). The proportion of prey left partially unconsumed was similar for predators on the two substrate types (Table 6.4).

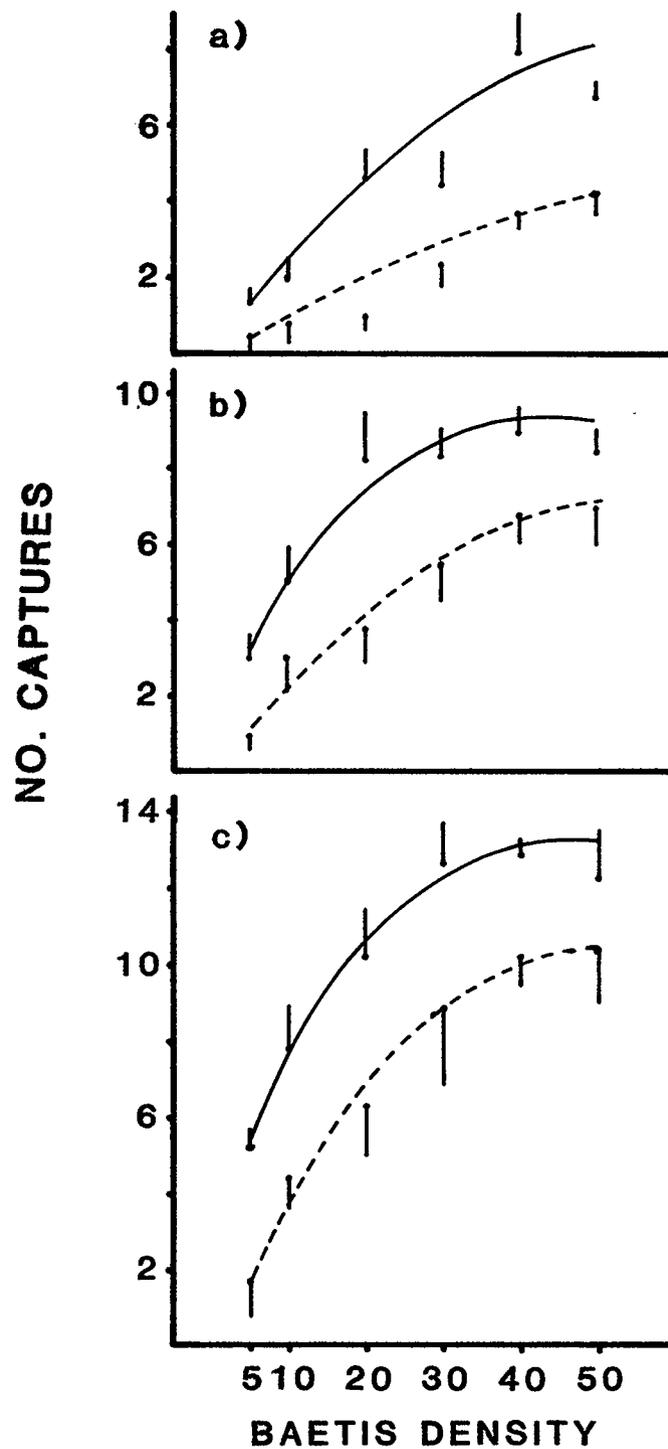


Fig. 6.5. Functional response curves obtained for starved Kogotus on sand (—) versus gravel (---) substrate over a) 8 h, b) 24 h, c) 48 h. Error bars are 1 SE.

Table 6.2. Fit of the capture data to Type I, Type II, and Type III functional response curves. Handling time (H) is given as calculated from the Type II fit.

SUBSTRATE	TIME (h)	COEFFICIENT ( $r^2$ )			H
		I	II	III	
SAND	8	.40	.12	.15	.13
	24	<u>.28</u>	.35	.31	.01
	48	.45	<u>.60</u>	.10	.07
GRAVEL	8	.60	.08	.39	.08
	24	<u>.59</u>	.28	.39	.04
	48	<u>.55</u>	.14	.26	.04

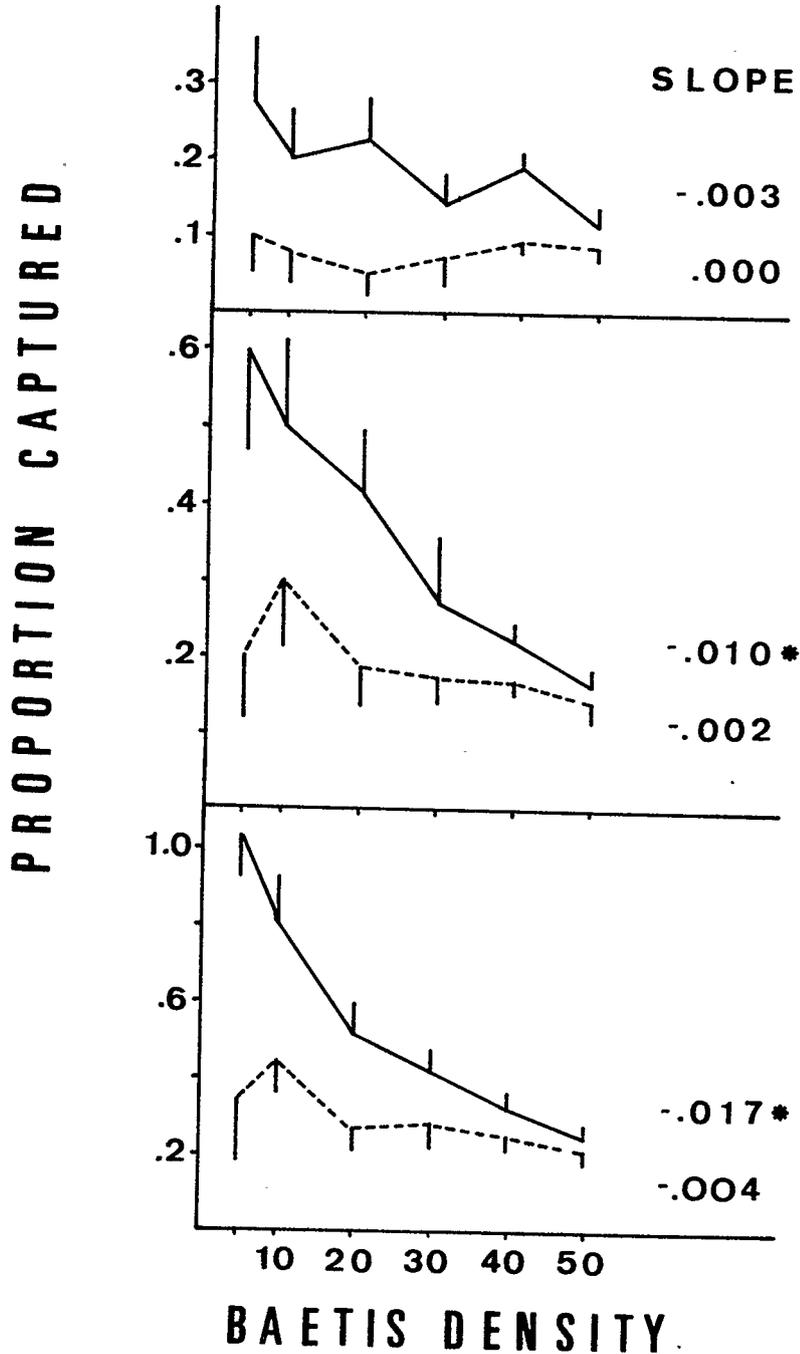


Fig. 6.6. Proportion of available prey captured versus prey density on sand (—) and gravel (---) substrate over a) 8 h, b) 24 h and c) 48 h. Slopes significantly different from 0 are indicated by an asterisk.

Table 6.3. Distribution of Baetis consumption over the 24 h period for Kogotus on sand (S) versus gravel (G) substrate.

<u>BAETIS</u> DENSITY	TIME PERIOD					
	1400-2200 h		2200-0600 h		0600-1400 h	
	S	G	S	G	S	G
5	.17	.50	.58	.50	.25	.00
10	.35	.28	.36	.41	.29	.31
20	.56	.25	.27	.58	.17	.17
30	.56	.42	.24	.47	.23	.11
40	.68	.56	.24	.35	.08	.09
50	.65	.61	.10	.29	.25	.10

Table 6.4. Fraction of Baetis left partially consumed on sand versus gravel substrate in 48 h trials.

<u>BAETIS</u> DENSITY	PROPORTION	
	SAND	GRAVEL
5	.00	.00
10	.02	.09
20	.00	.04
30	.08	.05
40	.19	.00
50	.17	.16

## Discussion

Feeding rates for fed Kogotus were much lower than for starved Kogotus at the same density of Baetis prey. This result could have been produced by lowered probabilities (P) for any step of the predator foraging process:

$$P(\text{encounter}) - P(\text{attack}) - P(\text{capture}) - P(\text{consumption})$$

Of these four stages, probability of encounter was found not to change with hunger level of the predator. Fed Kogotus did not spend less time moving on the substrate as was observed for zygopterans (Akre and Johnson 1979). This indicates that the response reported earlier (Section 5.1), where Kogotus reduced time spent moving as prey density increased was a direct response to prey density. That is, while movement rates appear to be at least partially determined by encounter rate with prey, they are not affected by level of predator satiation.

The second stage, probability of attack, was markedly affected by hunger level (Table 6.1). Starved predators were, on average, three times as likely to attack an encountered prey as were fed predators. This is in agreement with observations for Chaoborus which reduced attack rate on Daphnia when satiated (Pastorak 1980). Hesperoperla and Megarcys (Plecoptera) also reduced the frequency of attacks on Ephemerella when fed (Molles and

Pietruska 1983). Interestingly, these Plecoptera showed no such tendency with respect to Baetis tricaudatus, the prey type used in the present study. This discrepancy could be due either to a difference in strategy between the considerably larger Hesperoperla and Megarcys and the smaller Kogotus, or it could be due to differences in experimental design, particularly in what was considered to be a satiated predator.

The third stage, probability of successful capture could not be evaluated, due to the low number of observed captures in these experiments.

A difference in the final stage, the probability of actually consuming a captured prey, was also observed. The incidence of prey left partially consumed was much higher for fed Kogotus than for starved animals. The similar rates of partial consumption seen on gravel indicates that this result is not just an artifact of the unnatural substrate type used in these experiments. Partial consumption at high prey densities has been reported for other aquatic predators, particularly the fluid feeding hemipteran, Notonecta. Since extraction of body fluids becomes more difficult as feeding proceeds, partial consumption was shown to be an advantageous strategy when prey were abundant (Cook and Cockrell 1978). A similar situation may exist for Kogotus, since when a prey was

partially consumed, the soft abdomen was usually eaten, and the more sclerotized head and thorax discarded. Wasteful killing (i.e. without complete consumption) has also been observed for damselfly naiads (Johnson et al. 1975). In this case, it was suggested that captures were motivated by empty midguts but that full foreguts precluded consumption.

In summary, consumption rates are much higher for starved than fed Kogotus. This difference is not due to changes in the movement pattern affecting encounter rate, but is produced by changes in the probability of attacking prey, supplemented by an increased tendency to leave prey partially consumed.

Predator capture rates were lower on gravel than on sand at all prey densities, but the effect was strongest at the lowest prey densities, shifting the functional response curves toward Type III. Although this result is consistent with the suggestion that Baetis were hiding in a fixed number of refuges, behavioral observations do not support this view. Baetis invariably sat on top of the gravel, despite the fact that the interstices were large enough for entry. Kogotus, in fact, showed a much greater inclination to burrow into the substrate than did Baetis. As the prey were not in places that were inaccessible to the prey, the sigmoid curve must be the result of changes in predator behavior as prey density increased. A tendency to key in on Baetis microhabitat (as was suggested by the field gut

content data - Chapter 2) is a possible explanation. The overall decrease in capture rates on gravel versus sand, on the other hand, is probably attributable to the increased surface area available for the prey, and by the reduced efficiency of the search pattern of Kogotus, which involved climbing in and out among the rocks while all the Baetis were sitting on top.

This study has attempted to add some detail to earlier descriptions of Kogotus functional response and behavior. Capture rates are strongly influenced by hunger level, primarily via changes in attack rate. Increase in the heterogeneity of substrate not only reduces capture rates, but results in a different type of functional response.

## CHAPTER 7

DIEL FEEDING PERIODICITY OF KOGOTUS

## Introduction

Diel periodicity in the activity of aquatic invertebrates was recorded as early as 1940, when Moon observed that colonization of introduced substrate in a lake occurred much more rapidly at night than during the day. In laboratory experiments, Harker (1953) demonstrated that three mayfly species had endogenous species-specific diel activity rhythms, which were not altered by either continuous light or darkness, or by reversed illumination. Similarly, Hartland-Rowe (1955) found that a species of mayfly, remained in its burrow during the day, emerging at night to feed, and that this pattern persisted for at least two weeks of continuous darkness.

In the 1960's, quantitative studies demonstrated that most components of invertebrate drift were higher at night than during the day (Waters 1961; Elliott 1967), and research in diel periodicity of stream invertebrates focussed primarily on determining the cause of this rhythm. In a detailed study of five mayfly species, Elliott (1967) suggested that increased foraging activity on the tops of stones during the night resulted in higher drift rates. He

identified two types of periodicity (1968), light-induced movement onto the upper surfaces of stones (exogenous control), and a pattern of increased nocturnal activity which persisted in continuous light and dark (endogenous). Virtually all other studies have found either an undetectable or weak endogenous component which is easily overridden by light, (Holt and Waters (1967), Chaston (1968), Bishop (1969), Muller (1974), and Bailey (1981) working on mayflies, Bishop (1969) on stoneflies, Elliott (1970) on caddisflies, Chaston (1968) on simuliids, and Holt and Waters (1967) on amphipods).

In all these studies, light was identified as the exogenous control, and Bishop (1969) showed that intensity (or possibly change in intensity) was the critical factor rather than wavelength. Additional support came from studies which indicated that the normal nocturnal pattern was suppressed on a moonlit night (Anderson 1966) and during the continuous light of Arctic midsummer nights (Muller 1974). Hughes (1966a, b), however, showed that the response to light is not uniform, even among mayflies, since Tricorythus discolor shows a typical photonegative response, but Baetis harrisoni is actually attracted to areas of high light intensity. There have also been two unsuccessful attempts to measure diel changes in density of

invertebrates in the benthos, presumably as a result of drift or vertical migration in the substrate (Clifford 1972; Kovalak 1978).

More recently, some attention has been directed toward periodicity of lotic insect activities other than drift. Two species of Plecoptera were found to have higher oxygen consumption rates at night (Zoladek and Kapoor 1971), presumably reflective of activity pattern. No diel changes in respiration were observed for Chaoborus when activity was restricted, indicating the absence of any endogenous respiratory cycle (Sigmon et al. 1978).

No general pattern of diel periodicity in feeding of aquatic insect predators has yet emerged. Visual predators such as dragonflies and damselflies appear to be both more active and to feed more frequently under lighted conditions (Cloarec 1975; Crowley 1979). On the basis of gut content analysis, tactile or chemotactile predators such as stoneflies have usually been classified as nocturnal feeders. Vaught and Stewart (1974) found that more Neoperla (Perlidae) had full stomachs in samples taken in the morning and evening than in the afternoon. Allan (1982) also found that the guts of a perlodid, Megarcys signata, tended to be fullest in the early morning, suggesting either feeding periodicity or differential digestive times. A more variable pattern, but one still suggesting the predominance of nocturnal feeding was

observed for Hesperoperla and Skwala (Johnson 1983). Laboratory behaviour experiments, however, have yielded contradictory results. Sjostrom (1983) found that the hunting behaviour of a perlid, Dinocras cephalotes, varied with light intensity under controlled laboratory conditions, while Molles and Pietruska (1983) found that neither Hesperoperla pacifica (Perlidae) nor Megarcys signata altered attack or feeding rates in response to light regime.

Previous feeding experiments in the laboratory (Section 5.2) provided some evidence that the consumption rate of Kogotus nonus did not vary with light regime. In view of the rather voluminous literature reporting diel activity cycles in various aquatic insects, and the conflicting and sparse evidence with respect to predatory stoneflies, a detailed examination of periodicity was conducted to determine if Kogotus does show a diel cycle of feeding in the field, and if such a cycle can be explained in terms of light regime.

## Methods

A series of experiments and gut content analyses were conducted in two localities, Big Hill Springs Creek (this study) and the East River at the Rocky Mountain Biological Laboratory, Colorado, USA, using two closely related species of perlodid stonefly, Kogotus nonus and Kogotus modestus. The two species have similar life cycles, emerging in summer, and in both cases experiments were conducted with relatively large nymphs measuring 1.0-1.5 cm in length. At each locality, evidence was first gathered to determine whether the predators under consideration did exhibit feeding periodicity in the field. Secondly manipulative experiments were conducted to determine whether this periodicity could be explained by response to light regime.

## A) Evidence of periodicity of feeding in the field

1) Gut content analysis (K. nonus, Alberta)

K. nonus were collected and immediately quick-frozen to prevent further digestion of existing gut contents. A minimum of 50 animals were obtained at each of four time periods, 0600 h, 1200 h, 1800 h and 2400 h over two dates in May 1984 (sunrise 0600 h, sunset 2200 h). Average hourly water temperatures over the time period preceding each collection time were 3.1, 4.9, 8.6 and 4.8°C re-

spectively. In the laboratory, head capsule (interocular) width was measured, the foregut dissected out, and the number of prey present counted. As K. nonus are engulferers, and only the foregut was examined, prey items were usually fairly intact and easily identified.

For statistical analysis, predators were separated into two size classes (greater or less than 1.2 mm interocular width), since at this time of year, predators in the smaller size class rarely take Baetis as a prey item. After testing for normality of the prey count data, a chi-square test was performed for each of the two size classes to determine if the proportion of predators with prey in their guts varied with time of day.

## 2) Feeding and activity periodicity

### (K. modestus, Colorado)

A series of experiments using starved K. modestus were conducted to determine if a diel pattern of feeding and/or activity could be detected under a natural light and temperature regime. River water was pumped through small circular streams (Fig. 3.7) located on the riverbank under natural field conditions of light, temperature and water chemistry. Sand substrate and a current of 5-7 cm/s were used.

Single K. modestus were placed in individual artificial streams for 48 h of acclimation and starvation, before the addition of 20 Baetis. The predator was observed for 15 min, and number of captures, attacks, encounters, time spent moving on the substrate, and time spent stationary were recorded. Four to eleven replicate trials were conducted at each of five times, 0600 h (4-6°C), 0800 h (8-10°C), 1400 h (13-14°C), 1800 h (10-12°C), 2200 h (8-10°C). To determine if periodicity was dependent on hunger level, additional K. modestus were allowed to feed in the chambers for 24 h, after which similar 15 min experimental runs were conducted, with four to six replicated per time period.

To detect differences between the five time periods, the Kruskal-Wallis non-parametric analysis of variance procedure was used, and Spearman Rank correlations were run to determine relationships between number of captures and the various behavioural observations.

## B) Light/dark responses

### 1) Manipulation of light regime in the field

(K. modestus, Colorado)

An experimental procedure identical to that described in A(2) for starved K. modestus was followed, except that observations were conducted under altered light regimes, dark with a dull red light for 0600 h and 1400 h, and artificial white light at night (2200 h). Capture rates and activity under these altered light conditions were compared to the data collected under natural light, using the Mann-Whitney test.

### 2) Manipulation of light regime in the laboratory

(K. nonus, Alberta)

K. nonus of 20 to 25 mg wet wt were starved and acclimated for 48 h in the laboratory, using the circular streams with dechlorinated water at 8°C, and a current of 8-10 cm/s. Ten Baetis were added, and after an 8 h period the number of prey remaining determined. Light treatments were fluorescent light (1000 lx) and red light (15 lx). (It is unlikely that these insects are capable of perceiving red light (Chapman 1982), but as a check, four replicates were run in complete darkness. These were not significantly different from those in red light.) Ex-

periments were conducted both on sand (1-2 mm) and on gravel (10 mm) substrate. An additional light/dark experiment using 20 Baetis and a gravel substrate was run to check that trends were similar at higher Baetis densities. Each of the treatments was replicated five to twelve times. Data were analyzed using the Mann-Whitney U test.

## Results

## A) Field Periodicity

## 1) Gut content analysis

Gut contents were classified into four categories: empty, detritus (unidentifiable organic matter), Orthocladiinae, and Baetis. Of the 255 animals examined in this study, seven were excluded from the analysis as they had consumed prey other than Baetis or Orthocladiinae, (tipulids (3), filipalpiian stoneflies (2), oligochaetes (1) and rhyacophilids (1)).

The distribution of K. nonus among the four gut content categories did vary significantly with time of day for both large (chi-square = 208.1,  $p < .001$ ) and small predators (chi-square = 118.1,  $p < .001$ ). There appeared to be two feeding peaks, morning and evening, as the frequency of guts containing Baetis was highest at 1200 h and 2400 h (Fig. 7.1). Both large and small predators collected at 1800 h also contained fewer Orthocladiinae, but there was no evidence of a nightly feeding depression.

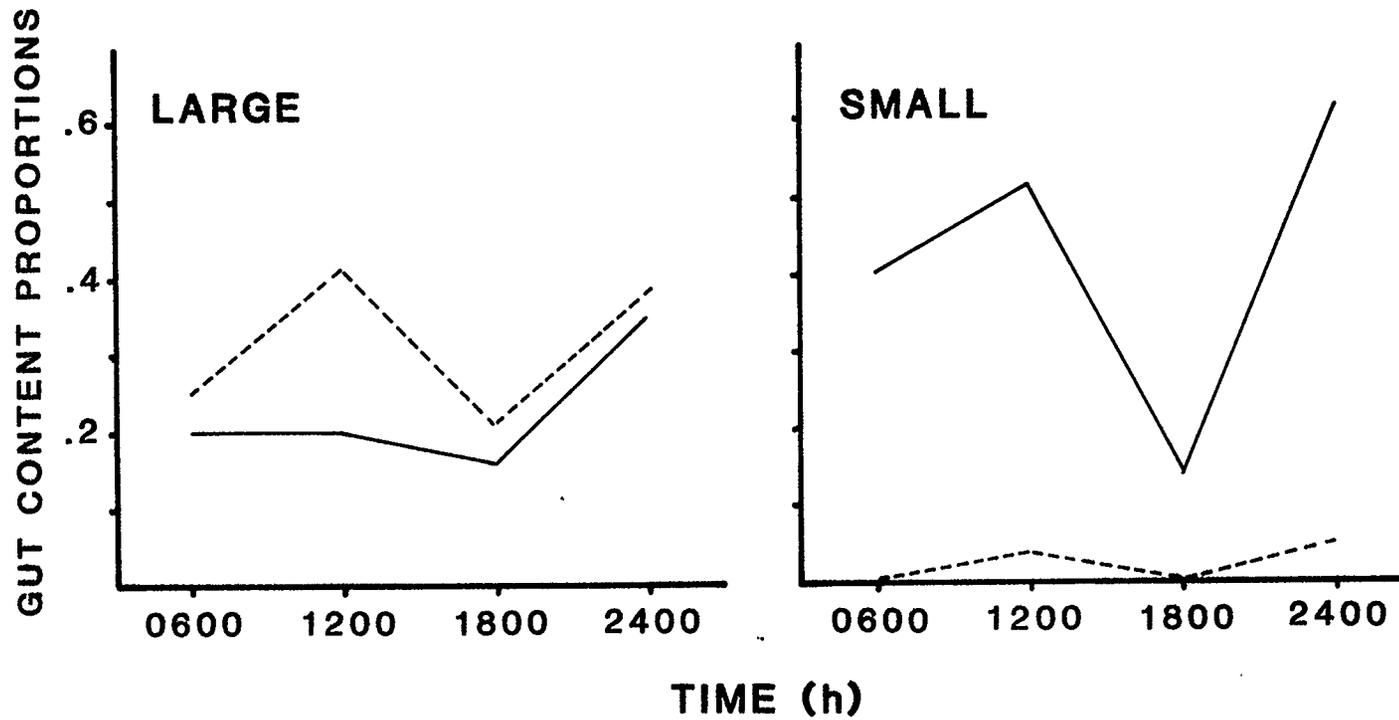


Fig. 7.1. Diel change in the proportion of large and small K. nonus guts containing Baetis (---) and Orthoclaadiinae (—).

## 2) Activity and feeding periodicity

Starved K. modestus did show evidence of diel periodicity when placed in artificial streams under a natural temperature and light regime. Predators tended to spend more time stationary in the afternoon (1400 h) and evening (1800 h), and although this activity pattern correlated well with the temperature regime, there appeared to be little relationship to the natural light regime (Fig. 7.2). Predators that spent more time moving did tend to capture more prey (Spearman Rank Correlation,  $p=.02$ ), but this relationship did not fully explain the pattern of capture rates. The significantly higher number of captures at dawn (0600 h) was largely due to an increased probability of actually capturing an attacked prey, rather than to an increased tendency on the part of the predator to attack an encountered prey (Fig. 7.3). Previously fed K. modestus showed the same diel pattern of activity (Fig. 7.2), but did not feed during the experimental trials.

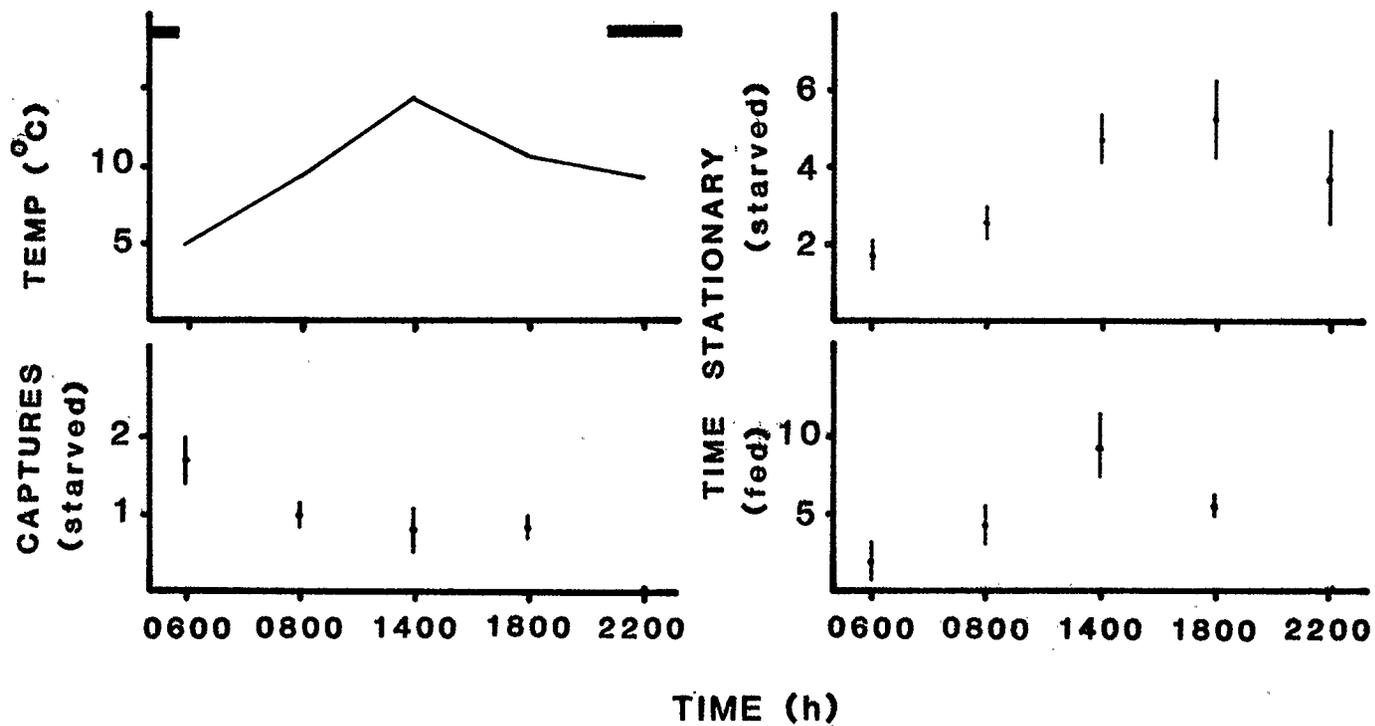


Fig. 7.2. Diel changes in water temperature, capture rate, and time spent stationary for starved and fed *K. modestus*. The period of darkness is indicated by solid bars, number of replicates for the starved and fed trials are in brackets, and error bars represent 1 SE.

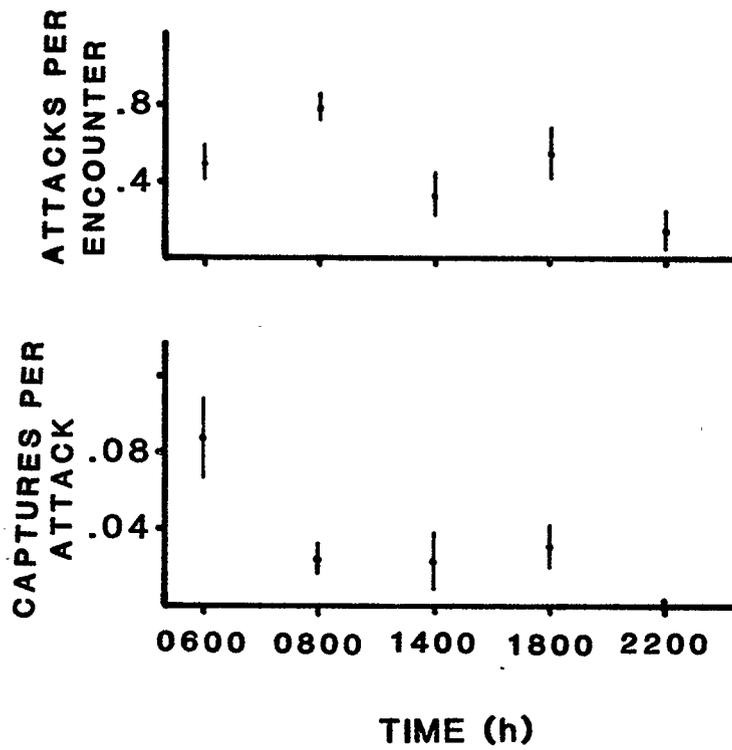


Fig. 7.3. Diel change in tendency for starved *K. modestus* to attack an encountered prey and to succeed in capturing an attacked prey. Error bars are 1 SE.

## B) Light/Dark Regimes

### 1) Manipulation of light in the field

Imposition of different light regimes in the field, dark during the day and light at night, did not affect either capture rate or the activity pattern of K. modestus (Fig. 7.4). Time spent stationary or moving, number of encounters, attacks and captures all did not vary significantly between light and dark conditions.

### 2) Manipulation of light regime in the laboratory

Manipulation of the light regime in the laboratory also had no effect on the capture rate of K. nonus, either on sand or gravel substrate at either density of Baetis (Fig. 7.5).

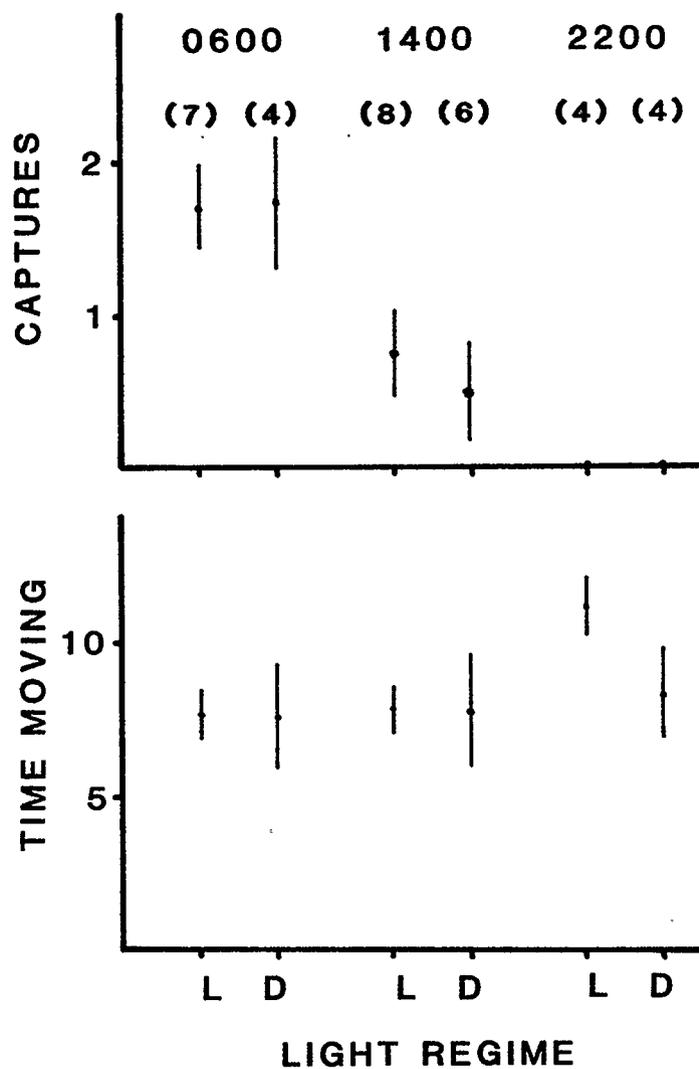


Fig. 7.4. Change in capture rate and activity under light regime manipulation (light:L, dark:D) for *K. modestus*. Number of replicates for light and dark trials at three times of day (0600, 1400 and 2200 h) are in parentheses. Error bars are 1 SE.

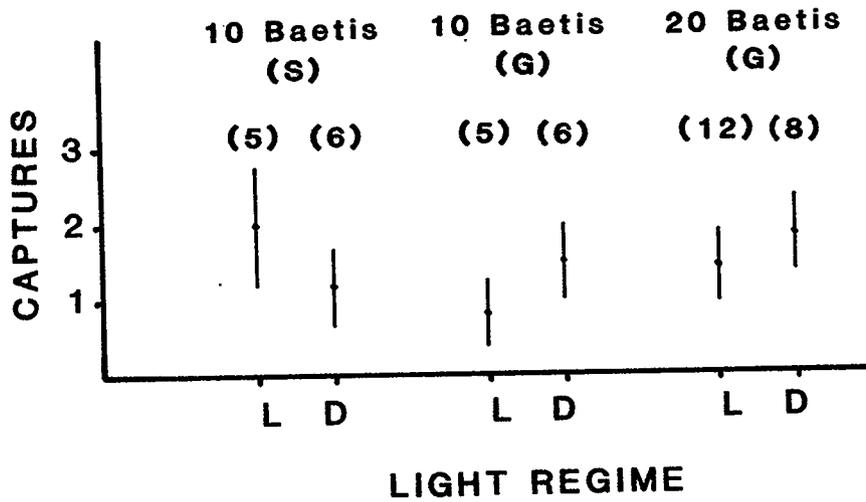


Fig. 7.5. Change in capture rate under two light regimes (light:L, dark:D) and two substrates (sand:S, gravel:G) for *K. nonus*. Number of replicates are in parentheses. Error bars are 1 SE.

## Discussion

It is evident that both K. nonus and K. modestus exhibit periodicity in feeding when in their natural environment, although in both cases feeding is not strictly limited to these times. Gut content analysis showed a difference in the pattern of consumption between prey. K. nonus guts contained Baetis more frequently at both noon and midnight, indicating morning and evening feeding periods, while feeding on Orthocladiinae was apparently depressed only in the afternoon (1800 h collections). With two feeding peaks on Baetis, these results cannot be due to diel temperature changes causing differential digestive times, since night temperatures were lower than evening or morning. These results indicate that K. nonus feeds less frequently during the day. The single overnight feeding peak observed with Orthocladiinae concurs with other studies where the prey consisted mainly of relatively sessile prey such as chironomids (Allan 1982), trichopteran eggs, hydropsychids, and chironomids (Vaught and Stewart 1974). Two feeding peaks with lowered night-time consumption have also been observed for Pargnetina (Perlidae) feeding on Baetis (Johnson 1981).

Observation of activity and feeding under a natural temperature and light regime (Colorado) also demonstrated periodicity in K. modestus feeding, but only one peak

(early morning) was identified. However, Baetis captures were again very low at night. Higher capture rate in the early morning appeared to be due to increased success in capturing a prey once attacked, rather than any increase in encounter rate or in tendency to attack prey.

This diel periodicity could be produced in at least four possible ways: 1) a direct response by the predator to the light/dark regime, 2) predator response to temperature changes, 3) diel changes in prey behaviour/activity, and 4) an internal clock or endogenous rhythm. The evidence for and plausibility of each potential mechanism will be discussed.

From the literature review, it was expected that if Kogotus did show a diel feeding pattern, it would be in response to changes in light intensity. However, experimental manipulations of the light regime had no effect on capture rates either in the field or in the laboratory. In the field, artificial light at night did not inhibit captures, nor did shielding from sunlight increase captures during the day. In addition, when activity was monitored, there was also no change in the proportion of time allocated to moving or remaining stationary, nor in tendency to attack prey or success in capturing an attacked prey. These results are in agreement with laboratory results for two other predatory stoneflies, Hesperoperla and Megarcys (Molles and Pietruska 1983). Unlike the

perlid, Dinocras, which under lighted conditions remains in a shelter until it starves to death (Sjostrom 1983), K. nonus, when provided with a gravel substrate, captured prey equally well under bright white light and dull red light. In addition, it was easily observed that feeding peaks in the field did not correspond very closely to the diel light/dark regime. In Alberta, the two peak feeding periods included one that was entirely light (0600 - 1200 h) and one that included both light and dark (1800 - 2400 h). In Colorado, peak feeding was near dawn, while twilight, a period of similar light intensity, showed no such peak, and feeding at night was lowest of all. It was concluded, therefore, that any diel periodicity of feeding shown by Kogotus is not due to a simple response to light regime.

Temperature also varies with time of day, and the diel activity pattern of K. modestus (Fig. 7.2), does correspond to these temperature changes. Metabolic costs have been shown to increase with temperature for the predatory stonefly, Acroneuria (Heiman and Knight 1975), and thus remaining stationary during the high temperatures of midday and early evening would make energetic sense. Reduced capture rates could be an indirect result of lowered encounter rates due to this reduced movement. The evening feeding peak may have been absent in Colorado because

evening temperatures remained high rather than dropping rapidly to approximate morning temperatures as in Alberta. No change in tendency to attack would be expected since energy requirements remain high. It is notable, also, that K. modestus was most successful in actually capturing attacked prey in the early morning, when temperatures were low. Since the activity and attack tendencies of the predator were similar between 0600 and 0800 h, it seems likely that the difference lay in the prey's ability to escape; it is possible that the temperature slowed the prey's response time. Although differences in temperature could account for reduced feeding during the day, and a high success rate in the early morning, it does not account for reduced feeding on Baetis during the night.

Diel changes in prey behaviour could also have contributed to the observed pattern. Baetis is known to drift at night (Harker 1953; Holt and Waters 1967; Elliott 1968; Pearson and Franklin 1968; Muller 1974; Allan 1984), while chironomids do not show consistent nocturnal periodicity in drift (Anderson 1966; Allan 1984). Baetis might, therefore, be less available at night, resulting in a low feeding rate as seen both in the Alberta gut content analysis and the Colorado field experiments. Under this hypothesis, reduced feeding on chironomids during the night would not be expected, and this was observed.

Diel periodicity could also result from an endogenous rhythm. This alternative can only be tested by experimentally eliminating all exogenous cues, which was not attempted in this study. While an endogenous rhythm remains a possibility, in view of the fragility of most reported circadian rhythms in aquatic insects (Chaston 1968; Waters 1972), it would seem less likely than the other explanations forwarded.

In conclusion, Kogotus does show diel periodicity in feeding, although it is certainly not exclusively a nocturnal forager. This periodicity does not appear to be produced by a direct response by the predator to light regime. Lower capture rates during the day are related to reduced activity of the predator, which is correlated with increased temperature. The low capture rates seen at night for Baetis but not for chironomids may be due to the nocturnal drift pattern of Baetis. It is suggested, therefore, that a strictly nocturnal feeding pattern is not general across all predatory stoneflies, and that the diel feeding pattern may, in fact, vary within a species depending on the type of prey consumed.

## CHAPTER 8

## CONCLUSIONS

The overall objective of this thesis was to determine if the structure of the benthic community in Big Hill Springs Creek was modified by the factor of invertebrate predation. Kogotus nonus, an abundant perlodid stonefly, was selected as a likely candidate for the role of influential predator.

From the field experiments, it can be concluded that Kogotus has the potential to influence the distribution of its prey, Orthocladiinae and Baetis, on a patch to patch basis. The effect on Orthocladiinae was consistent and strong for July, and may have been produced by consumption and/or increased dispersal on the part of the prey. The effect on Baetis was less consistent and was probably largely a disturbance effect, as shown by the laboratory drift experiments. While small enclosure experiments do not demonstrate that a predator is effectively excluding prey from areas of the stream, they do show that prey distributions are affected in a dynamic sense, that is, local patch densities of prey are lowered by the arrival or presence of a predator. In the experimental situation these patches were artificially maintained in particular

locations, and thus the effect on distribution was measurable. In the natural benthos, these areas of depletion are probably not stationary on the stream bed, and the location and length of existence of the patches will be affected both by the movement of the predator and the recolonization rate of the prey. Predator effects are not consistent throughout the year, as shown by the absence of effects in the June experiments. It is likely that in any stream community the importance of the various factors influencing structure changes through the year, as the physical (temperature, discharge) and biotic (species composition and abundance) factors change.

It has been suggested that communities can be classified in terms of the relative importance of abiotic versus biotic factors, and that in harsh environments, communities are less likely to be structured by biotic interactions. When the quality of the physical environment was reduced by adding sediment to field enclosures in this study, the impact of Kogotus on the prey community was eliminated in two out of three experiments. In the third experiment, however, addition of fine sediment actually enhanced the effectiveness of the predator, leading to questions about the relationship between environmental harshness and the particular species under consideration. There appears to be no logical basis for the assumption of

an inverse relationship between the importance of predation and environmental harshness. Short-term catastrophic events that either impair predatory ability or reduce prey densities to levels at which the predator is ineffective will show the predicted trend. However, disturbances may have the reverse effect if they increase the vulnerability of the prey to predation (eg. by filling in habitable interstices), or no effect if this increased vulnerability is countered by a reduction in predator efficiency. If different streams are compared on terms of harshness, predictions become even more difficult, since not only must harshness be defined in terms of many physical factors, it must be defined in terms of the species under consideration, each of which is presumably somewhat adapted to its respective abiotic regime. In attempts to classify communities, it may be more useful to reduce the question of the relative importance of abiotic versus biotic factors to questions about the measurable impact of species interactions in different streams. Generalizations about which types of streams are likely to have predatory or competitive interactions that affect community structure are certainly not possible with the number of streams that have been investigated to this point.

Additional investigations were conducted to determine if the prey were significantly affecting the distribution of Kogotus. Laboratory experiments demonstrated that

Kogotus does capture more prey in high density patches, and that it responds to differences in prey density with changes in movement rate. This response to prey density is not, however, reflected in distribution patterns in the stream. Within riffles the distribution of Kogotus shows no relationship to that of Baetis and the estimated patch sizes are very different. Kogotus distribution were correlated with those of Orthoclaadiinae more frequently than seen for Baetis, but there was still no correlation for the majority of sampling dates. Two possible explanations for these distributional patterns were forwarded. There is considerable mutual interference between Kogotus larvae, lowering the feeding rate of individuals in the presence of conspecifics. Aggregating in prey patches, therefore, carries a cost with it, making less aggregated predator distributions more beneficial in terms of prey capture rates. The lower correspondance to Baetis versus Orthoclaadiinae distributions may be due to the greater mobility of the former. Baetis is an extremely mobile animal, swimming and drifting both as part of its foraging behavior and in response to contact by predators. Even very consistent attempts on the part of the predator to aggregate in such ephemeral prey patches would not produce correlated distributions.

In conclusion, then, in Big Hill Springs Creek, an invertebrate predator has been shown to have some influence on the patch to patch distribution of its prey. There is also some evidence that the predator responds to local prey densities, but this response is likely modified by predator-predator interactions and prey movement between patches. It is difficult to speculate on whether these results are generalizable to other communities in other streams. Certainly invertebrate predators which live in the interstices of the substrate with their prey would appear to be more likely to show effects than drift-feeding or even benthic-feeding fish. However, Big Hill Springs Creek was selected as a study site since it had features conducive to experimental manipulations, small size, a stable discharge regime, high abundance but low diversity of species. It may be that these features are also ones that produce significant biotic interactions. However, as discussed above, at this point there is no sound logical argument or data base from which to draw the assumption that any type of stream is more likely to be influenced by predation, and patterns will only emerge as species interactions are studied in additional streams.

Although it is generally accepted that predators play an important role in communities of some ecosystems, particularly in the marine and terrestrial environments, this study is one of very few demonstrations to date that

predation may influence stream community structure. If biotic interactions were really unimportant in all stream communities, the conclusion that stream communities are fundamentally different from other communities could not be avoided. The bulk of ecological theory would then have no application to streams, since it has been derived, for the most part, from other ecosystems. The fact that current studies are showing that predation and competition do play an important role in stream communities as well, lends credence to the assumption underlying almost all community research, that there are basic similarities among communities across ecosystems. The search for such common principles thus remains a meaningful exercise.

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