Estimates of mayfly mortality: is stonefly predation a significant source?

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Field experiments and surveys were carried out in a Rocky Mountain alpine stream during the summers of 1990 and 1992 to estimate the proportion of natural losses of the mayfly *Baetis bicaudatus* resulting from the co-occurring, predatory stonefly, *Kogotus modestus*. Functional response experiments determined the number of prey consumed by male and female *Kogotus* by manipulating the densities of prey and the presence or absence of predators in stream-side chambers. Estimates of losses of *Baetis* and density of *Kogotus* were based on ten benthic samples collected weekly (except for last sampling date) from one study reach. Concurrently, drift density of *Baetis* was estimated upstream and downstream of the reach to determine gains or losses of *Baetis* resulting from migration.

In the functional response experiments *Kogotus* consumed the same number of prey regardless of prey densities. Female predators tended to consume more prey (~ 2 d^{-1}) than males (~ 1 d^{-1}), although the result was only statistically significant in one out of three experiments. Per-capita mortality rates of *Baetis* declined from 0.01 to 0.001 d^{-1} (predator m^{-2})$^{-1}$ with increasing prey density. In the study reach *Baetis* density declined 70% during the 4.5 wk and per-capita losses averaged 3.8% d^{-1}. We estimated that predation by *Kogotus* could cause between 1.6 and 9.5% of the losses of *Baetis* from the study reach. This occurred because high losses of *Baetis* were combined with low consumption rates and densities (1.83 individuals m^{-2}) of *Kogotus*. *Baetis* drift density was higher at night than during the day. Drift densities of *Baetis* tended to be higher leaving than entering the reach in nighttime estimates, although the results were not statistically signficant. Few replicates resulted in low power to detect differences in upstream and downstream drift densities; therefore, it is possible that some losses could be the result of drift out of the study reach. Nonetheless our results suggest that *Kogotus* populations had little direct, lethal effect on *Baetis* populations in this study reach.

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The significance of predation to prey populations depends upon the number of predators present and on the predators' ability to find and consume prey (Hassell 1978). For example, individual predators may consume only small numbers of prey; however, if predator density is high relative to prey density then predators may cause significant mortality in prey populations. Conversely, individual predators may consume large numbers of prey,

but if predator density is low relative to prey density the overall effect on prey populations may be slight. Consequently, to estimate the influence of predators on natural prey populations both the ability of the predator to consume prey and the number of predators and prey in the natural environment must be investigated.

The behavioral ecology of predatory stoneflies and their mayfly prey is well understood. In feeding experi-

ments predatory stoneflies preferentially attack and consume baetid mayflies (Malmqvist and Sjöström 1980, Molles and Pietruszka 1983, Walde and Davies 1987, Fuller and DeSteffan 1988, Peckarsky and Penton 1989a). Behavior of baetids is modified in the presence of stoneflies (Peckarsky 1980, Williams 1987, Malmqvist 1992), and encounters with predators may result in dispersal of *Baetis* from foraging patches (Malmqvist and Sjöström 1987, Peckarsky and Penton 1989b) and lowered feeding rates (Peckarsky et al. 1993).

Although baetids are clearly affected by stoneflies, stoneflies rarely depress *Baetis* populations in enclosures (Oberndorfer et al. 1984: no, Walde and Davies 1984a: no, Peckarsky 1985: sometimes, Walde 1986: sometimes). In fact, stoneflies appear to depress baetid populations only if prey dispersal is restricted (Cooper et al. 1990, Lancaster et al. 1991, Peckarsky 1991a). Although stoneflies from natural populations have substantial numbers of mayflies in their diets (Peckarsky 1985), the low predation rates observed in enclosures suggest little direct effect of stoneflies on mayfly abundance. Clearly, the enclosure technique has not produced definitive data to test hypotheses relating to estimation of the effects of predation on prey mortality in streams.

During the summers of 1990 and 1992 we conducted experiments and field surveys to estimate the proportion of natural mortality of *Baetis bicaudatus* Dodds (Ephemeroptera: Baetidae) resulting from predation by the stonefly *Kogotus modestus* (Banks) (Plecoptera: Perlodidae). Our main objectives were 1) to assess the ability of *Kogotus* to consume *Baetis* by experimentally determining the functional response of the predator across a range of naturally occurring prey densities, 2) to combine predatory mortality rates from the functional response experiments with natural density of predators in a study reach of the East River to estimate potential mortality as a result of *Kogotus* predation, and 3) to compare the estimates of the potential mortality resulting from the predator with the actual loss rate of *Baetis* from the same study reach. We estimated migration into and out of our study reach by sampling drift concurrently with the benthos.

Study site and organisms

Benthic and drift sampling were conducted in a third-order reach of the East River, Gunnison County, Colorado, USA, at the site of the Rocky Mountain Biological Laboratory. This stream (described in detail in Peckarsky 1983) is a cold-water, high-elevation (2950 m) trout stream. The 82.5 m study reach was selected because it had no small tributaries; thus, invertebrate migration should occur only in the main channel. The section just upstream of the study reach provided similar habitat for both mayflies and stoneflies, with the exception of having a small tributary and a waterfall several hundred meters upstream.

Baetis is bivoltine at the study site. One cohort overwinters in the larval stage with emergence and oviposition beginning in early June (BLP, unpubl.). A fast growing summer generation (second cohort) emerges in August. *Kogotus* is univoltine, overwinters in the egg stage, larvae grow rapidly in June and July, begin feeding on mayflies by mid to late June and emerge in August (Peckarsky and Cowan 1991). Microhabitats used by *Baetis* and *Kogotus* also overlap extensively (Peckarsky and Cowan, in press). Thus, *Kogotus* and the summer generation of *Baetis* overlap both spatially and temporally. *Kogotus* selects *Baetis* over other mayfly prey (Peckarsky and Penton 1989a). Analysis of the gut contents of *Kogotus* suggests that *Baetis* is a major food resource (Peckarsky 1985) and all prey size-classes are represented (BLP unpubl.).

Methods
Kogotus functional response

Functional response experiments were conducted during the summer of 1992 in replicated, circular, Plexiglas chambers (0.0162 m^2) that were housed in a translucent vinyl greenhouse (Weatherport) beside the East River. Filtered stream water from the East River flowed through chambers creating a current velocity of ~ 15–20 cm s^{-1}. Chambers were filled with ~ 1 cm of gravel and one granite rock. Four, 24-h trials were run beginning on 14 and 16 July and 4 and 5 August. In the 14 July trial, chambers received either 5, 10, 15 or 20 *Baetis* (308.6, 617.3, 925.9, 1234.6 larvae m^{-2}, respectively). Because *Kogotus* ate few *Baetis* during this trial, prey numbers were reduced to 2, 4, 6 or 8 *Baetis* (123.5, 246.9, 370.4, 493.8 larvae m^{-2}, respectively) in the trial beginning on 16 July. The trials conducted during August used 2, 5, 8 and 11 *Baetis* (123.5, 308.6, 493.8, 679.0 larvae m^{-2}, respectively). Densities of prey were within naturally occuring ranges (Peckarsky 1991b and Results). Either one male or one female *Kogotus* was placed in a chamber (61.7 larvae m^{-2}). Three replicates of each treatment combination (prey density, sex of predator) were run. Two controls (no predator) were run with each prey density. *Kogotus* nymphs were held without food for 24 h prior to a trial.

All *Kogotus* and a subsample of *Baetis* were preserved (70% EtOH) and taken back to the laboratory where head capsule widths were determined. *Baetis* nymphs were intermediate in size (head capsule width mm ± 1 SE; 0.88 ± 0.01, n = 20; 0.97 ± 0.02, n = 20; 0.89 ± 0.02, n = 48; trials 1, 2, and 3 & 4, respectively) and would be classified in later developmental stages (Allan et al. 1987; Stage III, see Drift Methods). Head capsule widths of male *Kogotus* (2.15 ± 0.02, n = 12; 2.09 ± 0.02, n = 11; 2.10 ± 0.02, n = 24; mm ± 1 SE; trials 1, 2, and 3 & 4, respectively) were smaller than those of females ($2.25 \pm$

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0.08, n = 12; 2.45 ± 0.06, n = 12; 2.50 ± 0.02, n = 24; mm ± 1 SE; trials 1, 2, and 3 & 4, respectively).

We compared number eaten (transformed ln + 1) among initial prey densities and predator sexes using analyses of variance (ANOVA). Separate ANOVAs were used on data from trials one and two because prey densities differed. Data from trials three and four were combined for analysis. Data from all trials were combined to compare *Baetis* per-capita mortality rates. Daily per-capita mortality was calculated as $(\ln[B_I] - \ln[B_F]) (P)^{-1}$, where B_I was the initial prey density, B_F was the average final prey density in each treatment combination and P was predator density. Mortality estimates were based on predator density to facilitate comparison with *Baetis* mortality estimates derived from benthic sampling. Per-capita mortality rates were compared among prey densities and between sexes using analysis of covariance (weighted to correct for heteroscedasticity of variances).

Baetis and Kogotus benthic densities

On each of six dates (12, 19, 26 July and 2, 9, 13 August 1990), 10 stones were randomly selected from the East River reach and sampled for *Kogotus* and *Baetis*. Invertebrate samples were collected by placing an aquatic D-frame net (meshes = 100 μm) downstream of an individual stone while lifting it out of the stream, so that more loosely associated insects were washed into the net. Insects were removed from stones and nets, preserved in 70% EtOH, taken back to the laboratory and identified under the dissecting microscope.

The head capsule width of each *Baetis* was measured and larvae were classifed into one of four developmental stages (I – no wing pads, II – wing pads shorter than wide, III – wing pads longer than wide, IV – wing pads darkened; Clifford et al. 1979, Delucchi and Peckarsky 1989). In both benthic and drift samples head capsule widths varied between 0.13 and 0.45 mm for stage I and 0.35 and 0.71 mm for class II larvae. Head capsule widths of stages III and IV overlapped extensively (0.56 to 1.00 mm).

Densities of *Kogotus* and of each developmental stage of *Baetis* were calculated using the upper surface area of stones (the foraging habitat of *Baetis*). To determine upper surface area, the stones were placed on acetate sheets in the same configuration as they lay in the stream. Then the horizontal surface areas were traced (McAuliffe 1984, Peckarsky 1991b) and acetate sheets were subsequently digitized. We compared benthic densities of each developmental stage of *Baetis* among dates using one-way MANOVA and individual ANOVA's for each stage. If significant differences among sampling dates were found, pairwise comparisons were made using Tukey's HSD Test (critical α < 0.05).

For each week, we estimated daily per-capita mortality rates of the summer generation of *Baetis* using mean benthic density (all developmental stages combined) in consecutive weeks (daily mortality rate = $(\ln[Baetis \text{ density}]_n - \ln[Baetis \text{ density}]_{n+1})$ (number of days between samples)$^{-1}$, where n and n + 1 denote consecutive weeks). Mortality over the entire sampling period was estimated in a similar manner using the first and last dates. We assumed that losses between successive weeks were not the result of adult emergence. This assumption seems reasonable during the early weeks of the study, given that few large larvae (those capable of emerging) were found, but might have been violated during the last week of the study, which should be taken into account when interpreting the data.

Natural *Baetis* mortality attributable to *Kogotus* predation was estimated by multiplying average field stonefly density and per-capita mortality rates from functional response experiments. Rather than using one mean value, we used a range of predator densities ($\bar{X} \pm 1$ SE) to simulate natural variability in predator densities (see Results). Further, we used the per-capita mortality rate from high prey density functional response trials because natural *Baetis* densities were > 1200 larvae m^{-2} in all but the last 1.5 wk. Finally, while we determined the *Baetis* mortality in the field on a per week basis (see Results), the amount of mortality due to *Kogotus* predation (over the range of predator densities) was estimated as one measure for the entire study based on the average *Baetis* field mortality.

Baetis drift

To account for migration of *Baetis* into and out of the study site, two permanent drift sampling sites were located 3.4 m upstream and 6.0 m downstream of the reach. Beginning 18 July 1990, we sampled both nighttime (21.00–22.00) and daytime (10.00–11.00 mountain daylight time) drift on the evening and morning before benthic sampling. Drift nets (30 × 45 cm, height × width) with both inner (320 μm mesh) and outer nets (180 μm mesh) were first placed at downstream sites and then upstream sites to minimize disturbance. Amount of water filtered through nets (m^3) was estimated using the cross-sectional area of water passing through the nets (m^2), stream flow at the net mouth (m s^{-1}, Marsh McBirney 201 flowmeter) and the amount of time the net was in the water (s). We took 5-min samples at night and 30-min samples during daylight (except during first trials when nighttime samples ran for 15 min and daytime samples 1 h). Differential durations of daytime and nighttime drift samples were used because of diurnal differences in *Baetis* drift density (e.g., Allan 1987).

At the end of sampling, nets were taken back to the laboratory where invertebrates were collected by hand-picking and thorough washing of nets into large collection chambers. Chamber contents were filtered through fine mesh (180 μm) and organisms were preserved in 70% EtOH. Invertebrates were sorted under a microscope in the laboratory. Complete samples were counted, ex-
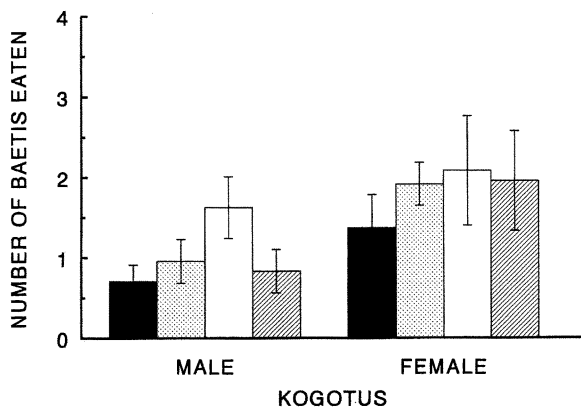
Fig. 1. Mean number of *Baetis* eaten by male and female *Kogotus* in functional response trials begun on 14 July (solid bars), 16 July (stippled bars), 4 August (clear bars) and 5 August (hatched bars). All values ± 1 SE.

Table 1. ANOVAs for the number of *Baetis* eaten (tranformed [ln + 1]) by *Kogotus* in 24-h trials.

Experiment	Source	ss	df	F	P > F
Trial 1	Sex	0.29	1	1.06	0.3183
	Initial *Baetis*	1.01	3	1.24	0.3291
	Sex × *Baetis*	1.06	3	1.30	0.3096
	Error	4.36	16		
Trial 2	Sex	1.07	1	4.62	0.0484
	Initial *Baetis*	0.16	3	0.22	0.8775
	Sex × *Baetis*	0.10	3	0.15	0.9292
	Error	3.46	15		
Trials 3, 4	Trial (Block)	0.25	1	–[a]	–
	Sex	0.41	1	0.89	0.3522
	Initial *Baetis*	3.26	3	3.26	0.0892
	Sex × *Baetis*	1.54	3	1.12	0.3572
	Sex × Trial	0.33	1	–	–
	Baetis × Trial	0.37	3	–	–
	Sex × *Baetis* × Trial	0.38	3	–	–
	Error	14.71	32		

[a] Untestable block effects.

cept for the first dates when contents of nets were sub-sampled because of the large numbers of invertebrates found in the longer duration drift samples. Head capsule widths of *Baetis* were measured and larvae were sorted into the same developmental stages as in the benthic samples.

We calculated *Baetis* drift densities (m⁻³) and determined the proportion of each developmental stage in the drift. Because sites were permanently located, we considered weekly samples as repeated measures on the same sampling unit. Consequently, we described drift at each site using summary parameters: slopes and intercepts of regressions relating transformed (ln) weekly drift densities (all developmental stages combined) to sampling date (von Ende 1993). As the sampling progressed, we expected that drift densities would decline with benthic densities. If regression models fit data adequately, then the slopes and intercepts should effectively capture the relationship of drift density to time, thus, combining the repeated measures into two relatively independent parameters. Slopes and intercepts were used as response variables in two-way ANOVA's (net location and time-of-day). We also calculated the power $(1 - \beta$, the Type II error rate) of our survey to detect differences between main effects and the interaction because trends that seemed apparent were not statistically different (Cohen 1988).

Results

Kogotus functional response

Only one prey was lost in controls; therefore, we assumed that all losses in predator treatments were the result of predatory mortality and made no corrections for losses in controls. On average *Kogotus* ate ~1–2 *Baetis* in 24 h

(Fig. 1). We did not detect any differences among prey densities in the number of prey eaten by *Kogotus* (Table 1) in contrast to other similar studies of stonefly functional responses (Malmqvist 1991). The general trend was for females to consume slightly more prey than males (Fig. 1), although the trend was statistically significant in only one trial (Table 1). As a result of the constant number of *Baetis* consumed, daily per-capita mortality rates of *Baetis* declined as prey density increased (Fig. 2; $F_{1,28} = 14.11$, p = 0.0008). We did not detect any difference in predation rates between *Kogotus* males and females, although the effect was marginally non-significant ($F_{1,28} = 3.43$, p = 0.0745). The effect of prey density on *Baetis* mortality rates did not differ between males and females (interaction, $F_{1,28} = 1.53$, p = 0.2267).
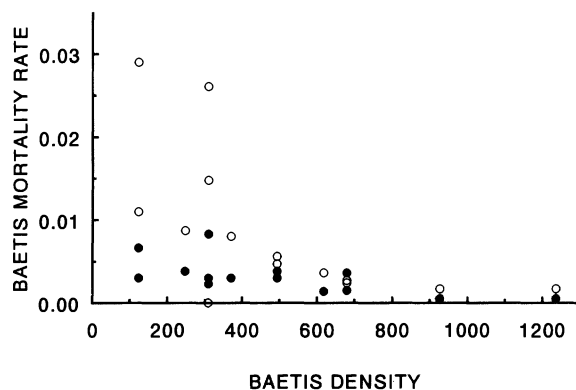

Fig. 2. Daily per-captia mortality rate of *Baetis* (d⁻¹) resulting from predation by male (closed circles) and female (open circles) *Kogotus* in functional response experiments. All trials were combined.

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Table 2. One-way MANOVA (*Baetis* developmental classes I, II, III, IV) on the effects of sampling date on benthic densities (ln[number m^{-2} + 1]) of the summer cohort of *Baetis*. Tukey's HSD test was used for pairwise comparisons ($\alpha < 0.05$).

Response variable	Source	ss	df	F	P > F	Significant pairwise comparisons
MANOVA	Date	0.2617[a]	20,170.1	4.24	0.0001	7/12 > 8/9 = 8/13
Stage I	Date	68.96	5	4.43	0.0019	
	Error	168.1	54			
Stage II	Date	7.767	5	0.98	0.4369	
	Error	85.37	54			
Stage III	Date	145.6	5	7.32	0.0001	8/2 > 7/12
	Error	214.9	54			
Stage IV	Date	26.57	5	3.05	0.0170	8/13 > 7/19 = 7/26
	Error	94.08	54			= 8/2

[a] = Wilks' λ for MANOVA.

Baetis and Kogotus benthic densities

Densities of the four *Baetis* developmental stages varied across dates in a manner that was expected as larvae progressed through subsequent stages (Table 2, Fig. 3). Stage I nymphs had highest densities on 12 July. Stage II peaked on 19 July, although differences among dates were insignificant (Table 2). Stage III larval density peaked on 2 August and Stage IV had highest densities on the last date. During the entire sampling period, Stage I and Stage II nymphs were higher proportions of the benthos ($\bar{X} \pm 1$ SE, n = 6; 0.396 ± 0.082 and 0.523 ± 0.063, respectively) than Stages III and IV (0.070 ± 0.027 and 0.012 ± 0.008, respectively).

Benthic densities of the summer cohort declined from 2897.4 m^{-2} (± 867.2 [1 SE] n = 10) on 12 July to 862.8 m^{-2} (± 201.4 [1 SE] n = 10) on 13 August for total decrease of 70% within the 4.5 weeks. Daily per-capita loss rates were 0.027 d^{-1} (week 1), 0.034 d^{-1} (week 2), 0.012 d^{-1} (week 3), 0.081 d^{-1} (week 4) and 0.034 d^{-1} (week 5) and averaged 0.038 d^{-1} over the entire 4.5 wk.

Kogotus densities were very low and highly variable throughout the study (1.828 m^{-2} ± 1.30 [1 SE] n = 60). Further, density estimates from samples taken over four
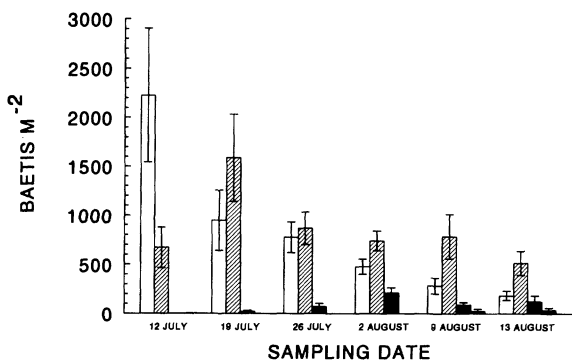

Fig. 3. Benthic densities (± 1 SE) of the summer cohort of *Baetis* over the six sampling dates. The four developmental stages are plotted separately. Stage I (the youngest stage, clear bars); Stage II (hatched bars); Stage III (stipled bars); Stage IV (solid bars).

different seasons in this study reach were 0 m^{-1} (1987, 1990), 4.6 m^{-1} (1985) and 6.1 m^{-1} (1986; Peckarsky 1991b). Using the standard error of the mean density as lower and upper bounds for *Kogotus* density we estimated that per-capita mortality rates resulting from *Kogotus* predation varied between 0.0006 d^{-1} to 0.0036 d^{-1}. Thus, we estimate that direct mortality by *Kogotus* accounted for 1.6 to 9.5% of *Baetis* losses from the study reach.

Baetis drift

Regressions of drift density against sampling date adequately described drift; all regressions were significant except one (p < 0.05 and p = 0.058, respectively) and explained between 75 and 97% of the variation in drift (Table 3A). Drift densities were much higher at night than during the day; intercepts of night regressions were significantly larger than intercepts of day regressions (Table 3B, Fig. 4). We were unable to detect differences in drift densities between upstream and downstream locations (Table 3B), although there appears to be a consistent trend of greater numbers of larvae drifting out of than into the stream reach at night (Fig. 4). Our inability to statistically detect this trend probably occurred because the statistical power of our design was low (Table 3B). Thus, our survey had a high probability of a Type II error (high β), which means that we were likely to not reject the null hypothesis when it in fact was false.

Nymphs in the early developmental stages made up the largest proportions of the drift (Stage I, PM: 0.22 ± 0.03, AM: 0.39 ± 0.04; Stage II, PM: 0.51 ± 0.03, AM: 0.51 ± 0.04; $\bar{X} \pm 1$ SE, each n = 20). Later developmental stages comprised smaller proportions (Stage III, PM: 0.27 ± 0.05, AM: 0.11 ± 0.02; Stage IV, PM: 0.003 ± 0.002, AM: 0.001 ± 0.001; $\bar{X} \pm 1$ SE, each n = 20). Stage I nymphs were a larger component of daytime than nighttime drift, Stage II nymphs were equally represented in daytime and nighttime samples, whereas Stage III nymphs were a higher proportion of nighttime than daytime drift. These results are as expected given the known diurnal patterns

Table 3. Analyses of drift densities (m⁻³) of the summer cohort of *Baetis*. (A). Individual regression equations of drift densities (ln[number m⁻³]) versus sampling date for the four net positions (two upstream and two downstream) during the two sampling periods (day versus night). *'s indicate significant t-tests (H_o: slope, intercept = 0, n = 5 in each regression). (B). ANOVAs for slopes and intercepts of the regressions with the power $(1 - \beta)$ of the individual tests.

A: Regressions

Time	Position	Slope	Intercept	r^2
Night	1-Up	−0.095*	3.334**	0.916
	2-Up	−0.071	2.897**	0.745
	3-Down	−0.063*	3.237***	0.889
	4-Down	−0.092*	3.582**	0.792
Day	1-Up	−0.071*	1.868*	0.802
	2-Up	−0.058*	1.490**	0.862
	3-Down	−0.045*	1.227**	0.843
	4-Down	−0.039**	1.180***	0.970

B: ANOVA's

Variable	Source	ss	df	F	P > F	$1 - \beta$
						(α = 0.05)
Intercept	Day/night	6.6339	1	116.62	0.0004***	0.60
	Up/down	0.0165	1	0.29	0.6191	0.13
	Interaction	0.2961	1	5.20	0.0847	0.32
	Error	0.2275	4			
Slope	Day/night	0.0015	1	7.19	0.0551	0.41
	Up/down	0.0004	1	1.93	0.2368	0.16
	Interaction	0.0001	1	0.71	0.4461	0.09
	Error	0.0008	4			

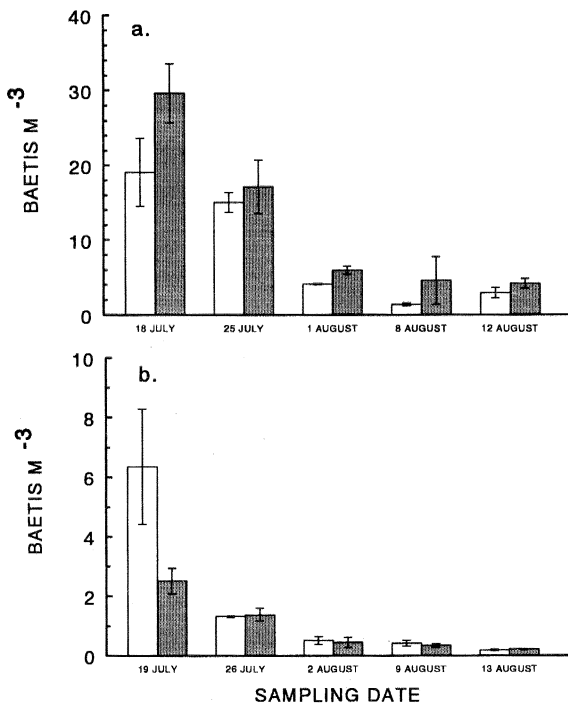* $0.05 \geq P \geq 0.01$; ** $0.01 > P \geq 0.001$; *** $0.001 \geq P > 0.0001$.

Fig. 4. a. Nighttime and b. daytime drift densities (± 1 SE) of the summer cohort of *Baetis* upstream (clear bars) and downstream (solid bars) of the East River reach used to determine *Baetis* densities and natural mortality rates. Note differences in scales for the two panels.

of drift of *Baetis* size classes (Allan 1978, 1987). At night, the proportion of Stage I nymphs in the drift was smaller than their proportion in the benthos (See Results for benthic densities). The opposite pattern occurred for the Stage III nymphs. Stage II nymphs comprised similar proportions of the benthos and drift. Stage IV nymphs had extremely low benthic and drift densities.

Discussion

We estimated that the loss of baetids resulting from direct, predatory mortality by *Kogotus* was a small proportion (< 10%) of the total loss of *Baetis* from this study reach of the East River. This result occurred because large losses (70%) of a relatively large *Baetis* population were combined with a small *Kogotus* population whose individuals consumed few prey in experiments. Few studies have compared the relative contribution of predatory mortality to overall mortality of natural prey populations, with estimates of mortality resulting from predation generally exceeding actual prey losses (e.g., Hildrew and Townsend 1982). In contrast, our results suggest levels of predation pressure well within the actual losses to *Baetis* populations.

Our results may be in line with natural losses resulting from predators because of a realistic study design. In

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previous studies of the *Baetis/Kogotus* system, Peckarsky and Penton (1989a) found predation rates of *Kogotus* that were about four times higher (when estimates were adjusted by predator density for comparison) than in this study. We suspect that earlier mortality estimates were inflated because they were obtained in containers that were biased toward prey capture and against predator avoidance. *Baetis* drifts or swims when encountered by a predator (Peckarsky 1987, Peckarsky and Penton 1989b). In the present study *Baetis* could avoid the predator by drifting in the circular chambers, whereas previous experiments used rectangular chambers with one-way flow. Consequently, baetids could not drift to avoid *Kogotus* and the stonefly could "trap" mayflies in corners. These observations suggest that low estimates of predatory mortality may result from effective predator avoidance behavior of *Baetis*.

Although *Baetis* may be able to avoid *Kogotus* predation by swimming or drifting, recent results suggest that significant sublethal costs to prey may result from such predator avoidance behavior (Peckarsky et al. 1993). Peckarsky et al. (1993) found that the presence of *Kogotus* (and another stonefly, *Megarcys signata*) caused a depression in gut fullness of *Baetis* nymphs similar to that caused by severe reduction of the periphyton resource. In long-term experiments (16 d) the presence of *Megarcys* (a related stonefly species) in stream-side chambers caused a decrease in the dry mass of both male and female *Baetis* upon emergence that was similar to the decrease among starved nymphs. These results suggest that predatory stoneflies may reduce the contribution of the *Baetis* population to the next generation more by effects on fecundity than by direct effects on prey survival.

It is possible that the actual proportion of *Baetis* mortality resulting from *Kogotus* predation could be even lower than our estimates because of consumption of naturally occurring alternative prey. For example depending on their availability, chironomids can compose between 45 to 90% of the gut contents of *Kogotus* (Allan 1982, Peckarsky 1985). Guts of the perlid stonefly *Doroneuria baumanni* contained about 1 *Baetis* and 4 chironomids, although these stoneflies still appeared to select mayflies at greater frequency than they were found in the environment (Lancaster 1990). Peckarsky and Penton (1989a) have shown that *Kogotus* also consumes other mayfly prey. These results suggest that predation pressure on *Baetis* may be reduced by the consumption of alternative prey.

Similarly, interference competition among stoneflies (Walde and Davies 1984b, Peckarsky 1991c), and presence of trout (Feltmate and Williams 1991) have both been shown to reduce predatory efficiency of stoneflies in streams. Our predation rate experiments eliminated both of these variables, which could have also resulted in inflated estimates of predation on *Baetis*. Therefore, we suspect that stonefly-induced mortality is even lower in natural stream systems where stoneflies are subjected to

other selection pressures. These observations strengthen our conclusion that stoneflies are not a significant source of *Baetis* mortality in streams.

From the perspective of an individual *Baetis* it may be better to reside in a high prey density patch than in a low prey density patch (all else being equal), because individuals reduce predation risk by being members of aggregations. Whether individuals benefit from aggregation in the natural community depends on two distinct mechanisms: dilution effects inherent in the functional response (e.g., satiation reduces predation risk in aggregations) and encounter effects (e.g., predators do not find larger aggregations of prey more easily than smaller ones; Turner and Pitcher 1986). Our results suggest that dilution effects occur, because the probability that an individual *Baetis* was consumed was higher when prey densities were lower; i.e., *Kogotus* consumed the same number of prey regardless of how many prey were available. Further, indirect evidence suggests that encounter effects also occur, because stoneflies did not aggregate in high prey density patches in this study or in any others over several spatial scales (Peckarsky 1988, 1991b) even though *Baetis* exhibits marked heterogeneity in its distribution (Peckarsky 1988). Similarly, Wrona and Dixon (1991) found that aggregation conferred a net advantage to pupae of the caddisfly *Rhyacophila vao* from predation by the planarian predator *Polycelis cornonata*.

Baetis mortality estimates were high (an individual had an average probability of mortality of about 4% d^{-1}), and the entire population was reduced by 70% in 4.5 wk. Clifford and Boerger (1974) roughly estimated that a population of *Baetis tricaudatus* declined 99.9% from egg to emergence of adults. Although our estimates are somewhat lower, we only estimated mortality for 4.5 wk and did not consider egg, early larval and adult mortality. Therefore, our results suggest that there is considerable mortality in the larval stage, and provide a strong justification for studies (in progress) of other potential sources of *Baetis* mortality (e.g., trout predation, parasitism, density-dependent effects).

We can make no clear statement concerning net migration of *Baetis* into and out of the study reach. Although a trend in the data suggested that at night more larvae left the reach than entered it, the results were not statistically significant. Two replicates do not estimate drift density with enough precision (Allan and Russek 1985; power < 20%) to detect differences equal to, or less than, the differences exhibited between upstream and downstream sites. Consequently, if a difference in the drift into and out of the study reach of the magnitude suggested by our mean values actually existed, the differences would be statistically undetectable about 80% of the time. Because the power of the test was low, non-significance might have occurred even though differences between the two drift densities were real. There was a small waterfall directly upstream of the study reach that could act as a barrier to drift into the reach. Certainly, assumptions, made by many researchers, that drift into and out of study

reaches are quantitatively similar are questioned by these results.

If we assume hypothetically that the estimated net losses or gains are real, we can estimate the total number of organisms lost (or gained) from the reach by multiplying drift densities by stream discharge and time. We can also estimate the number of organisms in the benthos by multiplying benthic densities by the area of the stream bottom. We estimated net losses (or gains) while varying the number of hours of daytime or nightime drift densities during a 24-h period. In most cases, estimates of net numbers of *Baetis* lost from the reach by drifting were higher than the estimated losses from the benthos from week to week. Thus, we have some bias in our data collection or estimation procedure that results in either underestimated benthic densities, over-estimated drift densities or both. However, comparisons within the drift and within the benthos should be valid if the bias is consistent within the benthos or within the drift.

This and other related studies suggest that *Baetis* dispersal is one key to understanding the population-level consequences of stonefly-mayfly interactions. Dispersal is not only a method of predator avoidance, but is also an important component of the foraging behavior of *Baetis* (Kohler 1984, 1985). Swimming is also the proximate cue for attack by stoneflies (Peckarsky and Wilcox 1989). In caging experiments, high dispersal rates of prey obscured the lethal effects of predators (Cooper et al. 1990, Peckarsky 1991a). Finally, predator avoidance may not be without costs. Avoidance often results in export from periphyton patches and reduction in feeding rates resulting in lower body size at maturity and adult fecundity (Peckarsky et al. 1993). Consequently, we conclude that the lethal effects of predatory stoneflies on *Baetis* populations (mortality) are relatively small in contrast to the potentially significant decrease in fitness (fecundity) that they cause to mayflies that are not consumed.

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