Sublethal Consequences of Stream-Dwelling Predatory Stoneflies on Mayfly Growth and Fecundity

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Ecology is currently published by The Ecological Society of America.

SUBLETHAL CONSEQUENCES OF STREAM-DWELLING PREDATORY STONEFLIES ON MAYFLY GROWTH AND FECUNDITY[1]

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Abstract. Predators can have consequences on prey populations and communities that extend well beyond direct predator-induced mortality. Predator–prey interactions often affect prey feeding rates, growth rates, or fecundities, thereby significantly affecting reproductive success of prey adults. Thus, investigation of the sublethal fitness consequences of behavioral responses of prey to predators is essential to our understanding of the total impact of predators on prey populations and communities. Feeding (algal grazing) rates, growth rates, and fecundities of *Baetis bicaudatus* (Baetidae) larvae were measured in replicated circular flow-through stream channels to determine the sublethal consequences on fitness correlates of the presence of predatory stoneflies (Perlodidae). Gut fullness of 24-h starved *Baetis* larvae was measured using fluorometry after 24 h (short-term experiments) in four treatments: (1) ambient resource rocks and no predators, (2) low resource rocks and no predators, (3) ambient resource rocks and one female perlodid stonefly (*Megarcys signata*), or (4) *Kogotus modestus* whose mouthparts were glued to prevent lethal effects of predation. Mid-instar male and female *Baetis* larvae were reared for 3 wk until wing pad maturation (long-term experiments) and subjected to all but the *Kogotus* treatment. Predator avoidance significantly reduced levels of *Baetis* gut fullness, over the short term, to levels intermediate between the high and low resource treatments. Longer term residence with predatory stoneflies caused larvae of both male and female *Baetis* to mature at significantly smaller sizes than in the treatment with ambient food but no predators. Mayflies with predators matured at sizes similar to those held with low food levels over the long term. Interestingly, both starved larvae and those avoiding predators did not grow during the experimental period in contrast to about a 50% growth rate of larvae experiencing ambient food levels, but no predators. Similarly, egg biomass per mature female larva was significantly reduced in both starved and predator treatments. The proportion of total body mass allocated to eggs was only reduced in starved mayflies indicating that the females avoiding predators accrued less total mass, but allocated a similar proportion to eggs as did well-fed *Baetis*. These data convincingly demonstrate that predator avoidance can have dramatic consequences on mayfly fitness. The mechanism explaining those fitness consequences is probably a disruptive drift/swim response by *Baetis* to encounters with stoneflies, which reduces *Baetis*' feeding rates. If we accept the assumption that natural selection has shaped the foraging behavior of organisms to maximize fitness, foragers need to make decisions that maximize both survivorship (minimizing risk of predation) and fecundity. In mayflies fecundity is entirely a function of resource acquisition by the larvae, which makes them particularly vulnerable to such sublethal effects of predation. Nonetheless, we suspect that the types of sublethal costs of predator avoidance documented by this and other recent studies are nearly universal consequences of organisms foraging under predation risk.

Key words: artificial streams; fecundity; feeding rates; fitness; growth rates; mayflies; predator avoidance; stoneflies; streams; sublethal effects.

INTRODUCTION

Selective predation, or consumption of certain prey types disproportionate to their densities in the environment, can have measurable effects on prey community structure. However, predation can also have

consequences on prey populations and communities that extend well beyond direct predator-induced mortality. Recently, Sih et al. (1985) pointed out that few investigations have focused on such "indirect" predator effects. Some recent (e.g., papers in Kerfoot and Sih 1987) and other classic studies have documented two general classes of predator impacts other than direct lethal effects on populations: (1) indirect community-level effects, such as keystone predator effects

(Paine 1969, Dodson 1974) and "top-down" or cascading trophic effects (Carpenter et al. 1987, Power 1990), and (2) nonlethal effects on prey populations. Kerfoot and Sih (1987) define both of these as indirect effects, but we consider the latter direct, though sublethal effects (as in Strauss 1991).

This second class of effects involves direct interactions between predators and prey that do not result in death to prey individuals, but have negative consequences on prey populations. Generally, those sublethal effects are due to changes in prey behavior as a result of predator avoidance (e.g., Fraser and Huntingford 1986, Formanowicz and Brodie 1988). If prey individuals take fewer risks in the presence of predators (Cerri and Fraser 1983, Abrams 1984, Real and Caraco 1986, Abrahams and Dill 1989), they may alter microhabitat use or behavior in such a way that their food intake is reduced. Such risk-sensitive foraging behavior may represent a trade-off between predator-induced mortality and reductions in prey foraging rates, and consequently growth rates and fecundities. However, as pointed out by Skelly (1992), field tests of fitness costs of predator avoidance are rare (but see Cooper 1984, Holomuzki 1986a, b, and Werner and Hall 1988). This type of direct sublethal effect may also extend to the community level (have indirect effects), since behavioral changes by prey often affect their competitors ("indirect apparent competition" sensu Holt 1984) or levels of their own resources (Dill 1987, Gilliam et al. 1989). Zaret (1980), Dill (1987), and Sih (1987) argue that direct sublethal and indirect effects of predation may be more costly to prey population densities and reproductive output than the generally small proportion of prey that are killed by predation.

Although many studies have documented selective predation by stream-dwelling stonefly larvae on *Baetis* spp. (Baetidae) (Malmqvist and Sjöström 1980, Molles and Pietruszka 1983, 1987, Walde and Davies 1987, Williams 1987, Allan and Flecker 1988, Fuller and DeSteffan 1988, Peckarsky and Penton 1989a), few have actually shown that stoneflies depress *Baetis* populations in enclosures (Oberndorfer et al. 1984: no; Walde and Davies 1984a: no; Peckarsky 1985: sometimes; Walde 1986: sometimes; Cooper et al. 1990: only if *Baetis* mobility is restricted). These data and those on feeding rates of stoneflies on *Baetis* spp. (Walde and Davies 1984b, Peckarsky and Penton 1989a, Cooper et al. 1990) suggest that rates of stonefly predation are not high enough, even on their favored mayfly prey species, to override the effects of prey mobility. Thus, we do not observe major changes in prey community structure as a result of stonefly predation on a small scale (enclosures).

However, *Baetis* behavior in the presence of predatory stoneflies is greatly modified from that in their absence (Peckarsky 1980, Williams 1987). Encounters with predators are disruptive, often resulting in dispersal from a periphyton patch on which they are foraging (Peckarsky 1987, Peckarsky and Penton 1989b). Other mayflies may suffer the same fate depending on their propensity for entering the water column in response to stonefly encounters; but most reports indicate that this disturbance has the greatest impact on *Baetis* spp. (Corkum and Pointing 1979, Walton 1980, Malmqvist and Sjöström 1987). Thus, such disruptive predator avoidance behavior may lower *Baetis* fitness by reducing their feeding rates, growth rates, and fecundities.

The purpose of this study was to test for direct sublethal consequences of foraging by stream-dwelling predatory stonefly larvae on larvae of *Baetis bicaudatus* (Baetidae), a mayfly that shows disruptive predator-avoidance behavior. *Baetis* larvae are the preferred mayfly prey species of the perlodid stoneflies *Megarcys signata* and *Kogotus modestus* in western Colorado streams (Peckarsky and Penton 1989a). When touched by a predatory stonefly, *Baetis* usually abandons the patch of substrate where it is grazing algae, and enters the water column (swims or drifts, Peckarsky and Penton 1989b). We predicted that this predator-avoidance behavior should reduce the intake of algae by mayflies, potentially resulting in lower growth rates and fecundities of maturing larvae. Our specific objectives were to (1) compare the short-term food intake of *Baetis* individuals in the presence and absence of predatory stoneflies, and (2) measure the effect of predator presence on the long-term growth rates of larval *Baetis* males and females as well as the fecundities of *Baetis* females at emergence to the adult stage.

MATERIALS AND METHODS

Study site and populations

Experiments were done on populations of stonefly and mayfly larvae that were common in high elevation streams (2450 m) in the vicinity of the Rocky Mountain Biological Laboratory in western Colorado. Test individuals were collected from a third-order site of the East River, or Benthette Brook, a first-order fishless tributary of the East River. At these sites, *Baetis bicaudatus* is bivoltine, having an overwintering generation that emerges from late June through early August and a strongly overlapping short summer generation that emerges from late July through early September. Individuals of both generations graze diatoms from rocky substrates. Diatoms are more abundant during late July and August (M. A. Penton, *unpublished data*), the period of greatest growth and development of the summer generation. As is typical of mayflies, *Baetis* has an extremely short nonfeeding adult phase (≈ 48 h), and attains all nutrients necessary for growth and reproductive development during the larval phase. Thus, potential fecundity is fully determined during the larval phase, and *Baetis* females emerge with eggs fully developed and ready to be fertilized.

Two predatory stonefly species are codominant in

these streams and have temporally staggered univol-
tine life cycles. *Megarcys* emerge from late June through
early August, concurrent with the overwintering gen-
eration of *Baetis,* and larvae of the next generation grow
rapidly enough throughout August and September to
become predatory on the late instars of the summer
generation of *Baetis. Kogotus* emerges from late July
through early September, concurrent with the summer
generation of *Baetis.* Similarly, *Kogotus* larvae of the
next generation are large enough by the following June
to be predatory on the late instars of the overwintering
generation of *Baetis.* Thus, both stonefly species exert
predation pressure on both generations of *Baetis. Me-
garcys* larvae achieve body sizes about two to three
time larger than those of *Kogotus* (Peckarsky and Cow-
an 1991), and inflict much higher rates of mortality on
Baetis than do *Kogotus* larvae (Peckarsky and Penton
1989*a*). Both stonefly species show dramatic sexual
size dimorphism, with females emerging at about twice
the size of males and causing about twice as much
Baetis mortality as males (Peckarsky and Cowan 1991).

Experimental conditions

Experiments were done in 15 cm diameter cylindri-
cal plexiglass flow-through chambers housed in a trans-
lucent vinyl greenhouse (Weatherport) beside the East
River. Filtered stream water was gravity fed from Ben-
thette Brook 100 m above the Weatherport in 1989
and 1990, or pumped from the East River in 1991.
(See Peckarsky and Cowan 1991 for further details.)
We preferred using Benthette Brook water because of
its lower concentration of suspended particulates.
However, a failure in this system dictated our use of
East River water during 1991 experiments. The water
source is of concern because *Baetis* shows more dra-
matic nocturnal feeding periodicity in water from the
fish-containing stream (East River) than in water from
the fishless stream (Benthette Brook) (C. A. Cowan and
B. L. Peckarsky, *unpublished data*). However, all cham-
bers within experiments were subjected to the same
water source, thereby eliminating any possibility that
water source caused differences between treatments
within experiments. Each chamber received four gran-
ite rocks of similar size (≈ 5 cm diameter), and flows
were maintained at 10–20 cm/s (measured with a Nix-
on Instruments micropropeller flowmeter).

Short-term feeding rate experiments

During July 1989 we conducted an experiment de-
signed to measure the impact of predator avoidance
on *Baetis* algal grazing rates. Both algal resource levels
and predator presence were manipulated in the cham-
bers. Mayflies were subjected to either ambient or low
levels of algae. An ambient food supply was provided
by using slimy rocks collected from the stream. We
achieved low algal levels by boiling then drying rocks
before use. Each chamber received five late stage III

Baetis larvae (wing pads longer than wide but not dark-
ened, Delucchi and Peckarsky 1989) of the overwin-
tering generation (comparable to a low density in the
stream = 300 larvae/m², Peckarsky 1991*a*). All may-
flies were starved (placed in chambers with previously
boiled rocks) for 24 h before trials, which was more
than adequate time to clear their guts of photosynthetic
pigments, and were subjected to one of four treatments
for 24 h. Trials were started and ended at 0600 Moun-
tain Daylight Time, a time when *Baetis* guts are nor-
mally the fullest (C. A. Cowan and B. L. Peckarsky,
unpublished data).

We added (1) one female *Megarcys* or (2) *Kogotus*
to chambers containing ambient resource levels, while
both (3) ambient and (4) low resource chambers re-
ceived no predators. Stonefly density (60 individu-
als/m²) approximated high density in the East River
(Peckarsky 1991*a*) and average density in Benthette
Brook. The low resource treatment was used to sim-
ulate extreme reduction in feeding in order to compare
the performance of mayflies in the presence of a pred-
ator that inhibited feeding to that of *Baetis* with a
known starvation state. In an attempt to clear more
completely *Baetis* guts of pigments, we repeated this
experiment in July 1990, replacing the boiled rocks in
the starved treatment chambers every 4 h during the
24-h treatment period.

We prevented stoneflies from feeding on test may-
flies by gluing stoneflies' mouthparts with household
Barge Cement. Trained observers could not distinguish
the foraging movements and attack behavior of glued
and unglued stoneflies during a pilot experiment car-
ried out in 1988. In addition, foraging periodicity of
glued stoneflies did not differ from that of unglued
stoneflies (B. L. Peckarsky and C. A. Cowan, *unpub-
lished data*). Therefore, this treatment effectively re-
moved the lethal effects of foraging stoneflies, enabling
measurement of any sublethal effects. At the end of the
experiment mouthparts of glued individuals were
checked to assure that they had remained disabled
throughout the trials. If any prey disappeared from
chambers, stomachs of the predators were also checked
for *Baetis* remains. To control for the possible effect
of the glue on mayfly performance, we placed a small
pebble with a drop of Barge Cement in each chamber
that did not have a stonefly.

After 24 h, all *Baetis* were preserved individually in
amber bottles containing 90% ethanol, and within 12
h of preservation, macerated to expose gut contents to
the extract, extracted for a total of 24 h, and subjected
to fluorometric analysis of the gut pigments, chloro-
phyll *a* and phaeopigments (breakdown products of
chlorophyll). With the fluorometer we were able to
resolve very small differences in pigment levels, which
enabled us to distinguish the gut fullness of the indi-
vidual *Baetis* subjected to different treatments. (See
Cowan and Peckarsky 1990 for a complete description
of this methodology. Note all other measures of chlo-

rophyll *a* taken in this study were similarly extracted in 90% ethanol and measured fluorometrically.) During the maceration process, we noticed that some females ($\approx$ 5% of the total sample) were parasitized by a mermithid nematode that occupied the complete abdominal and thoracic cavities; those were eliminated from the analysis. We used one-way analysis of variance with four treatment levels to analyze the treatment effect on the response variable: total pigment per gut (chlorophyll *a* + phaeopigment). Mean responses of the five individuals within each chamber were log transformed as indicated by a residuals analysis, and chamber means ($n = 7$) were used as replicates.

Long-term growth and fecundity experiments

During June and July 1991 we measured the impact of predator presence from fitness correlates of overwintering *Baetis* on: (1) time of emergence, (2) size at emergence, (3) growth rates of larvae, and (4) fecundities of females. Interestingly, a July through August 1990 attempt of this experiment was unsuccessful due to high levels of mermithid parasitism that completely castrated 9–30% (depending on the treatment) of the late instar or emerging *Baetis*. We did the 1991 experiment in early summer when parasite levels were very low (only one parasitized individual). We determined the sex of individuals before trials (larvae were inspected under a field dissecting microscope for the presence or absence of the precursor of the adult male compound eye), and on 25 June placed either 10 male or 10 female *Baetis* in each chamber. We increased the number of *Baetis* per chamber to compensate for anticipated losses due to starvation or predation. At the beginning of the experiment, mayflies were in early stage III, and initial sizes of larvae were estimated from subsamples of test organisms. Mesh nets were placed over each chamber to prevent loss of emerging individuals.

We collected only the first five individuals from each chamber that reached maturity, and immediately replaced mature *Baetis* with earlier instar individuals of the opposite sex (because they were distinguishable from the original 10 *Baetis*) to maintain constant mayfly densities and collected larvae just before they emerged at the time of maturation. We assessed state of maturation by the presence of elongate black wing pads through the integument of which the developing wings were visible (stage IV, Delucchi and Peckarsky 1989). During preliminary observations, we determined that *Baetis* individuals reaching this state were within 24 h of emergence, at which time they cease feeding (Cowan and Peckarsky 1990). Therefore, we were able to get an estimate of the effects of treatments on larval growth rates by comparison of initial to final mayfly sizes. Males and females were dry weighed using a Cahn microbalance and eggs were removed from all females and weighed as an estimate of fecundity.

To maximize replication (seven chambers per treat-

ment), we used only *Megarcys* as the predator treatment eliminating the *Kogotus* treatment to compensate for adding the *Baetis* sex treatment. Predators that died, emerged, or became inactive during times when normal stoneflies are foraging (as determined during four daily checks of the chambers) were replaced immediately with freshly glued individuals. We also replaced individuals who had become unglued and thus consumed some test prey individuals. Thus, while some stoneflies remained active for the entire 3 wk of the experiment, others were replaced at shorter intervals.

In 1990 we conducted a pilot experiment to (1) measure initial chlorophyll *a* levels and count diatom cells, (2) follow diatom succession over a 2-wk period on rocks in the Weatherport and from the East River, (3) measure chlorophyll *a* on rocks that had been grazed by *Baetis* (density = 5 mayflies per chamber) for 10 d, and (4) measure chlorophyll *a* on previously boiled rocks after 24 h in the chambers. During the long-term experiment we also took direct measurements of (1) chlorophyll *a* levels on rocks before and after 1 wk of grazing by *Baetis* (density = 10 individuals per chamber) in predator and no predator chambers and (2) chlorophyll *a* levels on previously boiled rocks after 48 h in the chambers. We monitored the chlorophyll levels on rocks in the Weatherport and the stream using a modified syringe sampler (Mayer and Likens 1987, Peckarsky 1991*a*) that collected the algae from a 1-cm^2 patch on the surface of the rock. Results from these experiments provided the rationale for the following protocol to maintain experimental resource levels throughout the long-term experiment. Boiled rocks were replaced every other day, because diatom cells recolonized the rocks through the water delivery system. To prevent ambient levels of algal resource from being overexploited, we enhanced light levels in the chambers with fluorescent lighting for $\approx$ 12 h/d. Slimy rocks were replaced in chambers where resource levels became too low (after 2 wk).

The experiment ended on 16 July after 21 d. As in the analysis of the short-term feeding rate data, we used the log-transformed mean of each response variable per chamber for statistical analyses, with chamber means serving as replicates. We applied a multivariate analysis of variance to assess the treatment effects on interdependent response variables of males and females: (1) size at maturation, (2) date of maturation; and of females only: (3) egg mass at maturation, (4) percent body mass attributable to eggs, and (5) total mass. Where MANOVAs were significant, subsequent separate ANOVAs and pairwise *t* multiple comparison tests (comparable to Fisher's LSDs for unequal sample sizes) determined which variables contributed significantly to the effects. We also field collected black wing pad (mature) larvae of male and female *Baetis* and compared their sizes and fecundities to those reared in our experimental chambers to check for container effects.
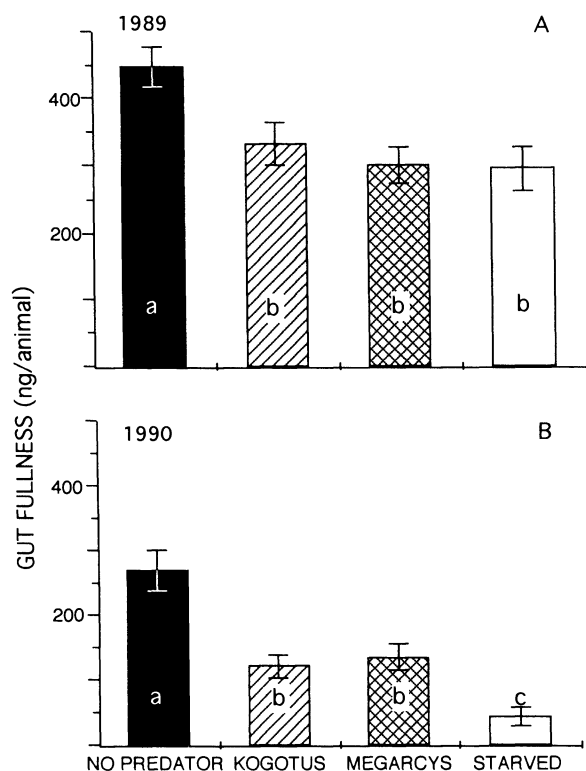
FIG. 1. Short-term feeding rate trials (1989 and 1990): total pigment (chlorophyll a + phaeopigments) per Baetis in chambers with no predators, Kogotus, or Megarcys, or where Baetis were starved ($n = 7$). Means with the same letters are not significantly different.

TABLE 1. Chlorophyll a on rocks from East River, Benthette Brook, and in the Weatherport greenhouse under various conditions.

	Source of rocks	Chl a (ng/cm^2, $\bar{X} \pm 1$ SE)	n
1990	East River, day 0	0.088 ± 0.011	3
	Boiled rocks, 24 h in Weatherport	0.034 ± 0.004	7
	Slimy rocks, 10 d in Weatherport	0.346 ± 0.057	3
	East River, day 10	0.073 ± 0.026	3
1991	Benthette Brook, day 0	1.730 ± 0.594	5
	Boiled rocks, 48 h in Weatherport	0.009 ± 0.004	5
	Slimy rocks, 7 d Megarcys treatment	0.348 ± 0.101	4
	Slimy rocks, 7 d, no predator treatment	0.489 ± 0.238	5

due to predator avoidance was comparable to that due to severe reduction of the periphyton resource. However, in the 1990 trials, where we replaced boiled rocks every 4 h during the 24 h trial, sublethal predator effects on Baetis algal consumption were significantly lower than the effect of virtually complete food deprivation (Fig. 1B).

Long-term effects on Baetis growth and fecundity

Effects of treatments on algal resource levels. —During the 1990 pilot experiment with only five Baetis per chamber, periphyton levels remained high throughout a 2-wk period of monitoring (Fig. 2). On most dates, total cell counts were higher in the Weatherport chambers than in the East River, probably due to low grazing pressure and the absence of scouring. Similarly, chlorophyll a measurements made on day 10 were higher in the Weatherport than in the stream (Table 1). During the long-term experiment in 1991, chlorophyll levels declined more rapidly (but were still relatively high) after 1 wk of grazing by 10 Baetis per chamber (Table 1).

RESULTS

Short-term effects on Baetis feeding rates

During both 1989 and 1990 the presence of a non-feeding predator (*Megarcys* or *Kogotus*) significantly reduced the gut fullness (total gut pigments) of Baetis over 24 h (Fig. 1: 1989; $F = 3.19$, $P = .0419$, df = 3, 24; 1990: $F = 17.19$, $P = .0001$, df = 3, 24). Interestingly, *Megarcys* and *Kogotus* had similar effects regardless of the differential predation pressure they exert on Baetis (Peckarsky and Penton 1989a). Thus, sublethal effects of predators may not be closely associated with their potential lethal effects, because sublethal effects depend on encounter rates rather than prey consumption rates.

Chlorophyll measures on previously boiled rocks (Table 1) and gut pigment levels of Baetis foraging on the boiled rocks (Fig. 1A) indicated that diatoms were recolonizing the chambers after as few as 48 h, and that Baetis was able to find food at a remarkably low resource level. The guts of Baetis grazing on rocks previously boiled, but placed in stream water for 48 h had no less pigment than those of Baetis foraging in the presence of predators on rocks with ambient levels of algae. Therefore, the reduction of Baetis' feeding rates
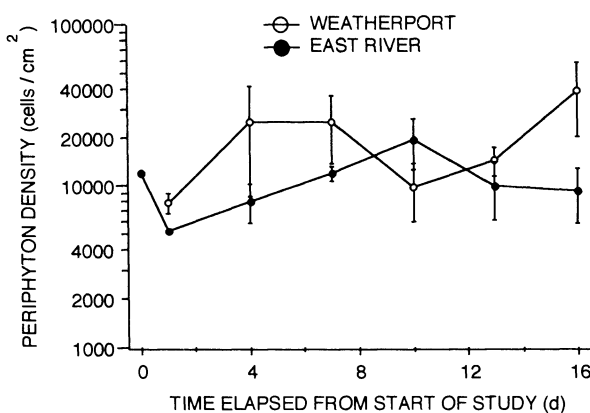

FIG. 2. Total diatoms on rocks in the East River and in the Weatherport greenhouse over a 16 d period ($\bar{X} \pm 1$ SE).
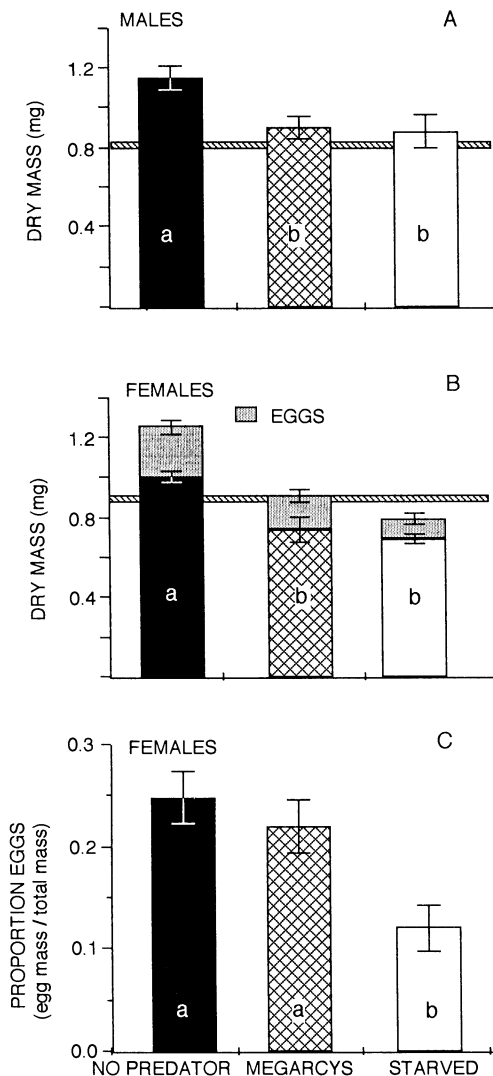
FIG. 3. Long-term growth and fecundity trial (1991): mean ± 1 SE dry mass of mature males (A), mature female dry mass without eggs and egg dry mass (B), and proportion of body mass comprised of eggs (C) of *Baetis* in chambers with no predators, with *Megarcys,* or starved. For males and females, *n* = 7, 6, 7 and 6, 7, 7, respectively. Horizontal hatched bar represents $\bar{X}$ ± 1 SE initial dry mass of *Baetis* used in experiments. Means with the same letters are not significantly different.

Sublethal effects on Baetis *fitness correlates.* — Results of this experiment clearly documented a consistent effect of predator presence on the performance of both male and female *Baetis*. The final dry mass of both males and females was significantly reduced in the presence of *Megarcys* (Fig. 3A and B, Table 2). Predator presence caused about a 21% reduction in weight of *Baetis* males at maturation, while starvation comparably reduced their body mass by 23%. Mature females weighed 25% less with predators than without, and egg masses suffered a 35% loss in the presence of predators.

Starvation of female *Baetis* produced a 31% loss of body mass and a 61% loss of egg mass. Interestingly, the egg : body mass ratio differed between starved females and those with predators, suggesting that *Baetis* in chambers with predators allocated proportionately more resource to egg mass than did starved *Baetis,* whose fecundity suffered the most (Fig. 3C, Table 2). There were no significant treatment effects on maturation times of *Baetis* (Table 2). Comparison of final masses with initial masses illustrates that *Baetis* virtually did not grow in the presence of predators or when deprived of food, and that there was no measurable difference between the effects of those two treatments on *Baetis* performance (Fig. 3A and B). These data suggest that predators have a severe long-term effect on *Baetis* growth and fecundity, comparable to that of food deprivation.

Comparison of body and egg masses of mature, field-collected male and female *Baetis* to those having matured in the experimental chambers showed that even the well-fed individuals matured at a smaller size than those maturing in the stream (Fig. 4). These data indicate that there is a container effect on *Baetis* growth rate and fecundity that is comparable (20–22% body size reduction) or greater than (43% reduction in fecundity) the sublethal effect of predator presence and of food deprivation within the containers. Further, sexual size dimorphism observed in field populations of *Baetis* (females larger than males, $F = 1.79, P < .0001,$ df = 33, 48) was less apparent in the experimental containers (Fig. 4). These data indicate that the conditions provided by the artificial streams promote lower growth and fecundity than those in the stream.

DISCUSSION

Our study shows that surviving prey mature at a smaller size than do those released from predation risk and thus suffer a loss in potential contribution of offspring to the next generation. The fitness consequences to mayflies of achieving a smaller adult body size are well known for females. Larger bodied female *Baetis bicaudatus* produce more eggs (Fig. 5) as has been documented for many other mayfly species (Brittain 1982, Harker 1989, but see Clifford and Boerger 1974). Therefore, females that are able to accrue more body mass will have higher potential reproductive output than smaller females. In males, an advantage of large body size has only been measured for one species (*Epeorus longimanus,* Heptageniidae, Flecker et al. 1988, Allan and Flecker 1989). These studies have shown that males collected at random in mating swarms are smaller on average than males collected in mating pairs, suggesting that larger males achieve more mating success.

Other studies have documented similar sublethal costs of predator-avoidance. Reductions in prey feeding rates in the presence of predators have been measured for a wide variety of aquatic taxa, including

TABLE 2. Summary of MANOVAs of effects of predators on dry mass of mature *Baetis* larvae, time to maturation (males and females), egg dry mass, percent eggs, and total dry mass (females only). M = *Megarcys* (no transformations needed).

| Sex	Response variable	Source	ss	df	F	P	LSDs
Males	MANOVA	Model	0.464*	4, 32	3.74	.013	
	Body mass	Model	0.303	2	4.81	.022	No predator > M = starved
		Error	0.535	17			
	Maturation time	Model	5.79	2	0.51	.61	
		Error	96.62	17			
Females	MANOVA	Model	0.061*	10, 26	7.92	.0001	
	Body mass	Model	0.337	2	11.76	.0006	No predator > M = starved
		Error	0.243	17			
	Egg mass	Model	0.085	2	6.94	.006	No predator > M = starved
		Error	0.104	17			
	Percent eggs	Model	0.071	2	7.69	.004	No predator = M > starved
		Error	0.078	17			
	Total mass	Model	0.730	2	10.95	.0009	No predator > M = starved
		Error	0.567	17			
	Maturation time	Model	10.66	2	2.12	.15	
		Error	42.78	17			

* Wilks' lambda.
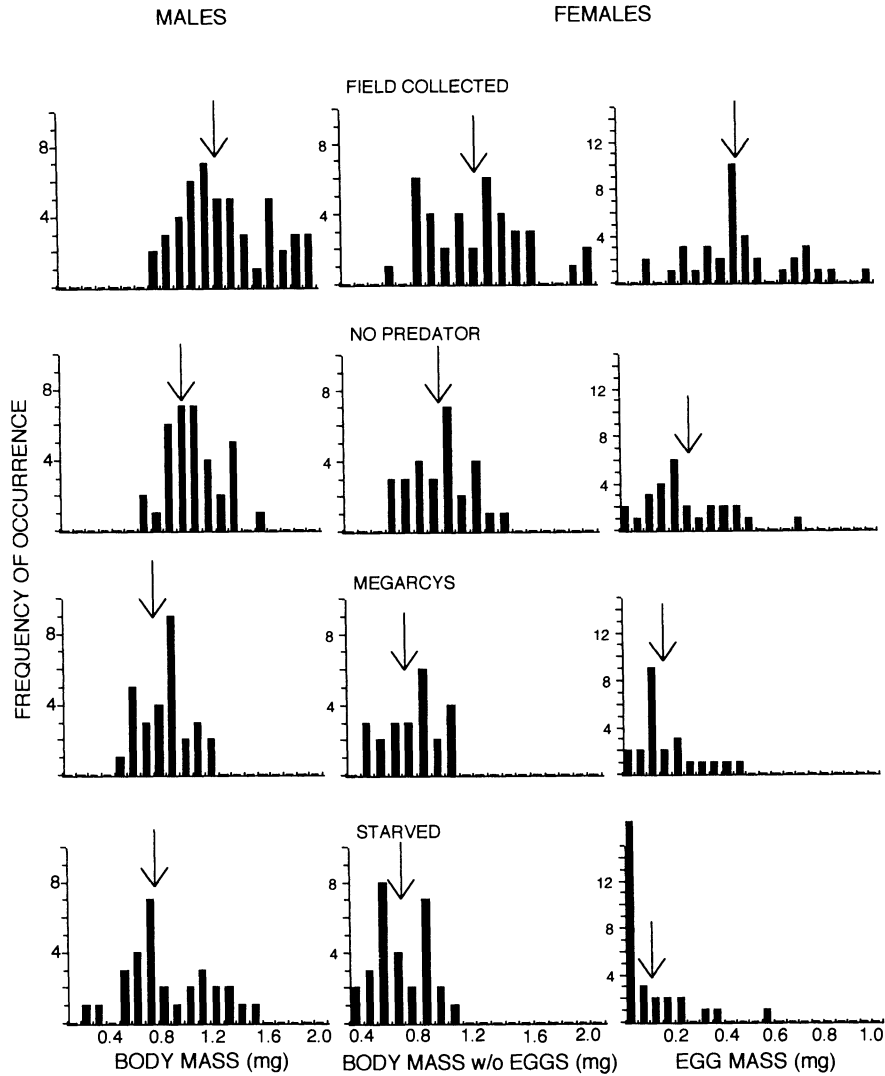
FIG. 4. Frequency distribution of dry mass of male and female *Baetis,* and egg dry mass of female *Baetis* for field-collected mature larvae and those maturing in chambers under the three treatments in the Weatherport greenhouse (1991). Arrows indicate means of each frequency distribution.
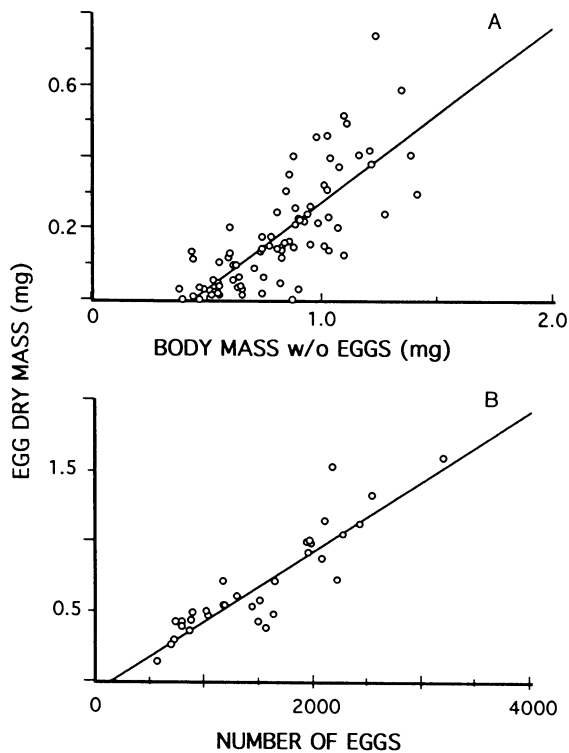
FIG. 5.   (A) Relationship between dry mass of female *Baetis* without eggs and egg dry mass ($r_s = 0.809$, $P < .0001$, $n = 80$). (B) Relationship between egg dry mass and egg number ($r_s = 0.892$, $P < .0001$, $n = 34$).

aquatic bugs (Bailey 1986), odonate larvae (Heads 1985, 1986, Dixon and Baker 1987, Jeffries 1990), stoneflies (Feltmate and Williams 1989), mayflies and caddisflies (Kohler and McPeek 1989), snails (Bertness 1981), crayfish (Stein and Magnusen 1976, Bellman and Krasne 1983), crustacean zooplankton (Jakobsen and Johnsen 1988), bluegill sunfish (Gotceitas 1990, Turner and Mittlebach 1990), and juvenile coho salmon (Dill and Fraser 1984). These feeding reductions have been attributed to changes in the level of foraging activity (Dixon and Baker 1988, Lawler 1989, Sih et al. 1990) or to changes in microhabitat or food patch selection by foragers in the presence of predators (Sih 1982, Power 1987, Wellborn and Robinson 1987, Pierce 1988).

A typically disruptive response by *Baetis* to predator–prey encounters is the mechanism most probably causing the feeding rate, growth rate, and fecundity costs reported here as a consequence of predator presence. Encounters with predatory stoneflies, which forage on the substrate, result in drift or swim avoidance responses by *Baetis* (Malmqvist and Sjöström 1987, Peckarsky and Penton 1989b, Lancaster 1990). Such behavior disrupts *Baetis*' foraging activity, significantly reducing rates of food intake. Although *Baetis* larvae sometimes respond less conspicuously by crawling away

from hydrodynamic pressure waves produced by foraging stoneflies (Peckarsky and Penton 1989b), most responses to stoneflies only occur after the predators make contact with *Baetis* and result in costly escape behavior (Peckarsky 1991b, Peckarsky and Penton 1989b; B. L. Peckarsky et al., *unpublished manuscript*).

We cannot entirely rule out the potential importance of observed microhabitat shifts by *Baetis* in the presence of predatory stoneflies. We and others (Soluk and Collins 1988; B. L. Peckarsky et al., *unpublished manuscript*) have measured shifts in the use of rock surfaces by *Baetis* (movements away from surfaces with highest resource levels) in the presence of stoneflies. Also, the proportion of *Baetis* individuals residing on a high food rock vs. a low food rock declines in the presence of a predatory stonefly. Therefore, costly microhabitat shifts can occur in chambers such as those used in this study, and probably play some role in observed sublethal costs of predator presence by *Baetis*; but the relative importance compared to that of drift/swim behavior needs to be investigated.

The most important result of this and only a few other related studies is that predators can dramatically reduce prey growth and fecundity resulting in significant losses of fitness beyond those mortality effects usually considered in studies of predator–prey interactions (Stamp and Bowers 1991). Crowl and Covich (1990) showed that snails alter their life histories resulting in delayed reproduction when sympatric with predatory crayfish. Heads (1986) and Dixon and Baker (1988) showed that damselfly larvae grew more slowly in the presence of predatory fish prolonging instar duration, which could potentially reduce fitness. Werner et al. (1983) measured a 27% growth reduction cost to small bluegill sunfish of dividing habitats with piscivorous bass. Van Buskirk (1988), Skelly and Werner (1990), and Wilbur and Fauth (1990) documented reduction in a number of larval performance parameters that could result in lower fitness of amphibians in the presence of predatory dragonflies. Juliano's (1989) study is unique in having actually measured a reduction in the reproductive output of tree hole mosquito larvae in the presence of other predatory mosquitoes. These studies suggest that such sublethal effects of predator avoidance are widespread among aquatic organisms.

If we accept the assumption that natural selection has shaped the foraging behavior of organisms to maximize fitness, foragers need to make decisions that maximize both survivorship (minimizing risk of predation) and fecundity, which is usually a function of resource acquisition (Gilliam and Fraser 1987). Thus, we suspect that the types of sublethal costs of predator avoidance documented by this and other recent studies are nearly universal consequences of organisms foraging under predation risk. Exceptions may occur if (1) behaviors that favor efficient foraging do not conflict with those maximizing survivorship, in which case no trade-offs are necessary (efficient foraging is not risky) or (2)

reproductive potential is not a direct function of feeding rate. In *Baetis bicaudatus,* efficient foraging behavior is risky, requiring costly trade-offs to be made when predators are present. Further, our study documents that reproductive potential of *Baetis* is directly related to feeding rate. Thus, the mayfly–stonefly predator–prey system is one in which we would expect to observe sublethal fitness consequences of predator avoidance.

Dill (1987) suggests that sublethal effects of predators are particularly relevant in aquatic systems because they are rich with organisms having indeterminate growth (e.g., fish and plants) and complex life cycles (e.g., insects and amphibians). Organisms with indeterminate growth can actually grow less and still allocate something to reproduction, whereas determinant growers must grow first, and only then can they reproduce. Many hemimetabolous insects, such as mayflies, do not have a fixed number of larval instars; and as a result, maturation occurs over a wide range of larval sizes. This observed variation in size at maturity and rates of development of *Baetis bicaudatus* larvae enables predators on mayfly larvae to exert particularly strong effects on adult reproductive success.

Finally, any interaction (predation, competition, or parasitism) among insect larvae that affects feeding rates, growth rates, or allocation of resources to egg development may significantly affect the reproductive success of adults (Prout and McChesney 1985, Peckarsky and Cowan 1991). Thus, investigation of the sublethal fitness consequences of behavioral responses of prey to predators is essential to our understanding of the total impact of predators on prey populations and communities.

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