

LINKING DRIFT AND BENTHIC DENSITY ALONG FISHLESS TO FISH
TRANSITIONS IN ROCKY MOUNTAIN STREAMS

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ABSTRACT

The influence of predators on drift and benthic density is important for understanding prey community structure in freshwater streams. Drift activity of stream invertebrates in fishless streams does not differ between day and night, but when visual drift-feeding trout are present, stream invertebrates drift nocturnally with peaks just after sunset. Drift and benthic collections from a fishless to fish transition zone in two Rocky Mountain streams were used to evaluate the hypothesis that 1) daytime and nighttime drift remain constant above the fish barrier and 2) benthic density is greater downstream of the fish barrier. Two drift samples (day and night) and six benthic samples were taken within a 100 m reach along the fishless to fish transition. Drift density showed no difference between day and night when sampling just above the fish barrier. Benthic densities were highly variable and no difference was found between the upstream and downstream reach or between sample sites. Average residence time was calculated using the number of *Baetis bicaudatus* drifting per day and the number of *Baetis bicaudatus* in a 50 reach downstream and upstream of the barrier. Average residence time in both the upstream and downstream reach of a fish barrier was approximately 6 to 12 days. The influence of an introduced predator downstream of a fish barrier may influence the decision of *Baetis* to drift. Future research should consider the distance traveled and size of invertebrates drifting in order to determine how transitioning into a fish stream affects the drift propensity of these organisms.

INTRODUCTION

Drift of aquatic invertebrates in Rocky Mountain streams has been of great interest to stream ecologists in forming models of stream community structure in an open, nonequilibrium system (Peckarsky 1996). Macroinvertebrate drift represents active dispersal into the water column and may be associated with foraging, searching for a new habitat, and/or escaping unfavorable conditions (McIntosh et al. 2002). Predation may also determine prey migration into and out of the water column. With increased risk of predation by visual feeders such as trout, adaptive prey behavior can affect life history strategies that can have important effects on their population dynamics. Diversity and abundance of predatory invertebrates in the stream may also influence drift and benthic densities. According to Wooster (1994), invertebrate predators such as stoneflies had a significantly higher influence on prey density than vertebrate predators such as fish.

Predator impacts on prey populations can influence entire community structure through indirect effects on lower trophic levels. For example, trout chemical cues have been added to fishless streams to measure the nonconsumptive impact on *Baetis* population growth and drift (Peckarsky 2002). These nonconsumptive effects on prey populations caused smaller size at emergence and may cause reductions in *Baetis* biomass that will influence community dynamics that outweigh the reduction in biomass from direct consumption.

By quantifying the density of *B. bicaudatus* found in stream drift and benthic substrate along fishless to fish transition zones, further information can be gathered as to the effect of predator introduction on prey population dynamics. Previous studies found mayfly drift in fishless streams to be aperiodic whereas drift was observed to be nocturnal in streams with trout (Mcintosh, 2002). Diel periodicity may be a response to minimize exposure to trout, which are visual feeders, during the light hours (Flecker 1992). In fact, Allan (1986) performed direct, in-stream observations by light amplification throughout the day and observed several species of *Baetis* to reside on stone tops by day and found them absent by night, which gives further support to an increase in nocturnal mayfly drift. Furthermore, larger *Baetis* nymphs were shown to drift periodically due to a strong selective pressure from trout (Allan 1984). In attempt to minimize their exposure to visual feeding trout, large mayfly nymphs show increased propensity to drift at night and decreased propensity to drift during the day (Allan 1978).

Although temporal and spatial variation of drift in response to predation has been well-studied, less is known about prey behavior and abundance along fishless to fish transition reaches. In this study, a comparison of benthic collections along the fish

barrier and in a downstream location with trout was used to study the flux of mayfly biomass in response to the threat of predation. By examining the biomass flux when transitioning over a natural barrier (e.g. waterfall) from a fishless stream to a stream with trout, I aim to quantify the abundance of *B. bicaudatus* along the transition zone and understand the average residence time of *Baetis* across a natural barrier. I hypothesize that *B. bicaudatus* will show a similar drift rate during the day and at night because drift is being sampled above the barrier in a fishless reach. I also hypothesize that benthic density will increase in the fish reach of the stream due to the influence of predatory fish on drift propensity.

METHODS

I conducted my research in two headwater streams, Avery Creek and Rock Creek, in western Colorado, USA near the Rocky Mountain Biological Laboratory from June 26, 2008 to July 18, 2008. The streams each possessed a cascade barrier in which a fishless reach transitions into a reach containing brook trout. Two drift samples were collected at 1000 and 2200 hours with mesh drift nets (mesh size = 368 μm) for 30 minutes at the top of the fish barrier. Six benthic samples were collected within 50 m upstream and 50 m downstream from the fish barrier at 12.5 m, 25 m, and 37.5 m. The samples were preserved in 95% ethanol and the number of *B. bicaudatus* nymphs was quantified from each sample in the lab. Wetted widths were also measured every 5 m within the upstream 50 m reach and downstream 50 m reach.

During each drift sampling period, stream discharge was taken below the barrier by dividing the stream width into 10-15 equal intervals and recording measurements of depth and current velocity (measured at 60% of depth using a flow meter). Discharge

measurements were also taken across the mouth of the drift net at the beginning of each sampling period. Benthic samples were taken using the “electrobugging” method of Talor *et al* (2001). Each sample was collected by electroshocking within a modified hess sampler (area = 0.072446 m², mesh size 368 µm) for 90 seconds. Invertebrates were preserved and enumerated as above, for the drift samples.

Drift density (*Baetis* drifting/ m³) was calculated using the following equation: $N / (\text{discharge at net (m}^3\text{/sec)} \times 1800 \text{ s/30 min})$ where N = number of *B. bicaudatus* per drift sample. With the assumption that drift and discharge remain constant throughout a 12 hour period, the following equation estimated how many *B. bicaudatus* were drifting during the day and at night: Drift density x whole stream discharge (m³/sec) x 43,200 sec/ 12 hr. *B. bicaudatus* drifting/ 12 hours during the day and at night were added to get the number of *B. bicaudatus* drifting/ 24 hrs.

Benthic density was calculated using the following equation: $N / \text{the area of the sampler (0.072446 m}^2\text{)} \times \text{area of the 50 m reach upstream or downstream of the fish barrier}$ where N = average number of *B. bicaudatus* found in one sample. Finally, average residence time was calculated: *B. bicaudatus* in the 50 m reach/ *B. bicaudatus* drifting/ 24 hrs.

Benthic densities were analyzed using a 2-way ANOVA to compare upstream and downstream benthic density for each site and to compare the two sites.

RESULTS

Daytime and nighttime drift densities were very similar for each site, which supported my first hypothesis (Fig. 1). Average drift density and average benthic density were both about three times greater in Avery Creek than in Rock Creek (Table 1 & Table

2). Although upstream and downstream benthic densities were greater in Avery, they were not statistically different from the benthic densities in Rock ($F_{2,9} = 4.7643$; $p = 0.0569$). Also benthic densities in the upstream vs. downstream reach varied and were not statistically different ($F_{2,9} = 0.0220$; $p = 0.8853$). Average residence time upstream and downstream in Avery Creek was about 6-7 days and about 8-12 days in Rock Creek (Table 2).

DISCUSSION

Although Avery and Rock varied in their drift densities, each stream showed equal nighttime and daytime drift densities, which supported aperiodicity of drift activity in fishless streams (Flecker 1992). Benthic density showed high variability in upstream and downstream samples. Although a larger sample size may be needed to observe differences in benthic densities from a fishless to fish transition, results showed no significant differences between the two locations or between upstream and downstream of the fish barrier. Therefore, my second hypothesis, that trout increase benthic density via effect on drift could not be supported.

Lack of replicate samples for my study resulted in low statistical power for comparison between upstream and downstream benthic densities. Also because several simplifying assumptions were made regarding the static nature of drift and discharge through daytime and nighttime periods, the results can only serve as a preliminary estimates as to the average residence time of *B. bicaudatus* in a 50 m reach. In combining results from Avery and Rock, average residence time was about six to twelve days (Table 2). This gives a rough idea as to how long *Baetis* may be residing in the

benthos before choosing to drift again. Small sample size prevented analysis between average residence times upstream vs. downstream of the fish barrier and between sites. Given a larger sample size, these results may give us information about upstream vs. downstream drift behavior and also may provide information about differences in prey behavior in each stream.

To improve this study, investigation of drift density below the barrier should be tested since trout are known to negatively influence drift of macroinvertebrate prey. Cooper *et al* (1990) has described numerous studies in which a strong predator effect from both vertebrate and invertebrates on prey density was shown to be correlated with the rate of prey emigration. Predators may be impacting the emigration of prey, and may have stronger impacts on prey communities with low rates of prey migration (Peckarsky 1996). Greater drift density in fast-flowing streams earlier in the summer and lower drift density in slow-flowing streams later in the summer may also affect average residence time in the stream and may change how predators impact prey migration and emigration.

The effect of predators on prey populations may influence as well as depend on how often prey are moving into and out of an area. Because the rate of drift is highly related to mayfly foraging (Kohler, 1985), individual fitness may be influenced by rate of drift (Peckarsky & McIntosh 1998). By drifting less in the presence of predators, individual mayflies may reduce their rates of resource acquisition and decline in individual fitness. Also Peckarsky *et al* (2001) observed different life history traits of the mayfly *Baetis bicaudatus* (Baetidae) in fishless streams when compared to those in streams with trout. *B. bicaudatus* in streams with trout reduce their exposure time to predation in the larval stage by maturing at a smaller size, which reduces their fecundity.

The influence that predators may have on prey drift is important to understanding the dynamics and interactions that will affect the overall community of the stream. Further investigation of drift and benthic densities across a fish barrier may be helpful to develop an improved understanding of how predators shape prey communities. Expanding this study to measure several other variables such as drift distance, size of drifting invertebrates, development at time of emergence, predator abundance, predator diversity, etc., which may all influence rate of drift, will provide a better evaluation as to whether or not mayflies may be altering their drift behavior across a fish barrier.

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Table 1. Drift density in Avery and Rock during the day and night.

Stream	Time	# <i>Baetis</i> /m ³	# <i>Baetis</i> /sec	# <i>Baetis</i> / 12hrs	# <i>Baetis</i> / 24 hrs
Avery	Day	1.86	0.11	4,671	8,000
Avery	Night	1.87	0.01	3,334	
Rock	Day	0.56	0.03	1,294	2,652
Rock	Night	0.66	0.03	1,358	

Table 2. Average benthic density upstream and downstream in Avery and Rock.

Stream	Upstream/ Downstream	# <i>Baetis</i> / m2	Estimated # <i>Baetis</i> in 50 m reach	Ave.residence time (days)
Avery	Up	313	47, 998	6
Avery	Down	428	52, 710	7
Rock	Up	175	32, 901	12
Rock	Down	93	20, 057	8

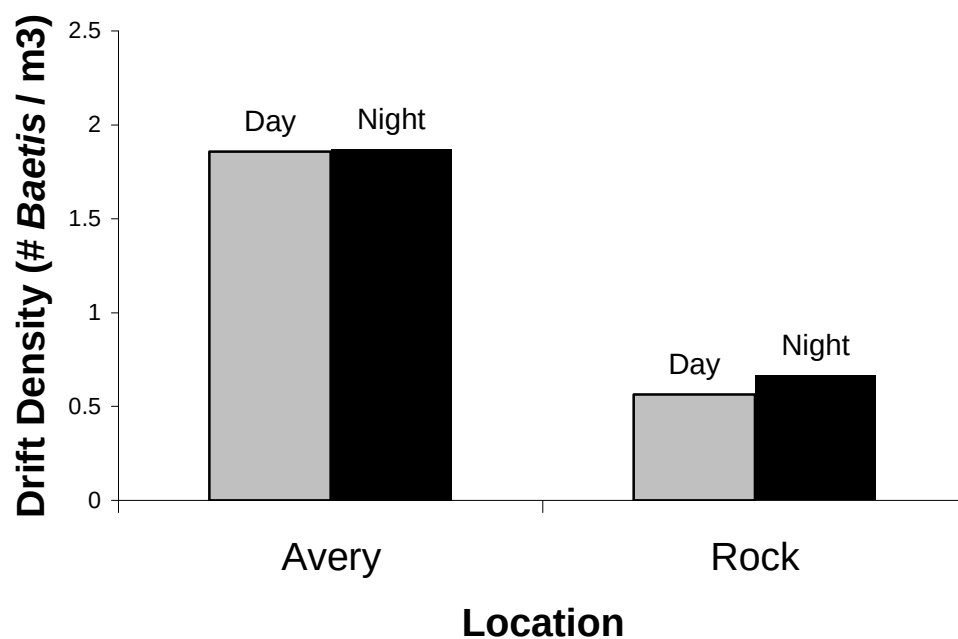


Fig. 1. Nighttime and daytime drift densities for Avery and Rock

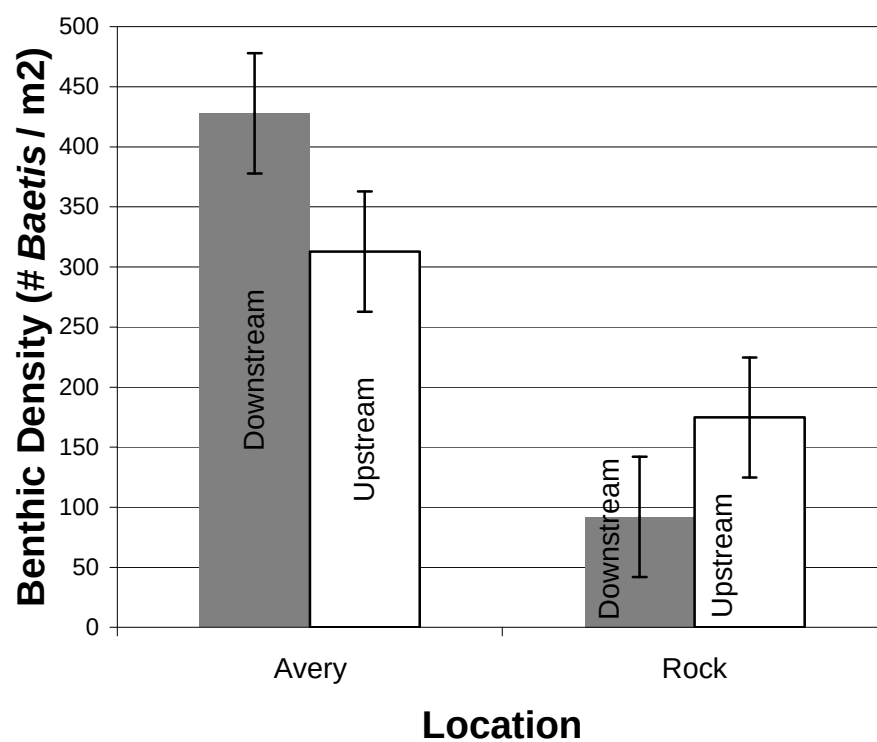


Fig. 2. Benthic density upstream and downstream in Avery and Rock