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Hydrologic and behavioral constraints on oviposition of stream insects: implications for adult dispersal

Received: 14 July 1999 / Accepted: 23 March 2000 / Published online: 6 July 2000
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Abstract The supply of recruits plays an important role in plant and animal population dynamics, and may be governed by environmental and behavioral constraints on animals. Mated females of the mayfly genus *Baetis* alight on rocks protruding from streams, crawl under water and deposit a single egg mass under a rock. We surveyed oviposition and emergence of a bivoltine population of *B. bicaudatus* in multiple stream reaches in one high-altitude watershed in western Colorado over 3 years to establish qualitative patterns at a regional scale (entire watershed), and quantitative patterns over six generations at a local scale (one stream reach). We also measured characteristics of preferred oviposition substrates, performed experiments to test hypotheses about cues used by females to select oviposition sites, and measured mortality of egg masses in the field. Our goals were to determine whether: (1) hydrologic variation necessitated dispersal of females to find suitable oviposition sites; (2) the local supply of females could provide the supply of local recruits; and (3) local recruitment determined the local production of adults. The onset of oviposition corresponded with the decline of spring run-off, which differed dramatically among years and among sites within years. However, eggs appeared before any adults had emerged in 8 of 22 site-years, and adults emerged 2–3 weeks before any eggs were oviposited in 3 site-years. Furthermore, the size distribution of egg masses differed from that predicted by the size distribution of females that emerged from seven of nine stream reaches. Protruding rocks and eggs appeared earlier each summer in smaller tributaries than in larger mainstream reaches, suggesting that hydrologic

and behavioral constraints on oviposition may force females to disperse away from their natal reach to oviposit, and possibly explain the predominantly upstream flight of *Baetis* females reported in other studies. Local oviposition rates in one third-order stream-reach increased rapidly as soon as substrates protruded from the water surface, and females preferred large rocks that became available early in the flight season. However, females oviposited on <10% of all available rocks, and <65% of preferred rocks as determined by an empirical model. These data indicated that the timing of appearance of suitable oviposition sites determined the phenology of local recruitment, but that preferred oviposition sites were not saturated. Thus, the magnitude of local recruitment was not limited by the absolute abundance of preferred oviposition sites. Only 22% of egg masses observed in the field suffered mortality during their embryonic development, and per capita *Baetis* egg mass mortality was significantly lower on rocks with higher densities of egg masses. Thus, we suspect that specialized oviposition behavior may reduce the probability of egg mortality, potentially compensating for the costs of dispersal necessary to locate suitable oviposition sites. Finally, the number of adults that emerged at one stream reach was independent of the number of egg masses oviposited over six generations of *Baetis*; and local recruitment was not a function of the number of adults of the previous generation that emerged locally. The patterns of oviposition and emergence of *Baetis* found in this study are consistent with the following hypotheses. Recruitment of eggs in a stream reach is not limited by the local supply of adults, but is a function of the regional supply of dispersing adults, which are constrained by the spatial and temporal distribution of preferred oviposition habitat. Furthermore, subsequent local production of adults is not a function of the supply of recruits, arguing for post-recruitment control of local populations by processes operating in the larval stage (e.g., predation, competition, dispersal, disturbance). Processes affecting larval and adult stages of *Baetis* act independently and at different scales, thereby decoupling local population dynamics of successive generations.

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Key words Colonization cycle · Hydrologic regime · Mayflies · Oviposition · Streams

Introduction

The supply of recruits can be an important determinant of the dynamics of plant and animal populations (Roughgarden et al. 1987; Underwood and Fairweather 1989; Holt 1993; Olafsson et al. 1994; Palmer et al. 1996; Chesson 1998). In some populations recruitment may be driven largely by biotic interactions, such as predation and competition (Wilbur 1977; Rausher 1979; Waser 1985; Pearman and Wilbur 1990; Holt and McPeck 1996). Alternatively, recruitment may be constrained by the disturbance regime or natural environmental fluctuations governing the accessibility of habitat suitable for new recruits (Butman 1987; Cushing and Gaines 1989; Miller and Stout 1989; Gaines and Bertness 1993; Kupferberg 1996; Bunn and Hughes 1997; Connolly and Roughgarden 1999). When populations at different locations are linked together by dispersal ("metapopulations" *sensu* Hanski and Simberloff 1997), factors affecting recruitment and dispersal generally reflect complex interactions between biotic and abiotic processes operating at local and regional scales (Menge and Sutherland 1987; Doherty and Fowler 1994; Palmer et al. 1996; Peckarsky et al. 1997; Chesson 1998).

Measuring recruitment is an especially intriguing problem for organisms with complex life cycles alternating between relatively sedentary and highly mobile dispersal stages. For example, the life cycles of marine and freshwater invertebrates, fish and amphibians often involve a habitat switch between the feeding and dispersal stages. The dispersing propagules in marine populations are generally larvae, whereas terrestrial adults of aquatic insects or amphibians may disperse to distribute their propagules widely (Underwood and Fairweather 1989; Palmer et al. 1996). For these organisms selection pressures acting on the dispersing phase may be relatively independent of processes operating on the more sedentary (usually feeding) stage. Thus, spatial and temporal variability in the habitat available for new recruits can influence large-scale patterns of dispersal and recruitment independently of species interactions occurring at a smaller scale (Gadgil 1971; Holt 1993; Holt and McPeck 1996; Palmer et al. 1996; Peckarsky et al. 1997; Chesson 1998). In some cases we know so little about the dispersal phases that it is unclear whether the offspring of adults produced in one location will grow up in nearby or distant locations (Gaines and Bertness 1993; Eckman 1996; Peckarsky et al. 1997).

Individuals of the next generation are recruited to most aquatic insect populations by oviposition of terrestrial adults into the larval (aquatic) habitat. Because most insects do not care for their offspring, females can increase their fitness by ovipositing in habitats that maximize larval growth and minimize egg and larval mortality (Dethier 1959; Rausher 1979; Werner 1986;

Higashiura 1989; Petranka and Fakhoury 1991). Thus, specialized oviposition behavior and site selection should be favored when larval or egg survival is higher at certain sites or times (Mangel 1987; Resetarits 1996; Blaustein 1999), and especially when the larvae are relatively sedentary or incapable of migrating away from unsuitable habitats (Bryant 1969).

Adult mayflies are relatively small, fragile insects that are notoriously short-lived, while the aquatic larvae are longer-lived and mobile relative to larvae of other insects (Brittain 1982). Mayflies generally oviposit by dipping their abdomens into ponds or streams releasing all or a few eggs at a time while in flight or while resting on objects above the water surface. However, all reported species of the genus *Baetis*, whose larvae are highly mobile (e.g., Hershey et al. 1993), have unusually selective oviposition behavior. Females alight on rocks protruding from the stream surface, and then crawl under water to the underside of the rock to lay their eggs (Morgan 1911; Murphy 1922; Elliott 1972; Bengtsson 1988). This behavior was first described eloquently by Eaton (1888, p. 11): "she creeps down into the water – enclosed within a film of air, with her wings collapsed so as to overlie the abdomen in the form of an acute narrowly linear bundle, and with her setae closed together – to lay her eggs upon the underside of stones, disposing them in rounded patches, in a single layer evenly spread, and in mutual contiguity. The female on the completion of her labour usually floats up to the surface of the water, ineffectively swimming with her legs, and, on emerging, her wings all at once are suddenly unfolded and erected; she then either flies away, or (as often happens) if her setae have chanced to become wet and cannot be extricated from the water, she is detained by them until she is drowned. In some instances, however, the female dies under water beside her eggs."

We have observed female *B. bicaudatus* ovipositing in this manner in streams in western Colorado near the Rocky Mountain Biological Laboratory (RMBL). Each female lays only one egg mass during her lifetime consisting of a few hundred to over 2000 eggs (Fig. 1). We suspected that this selective oviposition behavior reduced egg exposure to abiotic disturbances (scouring, sedimentation, and drying) and to large predators, thereby increasing the probability of survival and hatching success. However, these potential fitness benefits may be offset by costs associated with finding the optimal oviposition habitat. Temporal and spatial variation in the abiotic environment, affecting the timing of appearance of protruding rocks, may thereby constrain recruitment of *Baetis* populations. Females emerging before oviposition sites become available locally must either wait for sites to appear or disperse. Because adult mayflies do not feed and are short-lived, females may be forced to fly elsewhere to locate stream reaches where suitable oviposition sites are available. Thus, behavioral constraints on *Baetis* oviposition could decouple larval population dynamics of successive generations at the local scale, and have important implications for regional dispersal. We

used observational data obtained at multiple scales to determine whether: (1) hydrologic variation necessitated dispersal of females to find suitable oviposition sites; (2) the local supply of females could provide the supply of local recruits; and (3) local recruitment determined the number of adults that emerged.

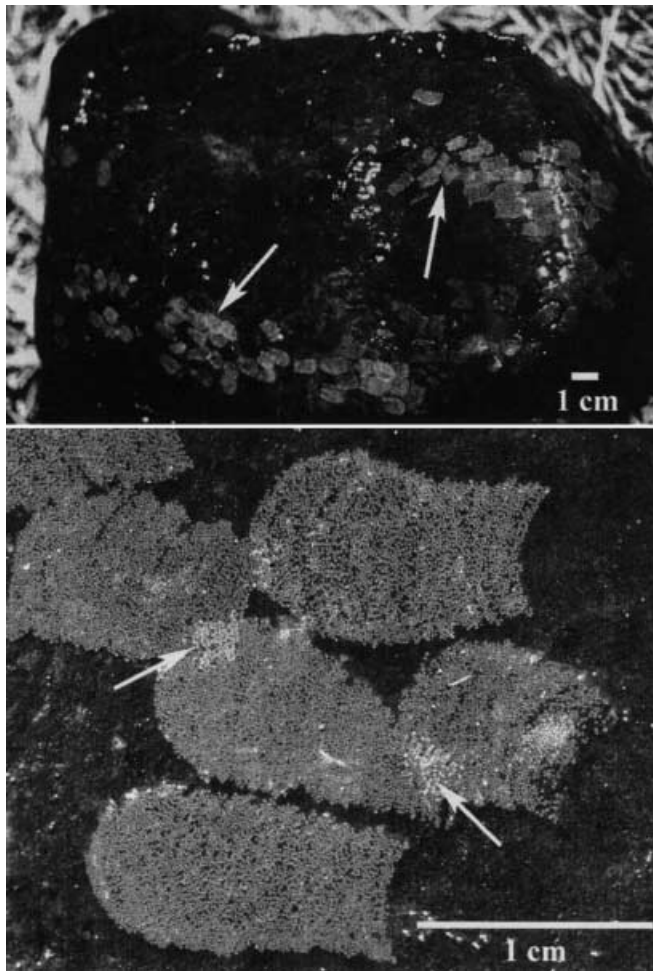


Fig. 1a,b *Baetis bicaudatus* egg masses on the underside of a rock from the East River study reach. **a** Entire rock with egg masses indicated by arrows (photograph by Brad Taylor). **b** Close-up with arrows indicating unfertilized (*bright*) and fertilized (*dull*) eggs (photograph by Angus McIntosh). Scale bar=1 cm.

Methods

We examined variation over space and time in qualitative patterns of emergence and oviposition among local *B. bicaudatus* populations in multiple stream reaches within one watershed over 3 years, and conducted quantitative studies at a single stream reach to evaluate factors that might constrain local oviposition (Table 1). Over the 3 years of this study the amount of winter snow fall, timing and intensity of snow melt, and amount of summer rainfall varied dramatically, which resulted in substantially different patterns of mean monthly discharges (Fig. 2), stream water levels, and availability of oviposition habitat.

Study sites

From 1994 to 1996 we studied multiple stream reaches (22 site-years) draining the East River catchment on the western slope of the Rocky Mountains, Gunnison County, Colorado (Fig. 3). Stream reaches ranged from 2,860 to 3,050 m in elevation (Table 2), and consisted of pools and riffles with heterogeneous cobble substrata. Since streams varied in size (Peckarsky et al. 2000), we adjusted the length of each reach (10–30 m) to standardize the surface area studied. Reaches varied by mean discharge, timing of availability of protruding rocks for oviposition, onset of *Baetis* oviposition, onset of emergence of females, presence or absence of fish (brook trout, *Salvelinus fontinalis* Mitchell) (Table 2), and the size and fecundity of emerging *Baetis* females (Peckarsky et al. 2000). We also focused on one local population of *B. bicaudatus* in a third-order 60-m reach of the East River, a trout stream at 2,890 m elevation flowing through the Rocky Mountain Biological Laboratory.

Study organism

Larvae of the mayfly *B. bicaudatus* Dodds (Ephemeroptera: Baetidae) are abundant algal-grazers in Rocky Mountain streams. Populations in most site-years were bivoltine with one generation that overwintered in the stream as small-instar larvae (winter generation), and emerged throughout June and July. These adults oviposited eggs that developed into a short summer generation that grew rapidly during July and August, emerged and then oviposited eggs of the next winter generation (Peckarsky and Cowan 1995). However, in one particularly high-snow, high-discharge year (1995), emergence of the winter generation was delayed and this species was unable to produce a summer generation at some sites (Table 2, Peckarsky et al. 2000).

As is characteristic of mayflies, *Baetis* has two winged terrestrial stages; mature larvae molt into pre-reproductive subimagos, which make the transition from the aquatic to the terrestrial habitat, and then molt into reproductive imagos 48 hours later (Vance 1996). Male imagos may live for 1–3 days (C.C. Caudill, unpublished work), but females probably live only 1 day (Vance 1996).

Table 1 Summary of methods used to determine patterns of *Baetis bicaudatus* oviposition and emergence, and mechanisms explaining oviposition patterns

	Watershed scale	Reach scale
Patterns	Phenology of emergence, oviposition sites and oviposition at 22 site-years in the East River watershed (Table 2, Fig. 3) Comparison of size of females emerging and ovipositing at 9 sites in the East River watershed (Fig. 4)	Weekly quantitative estimates of emergence, oviposition sites and oviposition in one 60 m reach of the East River for 6 generations (Table 3, Figs. 5,6,7,8)
Mechanisms		Factors affecting selection of oviposition habitat (Tables 4, 5) Factors affecting egg mass mortality in the field

Fig. 2 Mean monthly discharge and long-term (30 years) average discharge (± 1 SE) measured at a United States Geological Survey gauging station on the East River at Almont, Colorado, 40 km downstream of the study site. Horizontal filled bars indicate *B. bicaudatus* oviposition periods in the East River during the summers of 1994, 1995, and 1996

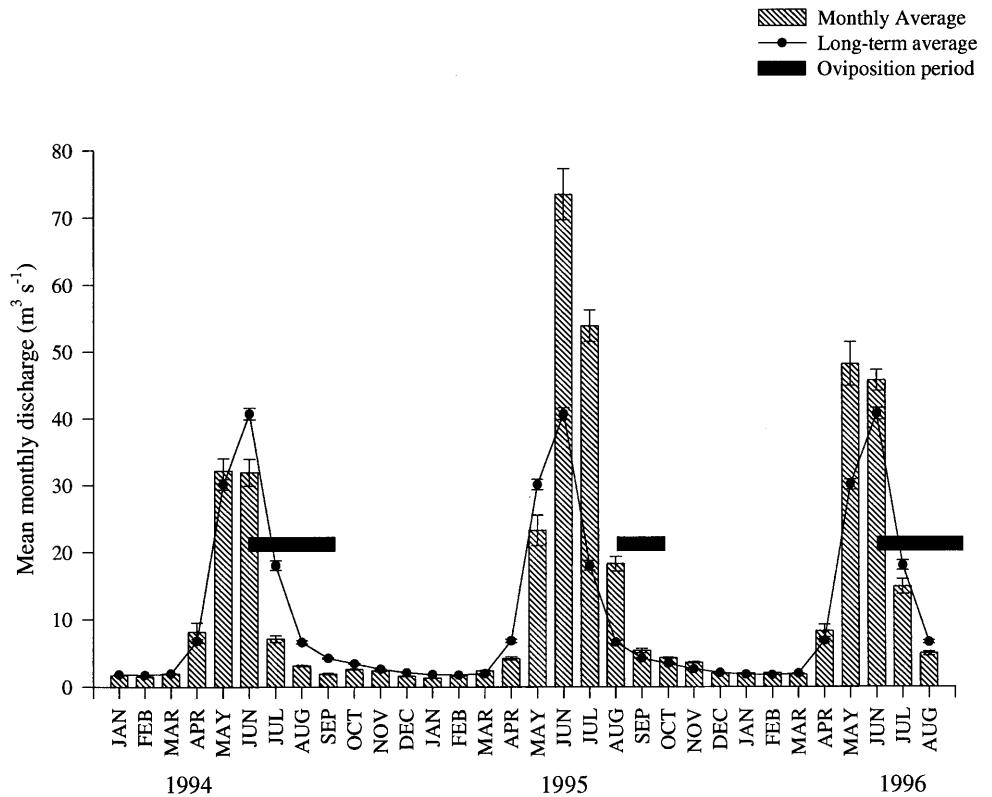
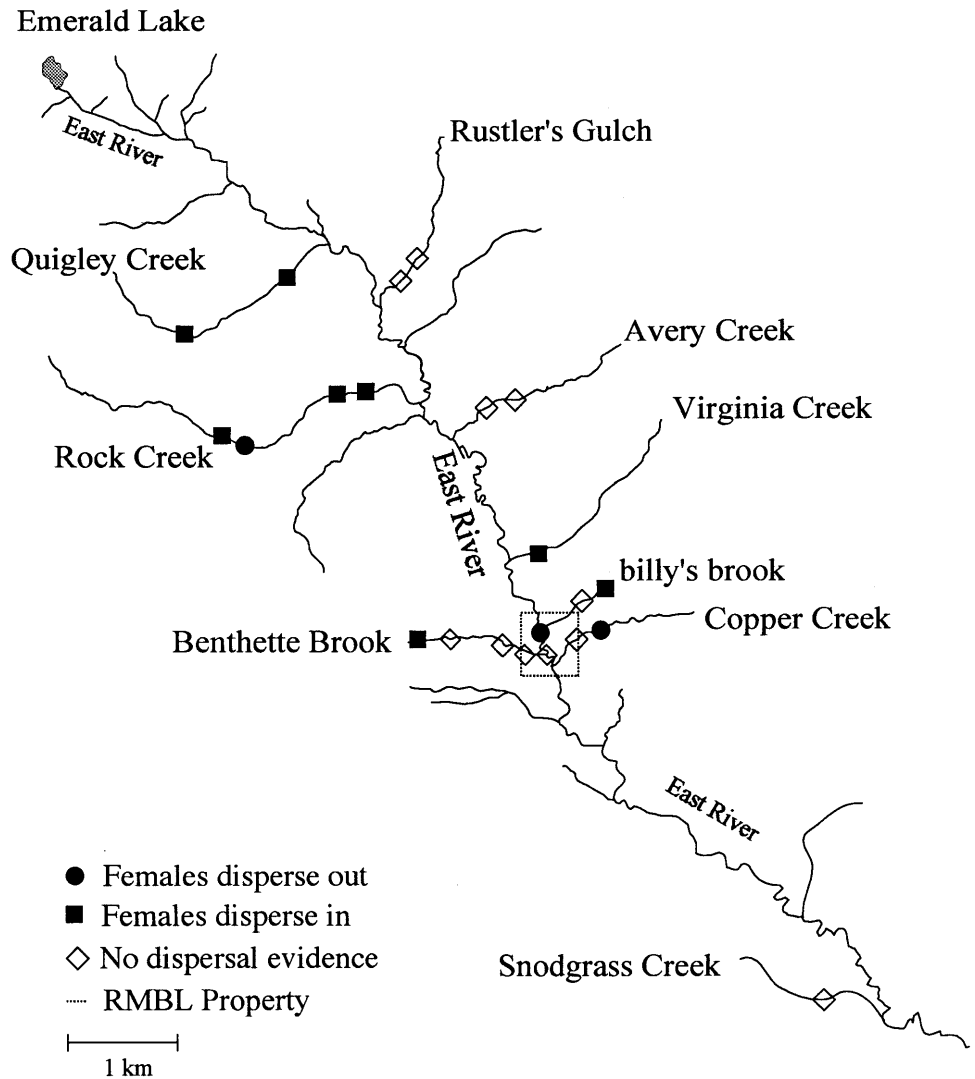


Table 2 Phenology of sites in the East River watershed studied in 1995 and 1996. Week 1 marks the first appearance of mature winter generation *Baetis* larvae (emergence) in the entire watershed each year. Week 1 (1995) starts 19 July; week 1 (1996) starts 25

June. Sites are ranked by size (discharge at the end of the summer; range 0.003–1.48 $\text{m}^3 \text{s}^{-1}$) (supercripts: *E* sites where eggs appeared before females emerged, *F* sites where females emerged at least 2 weeks before eggs appeared, *I* sites with no summer generation)

Stream (year)	Rank Discharge (low to high)	Elevation (m)	Rocks protruded (week)	Females emerged (week)	Eggs present (week)	Fish
1995						
Virginia Creek ^{1, E}	1	2930	1	3	2	No
Billy's Brook	2	2920	1	1	1	No
Upper Benthette Brook ^{1, E}	3	2930	1	5	4	No
Lower Benthette Brook	4	2910	1	1	1	No
Avery Creek	5	2940	3	2	3	Yes
Upper Rock Creek ^E	6	2990	4	6	5	No
Lower Rock Creek ^E	7	2930	4	5	4	Yes
Upper Quigley Creek ^{1, E}	8	3050	4	6	5	Yes
Lower Quigley Creek ^{1, E}	9	2990	5	7	5	Yes
Rustler's Gulch Creek ¹	10	2950	3	3	4	Yes
Copper Creek ¹	11	2860	4	3	4	Yes
East River ^F	12	2890	5	3	5	Yes
1996						
Billy's Brook ^E	1	2920	1	6	2	No
Snodgrass Creek	2	2940	1	2	3	No
Upper Benthette Brook	3	2930	4	5	5	No
Lower Benthette Brook	4	2910	1	2	2	No
Avery Creek	5	2940	1	4	4	Yes
Upper Rock Creek ^F	6	2990	3	4	7	No
Lower Rock Creek ^E	7	2930	3	5	4	Yes
Rustler's Gulch Creek	8	2950	3	4	5	Yes
Copper Creek ^F	9	2860	6	5	8	Yes
East River	10	2890	4	4	4	Yes

Fig. 3 Map of the East River drainage basin indicating locations of sites sampled in summers 1994, 1995, and 1996. *Filled circles* indicate sites where females emerged at least 2 weeks before eggs appeared and needed to disperse to other sites to find oviposition substrates (F in Table 2). *Filled squares* indicate sites where eggs appeared before females matured, therefore originating from females that dispersed there from other stream reaches (E in Table 2). *Open diamonds* indicate sites where the onset of emergence and oviposition were concurrent, or offset by only 1 week. Eggs at these sites could have originated from females that emerged from that site. North is at the top of the map (RMBL Rocky Mountain Biological Laboratory)



Males form mating aggregations (swarms) in clearings near small tributaries (winter generation) or near the mainstream (summer generation). Swarm size is variable ranging from ~20 to hundreds of individuals (Vance 1996). Females flying near swarms are pursued by males; males and females drop to vegetation near the ground in tandem and copulation terminates in <1 min (authors' personal observations). Then females fly off separately, generally in an upstream direction, to oviposit (Flecker and Allan 1988; Vance 1996).

During July 1992, we conducted a preliminary study to determine whether *B. bicaudatus* oviposited on protruding rocks as had been reported for other *Baetis* species. We sampled 40 randomly selected protruding rocks (30% of the total number of rocks available for oviposition), and 40 adjacent submerged rocks, in the 60 m reach of the East River near the RMBL. This survey confirmed that *B. bicaudatus* oviposited exclusively on protruding rocks in this stream. None of the submerged rocks had *Baetis* egg masses, whereas 25% of the protruding rocks did.

Patterns of oviposition and emergence

Watershed scale

We conducted a phenological survey of 12 (1995) and 10 (1996) stream reaches in the East River watershed (Table 2, Fig. 3), recording the first appearance of *Baetis* oviposition habitat (protrud-

ing rocks), first *Baetis* eggs, and first emergence of *Baetis* females (inferred from the presence of larvae with black wing pads, which are within 24 h of emergence). Each week we examined the undersides of all protruding rocks in each reach until the first egg masses appeared. We determined the first appearance of mature *Baetis* larvae from intensive benthic collections used to measure sizes of females emerging from each stream (Peckarsky et al. 2000). Male and female *Baetis* larvae are distinguishable in the late instars by development of the precursor of the male eye (Peckarsky et al. 1993; Vance 1996). We used these data to establish the temporal patterns of emergence and oviposition at each reach.

During summer 1995 we collected and dry-weighted (Cahn microbalance) the first 30 egg masses that we found at 12 different sites (Table 2) to obtain a frequency distribution of egg mass sizes for each site. Using data from weekly benthic collections (Peckarsky et al. 2000), we also measured the dry weights of females that had emerged from each reach during the period before egg masses were obtained. Sample sizes ranged from 2 to 60 females depending on how many females matured before all the egg samples were collected. We omitted three sites where <14 females had emerged before egg masses were collected, or where <18 egg masses were collected, and ran the following analysis on the remaining nine sites.

Females allocate about one-third of their body weight to eggs and egg size does not vary (Peckarsky et al. 1993). Therefore, dry weight (DW) of egg masses is equivalent to fecundity, and increases with female body size according to the function: DW egg

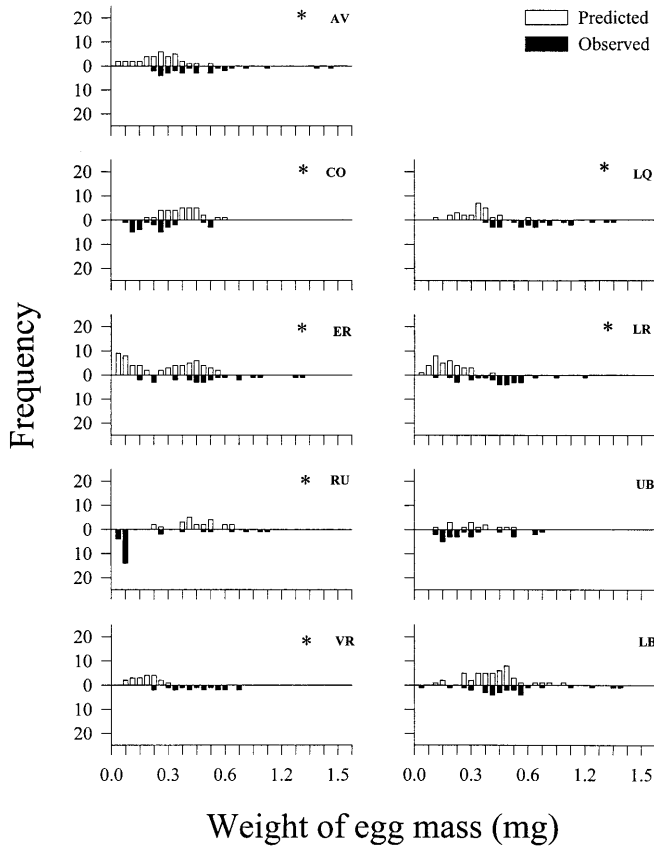


Fig. 4 Observed frequency distributions (filled bars) of *Baetis bicaudatus* egg mass sizes (fecundity) at 9 sites in the East River watershed during summer 1995, compared to expected fecundities (open bars) if eggs were oviposited by females that emerged from that reach. Predicted fecundities were obtained using female weight-egg mass weight regressions from data in Peckarsky et al. (1993) (Site codes: AV Avery Creek, CO Copper Creek, ER East River, RU Rustler's Gulch Creek, LB Lower Benthette Brook, LQ Lower Quigley Creek, LR Lower Rock Creek, UB Upper Benthette Brook, VR Virginia Creek, see Fig. 3, Table 2). Asterisk indicates significant differences between observed and expected size frequency distributions of egg masses for all 20 Kolmogorov-Smirnov 2-sample tests performed on data from that site ($P < 0.05$)

mass = $0.369 \times \text{DW female with eggs} - 0.180$ ($r^2 = 0.863$). We used this relationship between female body weight and egg-mass weight for *Baetis* to predict the size-frequency distribution of egg masses that would have been oviposited by the *Baetis* females that emerged from each site (Fig. 4). We used Kolmogorov-Smirnov two-sample (K-S) tests to determine the probability that the egg masses observed at each reach were oviposited by females that emerged from that reach. For each female we predicted egg mass weight from the regression equation. Then a residual value of the regression was drawn at random from the observed distribution of residuals, which were normally distributed with a mean of 0. We calculated the expected fecundity of each female as the predicted fecundity + the residual value. For each stream we generated 20 different expected size-frequency distributions using this procedure and compared them to the observed size-frequency distributions of egg masses. We rejected null hypotheses if 95% of these 20 K-S tests were significant ($P < 0.05$).

Stream reach scale

From 1994 to 1996 we obtained quantitative data on patterns of oviposition and emergence over the entire flight period of both generations of *Baetis* at one 60-m section of the East River at RMBL. The study site was a third-order reach with no major tributaries for ~5 km upstream (Fig. 3 – Rustler's Gulch). At weekly intervals we numbered all protruding rocks with a non-toxic waterproof Speedball pen as soon as they appeared at the water surface within the study reach, becoming part of the available population of oviposition substrates. We inspected the undersides of 33% (1994) or 20% (1995, 1996) of the new rocks that protruded each week, selecting rocks from the population by numbering and randomly choosing rocks. Once a rock was included in the sample, it was checked each week along with random samples of the new rocks that appeared, until the end of the adult flight period when no new egg masses were observed. If a rock had egg masses we recorded the location of each mass with a unique symbol indicating the date it first appeared. Larger rocks that could not be lifted were rolled over for inspection, but we did not check the undersides of rocks deeply embedded in the stream bottom. This procedure did not dislodge eggs, but sometimes disrupted females that were caught in the act of ovipositing. After rocks were checked, we replaced them in the same locations, oriented in the same direction. This method enabled us to census the new egg masses each week, and then to estimate the total number of new egg masses that accumulated in the study reach each summer.

To quantify emergence of *Baetis* females from the study reach we collected last-instar larval exuvia (distinguishable by wing pad development) at weekly intervals over the daily emergence period (1000–2000 hours MDT) when water temperatures exceeded 10°C . Collections were made for 5 min, four times daily (1000, 1300, 1600, 1900 hours MDT) by blocking an entire stream transect at the downstream end of the study reach with a 0.8-mm-mesh net. We estimated total daily catch rates by integrating under curves plotting numbers of exuvia collected four times daily. Then we corrected daily estimates by a factor that calibrated catch rates by empirically-derived differences in efficiency under different stream discharge regimes. Finally, we obtained estimates of total numbers of *Baetis* emerging from the study reach over the flight season by integrating under curves of corrected daily catches over the emergence period.

We calibrated catch rates empirically by releasing 100 marked *Baetis* exuvia (stained with Rose Bengal) or exuvia surrogates (pieces of flagging) at 10 m intervals (from 10–60 m upstream of the block net) to simulate emergence, and counting the numbers recaptured in 5 min by the block net. We obtained linear approximations of decay curves for log-transformed number recaptured (Y) over distance of release (X) at low ($0.37 \text{ m}^3 \text{ s}^{-1}$), medium ($0.91 \text{ m}^3 \text{ s}^{-1}$), and high ($1.95 \text{ m}^3 \text{ s}^{-1}$) stream discharge. Each decay curve was extended to the Y -intercept to estimate the number of exuvia originally released, but missed by the block net (A = the area between 0 and 60 m on the X -axis and between the decay curve and 100 on the Y -axis). Decay curves were also extended to the X -intercept to estimate the number of exuvia caught by the block net that would have come from upstream of 60 m (B = area under the tail of the decay curve >60 m on the X -axis). If C = the number of exuvia caught by the block net, the estimated number that emerged from the 60 m reach $E = C + (A - B)$. The correction factor (efficiency) for catches at each discharge level: efficiency = E/C , which was >1 for low discharges when catches underestimated simulated emergence, <1 at high discharges when catches overestimated simulated emergence, and ~ 1 at medium discharges. We calibrated weekly capture rates of exuvia by a correction factor that corresponded to the discharge on the day the data were obtained using the empirically-derived relationship between discharge (D) and efficiency of capture: $E/C = 1.853 \times 10^{-0.161D}$, $r^2 = 0.70$. We could not distinguish male from female exuvia, but assumed a 1:1 sex ratio (B.L. Peckarsky, unpublished work) to estimate numbers of females emerging from the study reach.

We used these estimates of oviposition and emergence to obtain patterns of seasonal phenology of both winter and summer generations of *Baetis* over the 3 years of the study. We also used a

reach-scale budget approach to compare estimates of oviposition and emergence of six generations of *Baetis* from the study reach to determine the relationship between local emergence of adults and local recruitment of egg masses.

Mechanisms explaining patterns

Oviposition cues

In 1996 we measured the physical characteristics of each rock sampled for egg masses in the study reach, including size (circumference), orientation (tall or flat), and geology (mostly granite or slate, with some marble, sandstone and conglomerate). We also noted the position of the rock in the riffle with respect to distance from the stream bank (center or edge), and whether the rock was embedded in fine sediment (no interstitial space on the underside). We dislodged and checked embedded rocks, thereby creating new interstitial spaces available for *Baetis* oviposition. In subsequent weeks, we continued to check these dislodged rocks for new egg masses. We derived a statistical model to determine the factors contributing to oviposition site-selection by *Baetis*, first using multiple logistic regression to determine the influence of rock characteristics on whether mayflies did (score=1) or did not (score=0) lay eggs (Hosmer and Lemeshow 1989; Trexler and Travis 1993). Then we excluded rocks that were not used (zeros) so that we could normalize the data, and applied a least-squares linear multiple regression on natural log-transformed egg densities (numbers cm^{-2} rock-bottom surface area) to partition the variance in density of egg masses among six rock attributes (size, time of appearance, location relative to shore, orientation (tall or flat), embedded (yes or no), and geology). We also obtained a correlation matrix among these six rock attributes and log-transformed egg density to check for multicollinearity among variables.

In 1996 we conducted an experiment to determine whether *B. bicaudatus* selected oviposition sites visually while in flight or used additional cues after landing on a protruding rock before ovipositing. On 17 August we numbered with a Speedball paint pen and covered the exposed surfaces of three different types of randomly-selected protruding rocks with Tanglefoot tree coating glue. The three treatments were: (1) 30 protruding rocks located in the center of the stream that were not embedded, (2) 30 protruding rocks in the center of the stream that were embedded, and (3) 30 dry rocks on shore to control for the possibility that females were attracted to the glue. On 20 August, we checked all 90 rocks for captured females. We analyzed these data using ANOVA to determine whether females landed preferentially on embedded or unembedded rocks, and whether rocks of each treatment were similar in size, water depth, geology, and current velocity.

Field estimates of egg mortality

By following the fate of egg masses in the field we estimated egg mass mortality rates as a baseline for future experimental studies to test the hypothesis that placing *Baetis* eggs under substrates reduces their risk of predation. Predation on insect eggs in streams has not been previously quantified, but interstitial invertebrate predators such as stoneflies (Perlodidae) and caddisflies (Rhyacophilidae) are common in these streams, and grazing invertebrates (mayflies and caddisflies) coexist in the same microhabitats as *Baetis* eggs. Egg masses that hatched left clearly distinguishable empty chorions, whereas eggs and chorions of others were missing. Generally, entire egg masses disappeared, but we occasionally observed partial egg mass damage. We suspect that our estimates of egg mass mortality might be too high given the potential for damage caused by repeatedly moving rocks for inspection.

First we estimated egg hatching success in the absence of predation. During July 1992 we collected 20 *Baetis* egg masses and incubated them in small plastic petri dishes with 45- μm -mesh windows in outdoor artificial streams with natural stream water (Peckarsky and Cowan 1991). We checked petri dishes every 2 days for hatchlings (as in Elliott 1972). Eggs required from

10–14 days to complete embryonic development after which hatchlings were removed, counted, and returned to the stream. We also followed 109 *Baetis* egg masses on 15 rocks during a low-flow period in the East River (21 July to 13 August 1992) to estimate the mortality of egg masses in the field. We used logistic regression to predict the probability of mortality of *Baetis* egg masses (dependent variable) from the density of egg masses per rock (independent variable) to test the hypothesis that aggregations of egg masses were less vulnerable to mortality in the field (SAS Institute 1990).

Results

Patterns of oviposition and emergence

Watershed scale

There was considerable temporal and spatial variability in dates of first appearance of *Baetis* oviposition sites (protruding rocks), the onset of *Baetis* oviposition, and the onset of emergence of females among stream sites in the East River watershed during summers 1995 and 1996 (Table 2). At three sites, including the East River study reach in 1995, the onset of oviposition lagged 2–3 weeks behind the onset of emergence of females from the stream. Females that emerged during those times were either forced to disperse to other sites to oviposit, or may have died waiting for oviposition habitat to appear in their natal reach (filled circles in Fig. 3). In contrast, eggs appeared at eight stream sites before female larvae had matured. Therefore, these eggs were oviposited by females that had emerged elsewhere and dispersed to these sites to oviposit (filled squares in Fig. 3). At 11 sites, eggs were first observed during the same week or 1 week after the appearance of mature female larvae. Therefore, all females emerging from those sites could have oviposited in their natal stream reach (open diamonds in Fig. 3). These observations suggest that water levels at the time of emergence may determine whether dispersal of *B. bicaudatus* females is required for successful oviposition.

In seven of nine streams sampled during 1995 where sample sizes of emerging females and egg masses were large enough, the observed and expected size-frequency distributions of *Baetis* egg masses were significantly different (K-S tests, Fig. 4). These data provide indirect evidence that some of the egg masses in those reaches were derived from females that emerged from other stream reaches and dispersed before ovipositing. At the other two streams, observed egg masses could have been derived entirely from the population of females that emerged from that site.

We ranked sites by discharge (from small to large) to examine whether there was a relationship between stream size and the timing of availability of oviposition sites (Table 2). In both 1995 and 1996, protruding rocks appeared significantly earlier in small streams than large streams (1995: $r_s=0.8297$, $P=0.0008$, $n=12$; 1996: $r_s=0.6923$, $P=0.0265$, $n=10$). Variation in this relationship was probably due to variability in the local channel

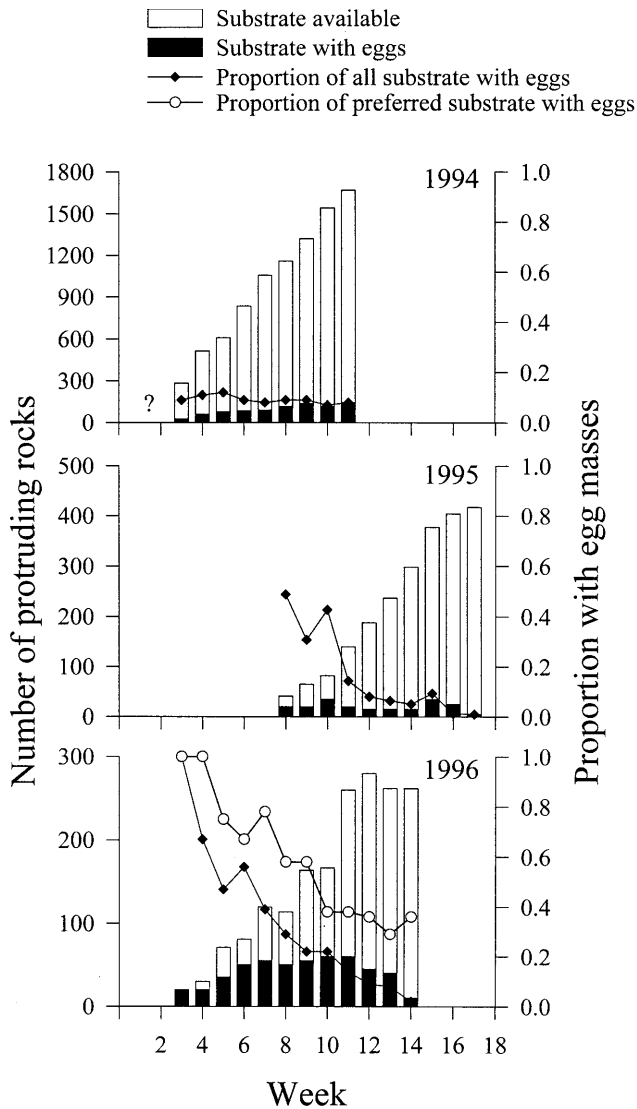


Fig. 5 Cumulative number of available oviposition sites (protruding rocks), cumulative number of rocks with *B. bicaudatus* egg masses, and proportion of available oviposition substrates with egg masses in the East River study reach during summers 1994, 1995, and 1996. Proportion of preferred substrates (large, unembedded, granite rocks oriented in the “tall” dimension) with egg masses are also shown for 1996. Week 1 began on 25 June. *Question-mark* indicates that we missed the onset of *Baetis* oviposition in 1994. Early dates with no data in 1995 and 1996 indicate that no rocks were protruding

geomorphology and composition of substrata among reaches, independent of stream size. Similarly, there was a correlation between stream size and the onset of oviposition (1995: $r_s=0.6828$, $P=0.0144$, $n=12$; 1996: $r_s=0.5865$, $P=0.0747$, $n=10$), with smaller streams being colonized earlier than larger streams; however, this correlation was not significant in 1996. Because small streams are tributaries of larger streams, these data suggest that in early summer when water levels are high, upstream flight by female *Baetis* would increase their probability of finding oviposition sites. Note, however, that

small streams occur throughout the watershed (Fig. 3), so that females may not have to fly very far upstream to locate oviposition sites. Interestingly, there was no relationship between stream size and the timing of first emergence (Table 2), suggesting that the onset of emergence was not related to hydrologic conditions signaling the local availability of oviposition sites.

Reach scale

At the study reach on the East River the date of first appearance of oviposition sites varied by more than 5 weeks over summers 1994, 1995, and 1996 (Fig. 5) due to dramatic interannual differences in the mean monthly discharge (Fig. 2). In fact, protruding rocks appeared in the East River before the investigators arrived in 1994 (6 July), which was the driest year. Thus, we missed the onset of *Baetis* oviposition in that summer. 1995 was the highest snow year on record in Gunnison County, resulting in record high stream discharge and a delay in the availability of oviposition sites for *Baetis* until 14 August. In 1996 oviposition sites first appeared on 9 July. Also, the number of available oviposition substrates changed dramatically between 1994 and 1995 as a result of 1995 floods, which reconfigured the stream bed of the East River (Fig. 5, note different scales on Y-axes among years). The extended high water in 1995 reduced the cumulative number of rocks available in 1995 and 1996 by about 4 times compared to numbers of sites available in 1994. In 1995 and 1996 egg masses appeared as soon as rocks were available, and the proportion of available substrates that had egg masses started out very high (100% in 1996) and declined through time (Fig. 5). Similarly, the proportion of preferred substrates (large, unembedded, granite rocks oriented in the “tall” dimension, which were significant factors in empirical models) that had egg masses followed the same trend, suggesting that available oviposition substrates were not saturated except at the beginning of the season. Thus, the timing of their appearance determined the phenology of local recruitment, but the large proportion of preferred substrates that were not used by females suggested that the number of new recruits was not limited by absolute availability of habitat.

This interpretation is also supported by the distribution of egg masses among available substrates. The proportion of rocks used by females increased with rock size (Fig. 6, K-S test, $P=0.0005$); and over the entire recruitment period of all three years, most available rocks were not used by females (Figs. 6, 7). Remarkably, only a few rocks received most of the egg masses each year (Fig. 7). In 1994 females oviposited on only 10 of >600 rocks sampled. Of those 10 rocks, 50% of the egg masses were oviposited on two large rocks (30% on one and 20% on the other). We sampled about 100 rocks in each of 1995 and 1996. Only 14 rocks had egg masses in 1995 whereas females oviposited on 41 of the substrates sampled in 1996 (possibly because we dislodged the embed-

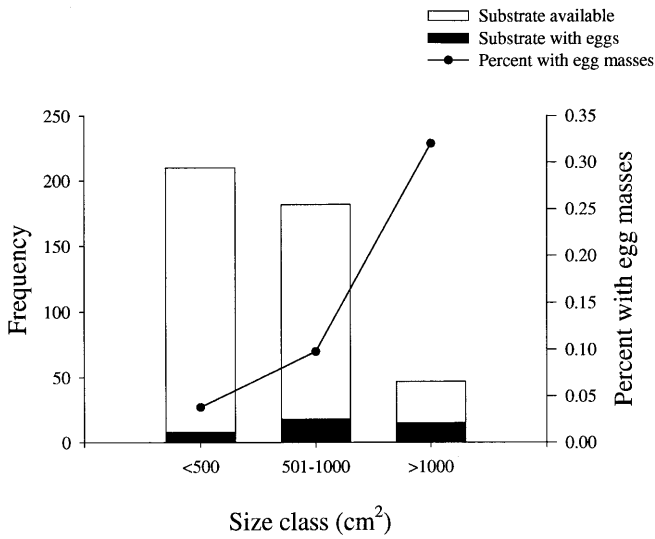


Fig. 6 Size frequency distributions of available oviposition substrates and substrates that received *Baetis* egg masses during summer 1996 in the East River study reach. Size frequency distributions differed between available and occupied substrates (Kolmogorov-Smirnov 2-sample test, $P=0.0005$). Percent of available oviposition sites that were occupied increased with rock size

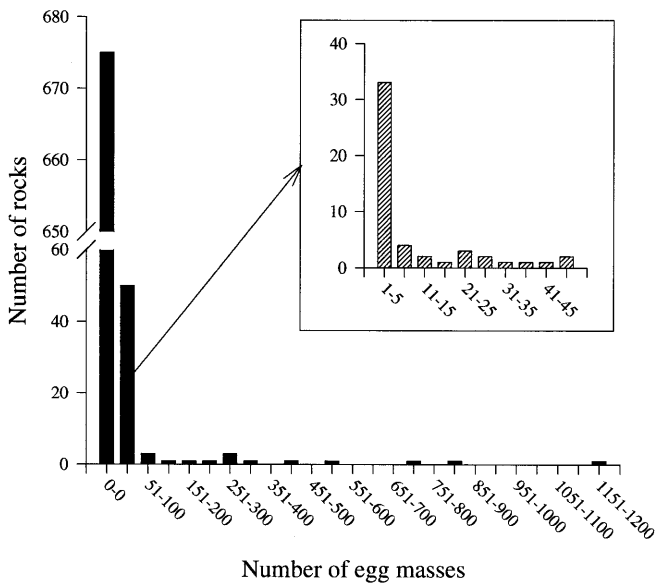


Fig. 7 Frequency distribution of *B. bicaudatus* egg masses per rock during 1994–1996 in the East River study reach. Inset illustrates frequency distribution of egg masses on rocks with 1–50 egg masses. Note that most rocks were not used by females, and that a few rocks received most of the egg masses

ded rocks providing more oviposition habitat). However, in both years one large rock had over half of the total egg masses observed (70% in 1995 and 53% in 1996).

Our data also suggest that females tended to lay eggs on rocks that already had other egg masses. Spearman rank correlation coefficients between number of egg masses at time t and new egg masses at subsequent times ($t+N$) were significant in all three years (1994: $r_s=0.640$,

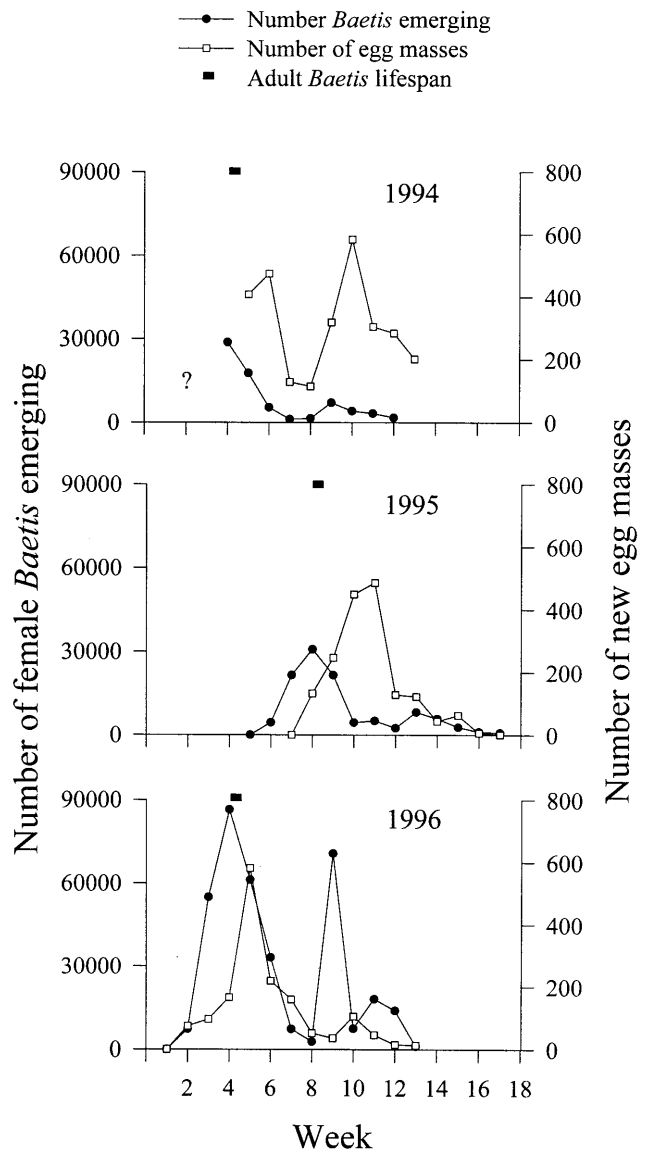


Fig. 8 Number of *B. bicaudatus* females emerging and number of new egg masses oviposited each week during 1994, 1995, and 1996 in the East River study reach. Week 1 starts on 25 June. Question-mark indicates that we missed the onset of *Baetis* emergence and oviposition in 1994. Horizontal bar over peak emergence each year indicates maximum adult *Baetis* life span for scale. Estimates of total numbers of emerging females and egg masses oviposited, for each generation and year are given in Table 3

$P=0.046$, $n=10$; 1995: $r_s=0.570$, $P=0.033$, $n=14$; 1996: $r_s=0.873$, $P=0.0001$, $n=41$). This pattern of oviposition could result from most females being attracted to a few preferred rocks, or from females responding to the presence of other egg masses.

During all three summers there were two peaks of emergence and oviposition corresponding with the overwintering and summer generations of *Baetis* (Fig. 8). The temporal dynamics of emergence of females were similar to the dynamics of oviposition in the study reach, but oviposition generally lagged behind emergence. In

Table 3 Budget for local recruitment and adult emergence of six generations of *Baetis* studied over 3 years in one third-order trout stream (Fig. 8). Total numbers of *Baetis* (and females) emerging were estimated from collections of exuvia (assuming a 1:1 sex ratio). Egg masses oviposited were estimated from cumulative censuses of protruding rocks sampled weekly. Winter females gave rise to summer egg masses, and summer females gave rise to winter egg masses. Percent return is the maximum hypothetical percent of females that could have returned to their natal reach to ovi-

posit, assuming each female lays one egg mass. Minimally, 92.2–99.5% of females that emerged from the reach either died or dispersed. Summer egg masses became summer adults, and winter eggs hatched and overwintered as larvae, producing the next year's winter adults. Note that total number of egg masses oviposited was similar each year (~8,000), while numbers of *Baetis* emerging fluctuated widely, and that generations that started with high numbers of egg masses did not consistently produce high numbers of adults

	Winter emergence (females)	Summer egg masses (% return)	Summer emergence (females)	Winter egg masses (% return)
1994	247,000 (123,500)	3,381 (2.7)	130,500 (65,250)	5,082 (7.8)
1995	293,750 (146,875)	6,310 (4.3)	167,375 (83,688)	1,335 (1.6)
1996	1,514,500 (757,250)	6,575 (0.9)	794,000 (397,000)	1,830 (0.5)

1996 there was about a 1-week lag between peak oviposition and peak emergence; whereas peak oviposition occurred 2–3 weeks after peak emergence during 1994 and 1995 (Fig. 8). These time lags are many times longer than the life span of adult *Baetis* (3–5 days). Thus, females that emerged before oviposition sites were locally available had to disperse to sites with protruding rocks or die. These data further show that the rate of oviposition was a function of the rate of recession of spring flood waters, which controlled the availability of protruding substrates. In contrast, the precise cues used to signal the onset of emergence are unknown; but, clearly, local emergence was not triggered by the local availability of oviposition substrates. It is possible that potential emergence cues, such as water temperature and photoperiod, correlate more reliably with the regional availability of oviposition sites.

Despite large interannual changes in the availability of oviposition sites (Fig. 5), the total number of egg masses oviposited in the study reach each year (including both generations) was fairly stable over 3 years; but the numbers of females emerging from the study reach fluctuated more dramatically among years (Table 3, Fig. 8). For the six generations covered by this study, we estimated that a maximum of 0.5–7.8% of the females emerging from the reach could have returned to their natal reach to oviposit (Table 3). If emerging individuals float long distances before shedding their exuvia, this low rate of return could be caused by an overestimate of the number of *Baetis* emerging, including individuals that emerged upstream of the reach. However, in all years combined, we caught 22,212 exuvia and only 301 subimagos in our block net, which suggests they do not travel far before shedding their exuvia. Thus, any overestimate of emergence should be small, and similar for all dates. Thus, we argue that low oviposition rates compared to emergence are explained by a combination of high rates of adult dispersal, low mating success and high mortality of adult females. Neither adult mortality nor dispersal rates have been measured directly for any mayfly population (the “black box”).

Similarly, over 3 years the estimated numbers of adults of each generation that emerged from the study

reach were independent of the estimated numbers of egg masses that initiated that generation (Table 3). These observations suggest that post-recruitment processes operating on *Baetis* larvae (e.g., predation, competition, disturbance and dispersal), determine the local production of adults; and that these processes vary over time even at the same location (Peckarsky et al. 2000).

Mechanisms explaining oviposition behavior

Oviposition cues

The probability of a rock having any egg masses and the density of egg masses on rocks were both functions of the date of rock appearance and rock size. The logistic multiple regression identified four rock attributes that contributed significantly to use of rocks by *Baetis* for oviposition: timing of appearance above the water surface ($\chi^2_L=49.03$, $P=0.0001$), size ($\chi^2_L=18.65$, $P=0.0001$), orientation ($\chi^2_L=10.15$, $P=0.0014$), and embeddedness ($\chi^2_L=7.03$, $P=0.0080$). Inclusion of additional variables increased the model R^2 by less than 1%. A goodness-of-fit test indicated that the data fit the model [Hosmer-Lemeshow (H-L) $\chi^2=4.98$, $P=0.7594$; Hosmer and Lemeshow 1989]. Similarly, the best-fit multiple linear regression (excluding rocks with no egg masses) indicated that a significant proportion of the variance in density of egg masses could be attributed to three rock attributes: size ($R^2=0.304$, $P=0.0002$), timing ($R^2=0.140$, $P=0.0037$), and geology ($R^2=0.059$, $P=0.0426$). Addition of other variables increased the model R^2 by less than 1%. The correlation matrix showed no significant association between the date of emergence and rock size (Pearson correlation coefficient $\rho=-0.141$, $P=0.378$, $n=41$). However, there was a significant association between rock orientation and time (tall rocks appeared early: $\rho=-0.319$, $P=0.042$), and between rock size and location (large rocks were in the center of the stream: $\rho=0.440$, $P=0.004$). These regression analyses indicate that females preferred to oviposit on large, unembedded, tall, granite rocks. Moreover, they further support the hypothesis that the seasonal variation in hydrology con-

Table 4 Number of substrates available and number of *B. bicaudatus* egg masses observed on unembedded, embedded, and dislodged (by hand) substrates ($P < 0.0001$, 2 *df*) during a 1996 experiment in the East River study reach

Substrate type	Available	Proportion available	Observed	Expected	(Obs-Exp) ² /Exp
Unembedded	263	0.60	1395	932	230
Embedded	142	0.33	0	513	513
Dislodged	32	0.07	159	109	23
Total	437	1.00	1554	1554	$\chi^2=766$

Table 5 Mean, SE, and total number of *B. bicaudatus* females (imago stage) captured on protruding rocks covered with tanglefoot during 1996 experiment at the East River study reach. Substrate treatments were: rocks on the stream bank (*Control*), rocks embedded within the streambed (*Embedded*), and rocks that were not embedded in the streambed (*Unembedded*)

Substrate type	<i>n</i>	Mean no. (SE)	Total
Control	30	0.00	0
Embedded	30	4.80 (0.67)	144
Unembedded	30	4.66 (0.65)	140

strained the timing of *Baetis* oviposition at the reach scale.

Interestingly, when we dislodged embedded rocks, *Baetis* females oviposited on them in greater proportion than expected by chance (Table 4). Also, the tanglefoot experiment showed that females landed on embedded and unembedded rocks with equal probability ($F=0.99$, $P=0.432$, 5,54 *df*, Table 5), suggesting that females distinguished among these rocks by sampling their undersides. Embedded and unembedded rocks did not differ in depth ($F=0.90$, $P=0.347$), geology ($F=0.09$, $P=0.767$) or current velocity ($F=0.54$, $P=0.467$), but embedded rocks were larger than unembedded rocks ($F=4.02$, $P=0.0499$). Thus, *Baetis* females may locate large rocks visually as a good target for potential oviposition sites; but once they have landed on a protruding rock they may use finer scale cues for actual oviposition.

Egg mass mortality

Egg masses incubated in stream water in the absence of predators hatched within 10–14 days with 97% hatching success, comparable to the 94% hatching success of *B. rhodani* eggs observed in the laboratory (Elliott 1972). A small proportion of the eggs in each mass (mean=0.7%) were white (the rest were beige) (Fig. 1), had no internal definition or indication of embryonic development, and did not hatch after 2 weeks. Comparison of white eggs to those from virgin female *Baetis* suggested that they were unfertilized. During 8 weeks of field observations of 109 egg masses on 15 rocks, 22% completely disappeared leaving no trace of eggs or chorions. Logistic regression predicted that the probability of egg mass mortality was lower on rocks with higher densities of egg masses ($\chi^2_L=17.60$, $P=0.0001$, 1 *df*). The equation predicting probability of mortality from egg mass density was: $\text{logit}(P)=0.1907-5.1454 \times \text{egg mass density}$, where probabili-

ty of mortality = $e^{\text{logit}(P)} / (1 + e^{\text{logit}(P)})$. The goodness-of-fit test indicated only a moderately good fit of the model to the data (H-L $\chi^2=7.53$, $P=0.0568$). These data provide a preliminary estimate of egg mortality in the field, and evidence that aggregating egg masses may reduce egg mortality.

Discussion

Little is known about processes that regulate aquatic insect populations in streams. Demographic models based on observational and experimental data have shown that biotic interactions occurring in the larval stages of *Baetis* have greater effects on fecundity than on the abundance of mayflies emerging from different stream reaches (Kerans et al. 1995; McPeck and Peckarsky 1998; Peckarsky et al. 2000). Furthermore, there is no evidence indicating whether recruitment determines the subsequent size of local or regional populations. However, the data presented in this study illustrate that the number of *B. bicaudatus* females that oviposited in one stream reach over six generations did not determine the number of adults that successfully emerged from that reach. Furthermore, our data suggest that local recruitment was determined by the temporal and spatial variation in environmental factors that influenced the timing and accessibility of oviposition habitat, rather than the number of females that emerged from that reach.

These data establish an observational basis for testing the hypothesis that a striking discontinuity exists between the benthic and dispersive stages of mayflies, thereby forming the conceptual framework for a new way of thinking about these populations of stream insects. That is, local production of adults may be independent of local recruitment (see theoretical perspective by Chesson 1998), but instead be determined by species interactions that occur during the larval stage (McPeck and Peckarsky 1998). Furthermore, larvae of these mayflies are highly mobile, and may travel as far as the adult stage (Hershey et al. 1993). Thus, extensive larval dispersal could also decouple reach-specific oviposition from subsequent emergence. Furthermore, processes that operate at the regional scale (e.g., weather patterns, hydrology) affect rates of dispersal and mortality of the adults, and thereby determine the regional pool of females available to oviposit. Local recruitment of *Baetis* is constrained behaviorally, and thereby dependent on large-scale abiotic factors (hydrology, channel geomorphology) that determine the times and places where they can oviposit. Thus, processes affecting larval and adult

stages of *Baetis* act at different scales, resulting in a decoupling of the local population dynamics of successive generations,

In seasonally fluctuating environments specificity of oviposition behavior observed in all reported species of *Baetis* may limit local recruitment; and time constraints imposed by extremely short adult stages may force them to disperse to find suitable oviposition sites. Mayflies are generally weak fliers (Brittain 1982), and dispersal can be very costly to insects (Rankin and Burchsted 1992). Thus, we argue that such specialized oviposition behavior must be accompanied by some compensatory benefit that increases the individual fitness of females. Our observational data provide several non-exclusive alternative hypotheses regarding the potential benefits of selective oviposition by *Baetis* that can be tested experimentally.

Many insects are known for ovipositing in locations providing high food quality for their relatively sedentary offspring (Dethier 1959; Rausher 1979; Moore et al. 1988; Kouki 1993). However, we assert that oviposition on the protected undersides of protruding rocks maximizes *Baetis* egg survival rather than larval growth and survival, because larvae are relatively mobile, and can select optimal habitats for foraging (Kohler 1984; Richards and Minshall 1988). Our estimate of 22% egg mortality, even though potentially elevated by physical disturbance, is lower than the few other published estimates of aquatic insect egg mortality in the field (30%, Martin 1991; 25%, Bennett and Mill 1995; 36%, Siva-Jothy et al. 1995).

Avoidance of egg predation is one of several alternative hypotheses that might explain why *Baetis* has evolved this specialized oviposition behavior. Preliminary experiments suggest that invertebrate predation from interstitial mayflies, stoneflies, or caddisflies (reported to eat amphibian eggs, Bell and Lawton 1975) is rare in this system (A.C. Encalada, unpublished work). Furthermore, *Baetis* did not avoid ovipositing in streams containing trout (Table 2), unlike other species that avoid ovipositing in habitats with high risk of predation (Chesson 1984; Resetarits and Wilbur 1989; Magnusson and Hero 1991; Petranka and Fakhoury 1991; Fraser and Gilliam 1992; Kats and Sih 1992; Blaustein and Kotler 1993; Ritchie and Laidlaw-Bell 1994; Sexton et al. 1994; Blaustein 1999; Stav et al. 1999), egg cannibalism (Dolumbia et al. 1998) or parasitism (Lowenberger and Rau 1994).

Alternatively, aggregations of egg masses on a few rocks may confer a fitness benefit. Our data showed that individual egg masses had a lower probability of mortality in an aggregation of many egg masses. Females of other insects oviposit in aggregations that function as protection against desiccation (Aldrich 1912; Otto 1987; Zwick and Zwick 1990), signal habitat stability (Dialdin and Ward 1991; Edgerly et al. 1998), reduce mortality from parasitoids (Damman and Cappucino 1991), minimize harassment by intruder males (Martens and Rehfeldt 1989; Rehfeldt 1992; Waage 1987) or reduce

the probability of egg predation (Turner and Pitcher 1986; Wrona and Dixon 1991). Aggregation could be an effective defense against predatory invertebrates that reach satiation relatively quickly (Kerans et al. 1995). Aggregation of *Baetis* egg masses could result from females recognizing and choosing to oviposit near other egg masses or as an indirect consequence of preference for specific physical conditions (A.C. Encalada, unpublished work). However, the fitness benefit of this behavior is independent of its mechanism.

We favor the hypothesis that the undersides of large, protruding rocks provide hydrologic stability (rarely roll or dry), as well as reduced exposure to scouring flow or ultraviolet radiation, thereby minimizing egg mortality due to abiotic factors. Higashiura (1989) demonstrated that gypsy moths living in snowy regions often oviposited in locations where eggs would be insulated by snow cover, even though larvae risked predation while traveling up tree trunks after hatching. Michiels and Dhondt (1990) observed that ovipositing dragonflies chose sites exposed to the north or south depending on temperature, thereby behaviorally regulating the thermal environment of their eggs. Similarly, Corbet (1967) reported that Arctic mosquitoes oviposited on slopes with southern exposure, which were the first to melt in spring. Our data are consistent with the hypotheses that *Baetis* females select sites with low exposure to scour, drying, and ultraviolet radiation, but have high stability and persistence for the 2-week embryonic period.

Implications for adult dispersal

Some theoretical models for the evolution of dispersal suggest that organisms should disperse even in stable environments if survival probability is very low in natal habitats (Johnson and Gaines 1990; McPeck and Holt 1992). Because adult female *Baetis* are short-lived, those who emerge before oviposition substrates are available have two alternatives: they can fly to locations where habitat is available, or they can die waiting. Thus, the hydrologic conditions in some years and at some sites combined with highly selective oviposition behavior constrain the ability of females to oviposit in the stream reaches from which they emerge, suggesting that extensive dispersal by *B. bicaudatus* occurs throughout the East River drainage basin. However, relatively short flights (<1 km) can result in females reaching locations with very different physical conditions. Studies measuring genetic differentiation among local populations of other mayflies also support the notion that aerial flight by these seemingly fragile insects may be a more important mechanism of dispersal than has been previously thought (Sweeney et al. 1986; Hughes et al. 1995; Schmidt et al. 1995; Bunn and Hughes 1997).

We would also argue that the predominantly upstream direction of dispersal by *Baetis* females (Madsen et al. 1973, 1977; Flecker and Allan 1988) could be maintained by direct selection on individual females caused

by behavioral and hydrologic constraints on oviposition, especially in high-water years. We propose this hypothesis as an alternative to the colonization cycle hypothesis (introduced by Muller 1954, 1982, and tested experimentally by Hershey et al. 1993), that upstream flight of stream insect adults is necessary to maintain larval populations in upstream reaches that might otherwise be depleted by downstream drift of larvae. Others have pointed out that fecundity is so high in most aquatic insects (hundreds to thousands of eggs per female) that only a few females flying in random directions are necessary to repopulate an upstream reach (Wilzbach and Cummins 1989; Anholt 1995; Schmidt et al. 1995). Furthermore, the colonization cycle hypothesis implies that upstream flight evolved by group selection on populations rather than by selection on individuals (Anholt 1995). Our hypothesis to explain the maintenance of upstream flight in *Baetis* is similar to that of Anholt (1995), but suggests that an abiotic factor (water level) rather than biotic factors (density dependence), is acting as the selective pressure maintaining this behavior.

Intriguingly, the scenario we have described may apply only to the overwintering generation of *B. bicaudatus* that emerges early in the summer. Winter generation *Baetis* males swarm near tributaries of the East River rather than on the mainstream (Vance 1996), and winter females fly predominantly upstream to oviposit (Flecker and Allan 1988; Vance 1996), when oviposition substrates are available earlier in upstream habitats. This could result in placement of eggs in habitats where not only the survivorship of larvae is higher (no trout), but also offspring will be larger and more fecund than in downstream reaches containing fish (McPeck and Peckarsky 1998; Peckarsky et al. 2000). Thus, there should be strong selection for upstream migration by female *Baetis* that emerge early in the summer (i.e., the overwintering generation). Later in the summer preferred oviposition substrates are plentiful in downstream reaches and are used by summer generation *Baetis* females. Consequently, upstream dispersal is not necessary for summer generation females to locate suitable oviposition sites, and mayflies of this generation may not fly anywhere to oviposit. However, it is conceivable that as water levels recede in late summer and if smaller streams dry, females may need to fly downstream to locate sites with adequate flow to sustain egg development. We have no direct evidence of downstream flight of summer generation *Baetis*, but male swarms of this generation occur on the mainstream instead of the tributaries (Vance 1996).

Implications for local and regional mechanisms controlling populations

We propose that adult dispersal and oviposition of *Baetis* mayflies may be driven by regional-scale processes (e.g., hydrology, meteorology, and the regional supply of propagules) and independent of local-scale processes affect-

ing performance of larvae. Furthermore, the supply of recruits, which remained somewhat constant from year to year in one reach, did not determine the abundance of adults produced in that reach, which was highly variable from year to year. This result suggests that interactions in the larval stage control insect populations at the local scale and determine regional differences in larval abundance and performance among stream reaches and years (Kohler and Wiley 1997; McPeck and Peckarsky 1998; Peckarsky et al. 2000). Thus, oviposition behavior and availability of oviposition habitat may strongly influence individual female fitness, but post recruitment processes appear more important in driving population dynamics. Similarly, for many marine invertebrates the availability of substrates may limit recruitment, but the local production of larvae by benthic adults plays little role in determining abundance of future generations at that location (Palmer et al. 1996).

The observational data reported in this study provide a different conceptual framework as a basis for future studies of stream insect populations. Whereas biotic interactions may influence the abundance or fecundity of the individuals arising from local populations, this study demonstrates that recruitment may be decoupled from local population dynamics, and dependent on large-scale processes that determine dispersal of individuals emerging from other locations in the region. One of the greatest challenges to studying organisms like aquatic insects and marine invertebrates is the open nature of these populations with recruits being supplied by a "black box" dispersal stage. To better understand the factors affecting populations of organisms with complex life cycles, we must not only include all life stages (Eckman 1996), but also study each stage at the appropriate spatial and temporal scales. Finally, we need to construct alternative models of population dynamics at scales relevant to open populations to explain fluctuations in the local populations of stream insects, and the spatial variation in abundance of local populations within a region (Chesson 1998; Connolly and Roughgarden 1999).

Acknowledgements We thank Tracy Smith, Marge Penton, Brooke Zanatell, Chester Anderson, Eric Odell, Wendy Brown, Angus McIntosh, Darcy Tickner, Emma Pierce, Bryan and Alison Horn, Peter Ode, Gail Blake, and Adam Burke for field and laboratory assistance during this project. We acknowledge Bern Sweeney for the original idea of estimating emergence by catching exuvia, and for creative suggestions for determining *Baetis* hatching success. We also thank Billie Kerans for the inspiration to celebrate gin-and-tonic-day every Thursday while sampling eggs and exuvia. Statistical advice was provided by Angus McIntosh, Karen Grace-Martin, and Chuck McCulloch. Comments from Steve Kohler, Mark McPeck, Angus McIntosh, Dave Lytle, Kate Macneale, Billie Kerans, Brad Anholt, Scott Cooper, Bruce Menge, Andrea Encalada, and two anonymous reviewers helped us improve earlier drafts of the manuscript. This research was supported by National Science Foundation Grant No. DEB-9306842 to B.L.P.

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