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The influence of periphyton abundance on *Baetis bicaudatus* distribution and colonization in a small stream

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Abstract. Colonization, distribution, and immigration of *Baetis bicaudatus* on rock surfaces was observed in a small Idaho (USA) stream. *Baetis* densities on rocks were assessed by direct observation through clear plastic viewing boxes. *Baetis* distributions among regions on individual rocks was related to periphyton abundance. Densities of *Baetis* on periphyton patches reflected the relative abundance of periphyton. Among rocks, distributions also were most strongly influenced by periphyton abundance. Water velocity and substrate size did not greatly influence distribution patterns. Chlorophyll *a* was the best indicator of periphyton abundance. Immigration rates, determined through time-lapse photography, were as high as 5.8 individuals/100 cm^2/hr. Over 50% of nymphs arrived from the drift. At such immigration rates, the proportion of immigrants that emigrate per unit time would have to be high to maintain densities observed on rocks after 48 hr. The results of this study show that *Baetis bicaudatus* abundance on rock surfaces is an interplay between immigration rate and nymphal response to food abundance.

Key words: *Baetis bicaudatus*, microdistribution, immigration, emigration, colonization, periphyton, grazer, stream ecology.

The distribution of lotic invertebrates is influenced by a variety of physical and biotic factors. Water velocity (Ciborowski and Clifford 1984, Corkum et al. 1977, Edington 1968) and substrate (Minshall 1984, Minshall and Minshall 1977, Reice 1980) often are cited as physical factors influencing local distributions of stream invertebrates. Biotic factors such as predation (Oberndorfer et al. 1984, Peckarsky 1980, Peckarsky and Dodson 1980) and competition (Hart 1983, 1985, Hemphill and Cooper 1983, McAuliffe 1983, 1984a, 1984b, Wiley 1981, Wiley and Kohler 1981) also affect local distributions. The relative contributions of biotic and physical influences on invertebrate distributions is a topic of continuing interest (see Minshall and Petersen 1985, Reice 1985, Robinson and Minshall 1986).

Recent studies in streams suggest that food may be limiting to many stream invertebrates, particularly within the grazing community (Hart 1985, Hill and Knight 1987, Mayer and Likens 1987, McAuliffe 1983, 1984a, 1984b, Vaughn 1986). The periphyton community on the surfaces of stony substrates in streams represents a high-quality nutritional resource for stream invertebrates. Carbon/nitrogen ratios typically are lower for periphyton than for other foods within streams (Gregory 1983). If grazers are limited by food, their local distributions should reflect the abundance of this resource.

Periphyton abundance varies over at least two spatial scales within streams: among rocks and on individual rock surfaces. Grazer foraging behavior often is concentrated in high resource areas over an individual substrate surface (Hart 1981, Hart and Resh 1980, Kohler 1984, Wiley and Kohler 1984). This type of foraging behavior should result in clumped distributions in areas of high periphyton abundance on individual substrates, although this has not been documented. Furthermore, if food is limiting and grazers have sufficient mobility to move among rocks, inter-rock distributions should be positively related to periphyton abundance. The interplay between the response to local (on a rock) and regional (among rocks) periphyton abundance should result in grazer distributions that reflect the abundance of food. Although some investigators have found that grazer distributions are related to periphyton abundance among rocks (Douglas 1958, Hawkins et al. 1982, Lamberti and Resh 1983, McAuliffe 1984b, Vaughn 1986), few studies have examined the dynamics of this relationship.

Our investigation was conducted to examine

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the influence of periphyton abundance on the nanno- and micro-distribution and short-term colonization of rocks by a mayfly, *Baetis bicaudatus* (Dodds), in a small Rocky Mountain stream. *Baetis bicaudatus* is widely distributed in small cool streams of western North America (Jensen 1966). Members of this genus are rapid colonizers (Ciborowski and Clifford 1984, McArthur and Barnes 1985, Shaw and Minshall 1980, Sheldon 1977) and often occur in large numbers. Densities are often greatest in stream reaches with high algal production (Behmer and Hawkins 1985, Wallace and Gurtz 1986). Drift behavior can be strongly related to food abundance (Bohle 1978, Kohler 1985). By drifting, *Baetis* can potentially move quickly among stream reaches or habitat patches. Several studies show that *Baetis* nymphs spend more time in high periphyton abundance areas when foraging on individual stony substrates (Hart 1985, Kohler 1984, McAuliffe 1984, Richards 1986), which indicates that crawling movements also may result in concentrations of *Baetis* in high food resource areas. Our study tested the hypothesis that distribution of *Baetis bicaudatus* both among rocks and on individual rocks is directly related to periphyton abundance.

Methods

Study site

Experiments were conducted in Spring Run, a first order, spring-fed stream in the Targhee National Forest, southeastern Idaho (43°16'0"N, 111°04'30"W). Spring Run is a high gradient (4–10%) stream characterized by turbulent flow. Channel width ranged from 0.4 to 1.2 m and water depths ranged from 0.1 to 0.5 m. Mean summer flow was approximately 0.1 m^3/s. Substrate was primarily gravel and cobble embedded in a marl matrix. Summer water temperatures ranged from 10 to 15°C.

The study took place where the stream flowed through a 100-m-long meadow. Stream-side vegetation was predominantly grasses and forbs. A canopy of riparian vegetation was not present here, although one was present both upstream and downstream of the meadow. Periphyton communities on stony substrates in Spring Run were composed primarily of diatoms. Mid-summer periphyton abundances as indexed by chlorophyll *a* (chl *a*) were similar or slightly lower than those reported for streams of similar size and geographic location (Andrews and Minshall 1978, Bott et al. 1985, Cushing et al. 1983). *Baetis bicaudatus* was the only species within the genus found in Spring Run where it attained abundances similar to those reported in other Rocky Mountain streams (Andrews and Minshall 1978, Sheldon 1977).

General procedures

In all distribution experiments, the number of *Baetis bicaudatus* present on rock surfaces was observed directly by eye with the aid of plastic viewing boxes. The open, clear plastic (2.5-mm thickness) viewing boxes (40 × 27 × 16 cm) were wedged between two lengths of angle iron placed across the stream so that the open side of the box faced directly up. The bottom of each box was held approximately 1 cm below the air-water interface. Rocks below the viewing boxes were easily visible as were *Baetis bicaudatus* nymphs on their surfaces. The distance between the upper rock surfaces and the plastic viewing box bottom ranged from 7 to 15 cm. Nymphs could move freely on and off the surface. Placement of the viewing boxes did not noticeably alter water velocity and water-column turbulence patterns.

Viewing boxes were set up at 7–10 small riffle/runs within the meadow area. Boxes were placed where they could be adjusted and maintained easily and thereby minimize observer disturbance.

All rocks used in the experiment were cobble from within the wetted perimeter of the stream chosen for similarity in size (5–15 cm, maximum diameter) and surface complexity (smooth). All rocks and rounded edges, few or no angular irregularities, and flattened upper surfaces.

An observation consisted of looking through a viewing box and counting the number of nymphs present on the upper flattened surfaces of the rock only. Less than a minute was required to count the individuals on any one rock. All individuals were counted regardless of size, although during all experiments the majority on rock surfaces were mature nymphs (3–5 mm).

Periphyton was sampled by scrubbing a known area of rock surface using a technique modified from Stockner and Armstrong (1971) as described by Robinson and Minshall (1986).

A 3-cm^2 sample was removed by placing a 35-ml syringe tube which had been cut in half and had a neoprene gasket glued to the outer edge of the flared plunger end. The flared end was pressed against the rock surface and the enclosed periphyton was scrubbed into a slurry with a coarse brush. The slurry was then removed from the tube with a pipette and vacuum filtered through 2.4-cm Whatman GF/C filters (pore size 0.45 μm). Filters were immediately frozen on dry ice before transportation to the laboratory.

Chlorophyll *a* was extracted by grinding a previously frozen filter in 5 ml or reagent grade acetone (100%), transferring the extractant to a centrifuge tube, and refrigerating the mixture at 4°C for 24 hr. Chlorophyll *a* and phaeopigment concentrations were determined with a Turner Model 111 fluorometer by multiplying the fluorescence readings by a calibration factor derived with a Beckman Instruments Model-DB spectrophotometer (APHA 1980). Since so little solution was required for fluorometer readings (<1% of volume), the remaining solution from each sample was then used without adjustment for measurement of total biomass (ash-free dry weight). Samples were oven-dried to constant weight at 60°C, cooled to room temperature, weighed, ashed at 550°C for 2 hr, rehydrated, redried at 60°, and reweighed.

Experiments on individual rocks

To examine whether *Baetis bicaudatus* distribution on individual rock surfaces is influenced by periphyton abundance, a series of rocks having patchily distributed periphyton was created. The purpose of this experiment was to determine whether distributions are influenced by relatively large differences in periphyton abundance within a range of patch sizes. Rocks were selected from the stream as previously described and an acetate sheet, on which a checkerboard pattern of square holes had been cut, was pressed against the rock surface and open squares were scraped with a stiff brush. Only one size of square was scraped on any one rock. Rocks with 0.5-, 1.0-, and 2.5-cm-wide squares were created. The width of the smallest patches corresponded roughly to 1 body length of a mature *Baetis bicaudatus* nymph. The pattern covered most or all of the upper surface of each rock so that approximately 50% of the available surface area was low resource (scraped) and 50% was high resource (unscraped). The total number of squares on each rock varied depending on the upper rock surface area and size of squares created. Total patterned area on rocks ranged from 35 to 150 cm^2. Only one rock was removed from the stream at a time for pattern creation. This process took only a few minutes for each rock.

In experiment A (June 1984), five viewing boxes were placed in the stream. One rock from each of the three patch size categories was placed beneath each viewing box for a total of 15 rocks. Rocks were in place by late afternoon and observations of *Baetis bicaudatus* on high and low resource squares on each rock were conducted at 0800, 1200, and 1700 hr the next day. The position of an individual's head was used to determine whether the nymph was on a high or low resource square. In the time required to count the number of nymphs on high and low resource squares, little or no movement occurred among squares on the rock. The total number of *Baetis* on a particular resource level of a rock was divided by the total area of those squares to obtain a density value. The average number of *Baetis* over the three observation periods on high and low resource squares for each rock was used in statistical analysis. One periphyton sample was taken from one high and low resource patch from each of the 2.5-cm-patch width rocks at the end of an experiment to obtain an estimate of periphyton abundance. Since the diameter of the periphyton sampling tube precluded sampling smaller patches, we used the content of the larger patches to give an estimate of the magnitude of difference between all high and low resource patches.

In experiment B, the rocks from experiment A were allowed to remain in the stream for 14 days. We expected that during this 14-d period, periphyton would accumulate on the scraped patches so that the difference in periphyton abundance between high and low patches would be decreased, thereby allowing determination of whether *Baetis bicaudatus* distributions reflected the decreased difference between high and low patches. All invertebrates were removed from the rocks, rocks were placed beneath viewing boxes, counts of *Baetis* were made, and periphyton samples were taken as in experiment A.

In experiment C (August 1985), seven viewing boxes were placed in the stream and all patch creation, observations and sampling were repeated as in experiment A with a total of 21 rocks.

Group comparisons were made by two-way ANOVA after comparing variances of treatment means.

Experiments among rocks

In experiment D (June 1983), a series of rocks was chosen from a 1-km section of the stream that included the meadow. Rocks were picked from the stream, and if they met physical criteria stated above, were assigned by direct visual estimation to one of two periphyton abundance categories (high or low). Rocks that were difficult to assign to an abundance category were not used. This method tended to maximize the difference between low and high periphyton abundance rocks as determined by visual estimation only. Rocks were submerged in water in a bucket for a few minutes while being transported to a viewing box. Before being placed beneath a viewing box, the rocks were carefully examined and remaining invertebrates washed from the surfaces or removed with forceps. Rocks were exposed to the air for only a few minutes while removing invertebrates or assessing periphyton abundance. Five high resource and eight low resource rocks were collected. Rocks were placed beneath viewing boxes by late afternoon and allowed to become colonized beneath the viewing boxes for 24 hr before the number of nymphs was counted on their surfaces. Following the observation period, three periphyton samples were taken from each rock surface. Group means were compared with a *t*-test.

In experiments E (June 1984), F (July 1984), and G (August 1984), a series of rocks was placed beneath the viewing boxes after invertebrates had been removed as previously described. An effort was made to represent the full range of periphyton densities but no attempt was made to divide rocks into low and high resource categories. Rocks were set in place by late afternoon or early evening and one observation of *Baetis* numbers was made a few hours after rock placement if light permitted, and at 0600, 1200, and 1700 the next day, and at 0600 and 1200 the following day. The mean of the last three observations was used in statistical analysis. Water velocity a few centimeters above the surface of each rock was assessed with a small Ott C-1 current meter. Rocks were then placed on the streambank one by one and two periphyton samples were taken from their surface as previously described. Since diatom communities on smooth rock surfaces in Spring Run appeared relatively homogenous, we felt that the average of two samples would adequately describe periphyton abundance. Upper surface area was then measured before removing the next rock from the stream.

The relationship between all variables and *Baetis bicaudatus* density was examined with a Pearson correlation analysis. Data were first compared with a normal probability plot to determine whether transformations were necessary.

Immigration rates

Immigration rates were estimated directly by counting the number of individuals which arrived on the surfaces of solid bricks (10 × 10 × 6 cm) in 1–2-hr periods at the same time as experiments E, F, and G. Bricks had been placed in the stream at least 1 mo before experiments to become colonized with periphyton. At the start of an observation period, all invertebrates were removed from a brick and the brick was placed beneath a viewing box as previously described. Bricks were then photographed (see Wiley and Kohler 1981) at 5-s intervals using an 8-mm movie camera (Minolta XL601) positioned above the viewing box with a tripod. At the end of 1–2 hr, invertebrates were again removed from the brick and a new filming period begun. At the end of filming, one periphyton sample was taken from each brick. Filming took place between 1000 and 1600 hr because of lighting limitations. The number of *Baetis* arriving on the upper brick surface in the film period was determined by examining individual frames of the films sequentially with a Copal film editor. Since *Baetis bicaudatus* nymphs typically move <8 mm/min in Spring Run (Richards 1986), nymphs that appeared on the brick surfaces farther than 10 mm from an edge between 5-s exposures were judged to have drifted to the brick surface. The remainder were assumed to have crawled to the surface.

Results

During all experiments, *Baetis bicaudatus* was the most abundant invertebrate on rock surfaces. *Neothremma* (Trichoptera:Limnephilidae) and *Drunella coloradensis* (Ephemeroptera: Ephemerellidae) also were present but in much smaller numbers. Examination of all numeric data showed that transformations were not required to meet assumptions of the statistical test.

Distribution among patches on a rock

Significant differences in *Baetis bicaudatus* density ($p < 0.05$) were noted between high resource (unscraped) and low resource (scraped) patches in all patchy rock experiments (Fig. 1). In all cases, the greatest *Baetis* densities were on high resource patches. The magnitude of the difference between densities on high and low resource patches was greatest in experiments A and C when the net difference in chl *a* density was greatest. The ratio of chl *a* density between high and low resource patches in these experiments was 4.5 and 5.0, respectively. In experiment B, the chl *a* density ratio was lower (1.7) and the difference in *Baetis* density was not as pronounced (Fig. 1).

No significant differences ($p > 0.05$) in *Baetis bicaudatus* density among the three patch sizes were noted in experiments A and C, however, a significant difference ($p < 0.05$) was noted in experiment B, where densities were greatest on 1.0-cm-width patches (Fig. 1). These results suggest that patch size had limited effects on *Baetis bicaudatus* distributions.

Distribution among rocks

In experiment D, high resource rocks had a significantly ($p < 0.05$) greater amount of chl *a* (mean ± 1 SE = 1.39 ± 0.11 $\mu g/cm^2$, $n = 5$) than low resource rocks (0.33 ± 0.03 $\mu g/cm^2$, $n = 8$). *Baetis bicaudatus* distribution reflected this difference. *Baetis bicaudatus* densities (individuals/cm^2) were significantly ($p < 0.05$) greater on high resource rocks (0.29 ± 0.04, $n = 5$) than on low resource rocks (0.19 ± 0.02, $n = 8$).

Indicators of algal abundance also had the highest correlations with *Baetis bicaudatus* density in the other among-rock experiments (Table 1). The strongest correlations with *Baetis bicaudatus* density in all three among-rock experiments (experiments E, F, and G) were with chl *a* density. Lower correlations were observed with ash free dry weight of algae in experiment E and G. Other indicators of food abundance or quality had no significant relationships with *Baetis bicaudatus* density (Table 1).

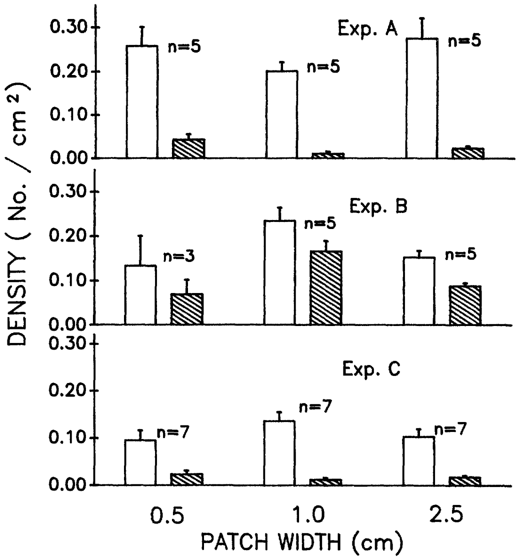

FIG. 1. *Baetis bicaudatus* density on high (open box) and low (cross-hatched box) periphyton abundance patches on rock surfaces. Bars represent one standard error of the mean. n = number of replicate rocks with a patch width size. Periphyton abundances were (mean ± 1 SE, $\mu g/cm^2$): exp. A high = 0.18 ± 0.02, low = 0.04 ± 0.01; exp. B high = 0.20 ± 0.3, low = 0.11 ± 0.2; exp. C high = 0.34 ± 0.04, low = 0.07 ± 0.01. F values for treatment effects: exp. A periphyton = 92.38 ($p < 0.001$), width = 1.70 ($p > 0.2$); exp. B periphyton = 8.33 ($p < 0.01$), width = 6.89 ($p < 0.01$); exp. C periphyton = 62.79 ($p < 0.001$), width = 0.62 ($p > 0.5$).

Of two physical variables measured, only velocity had a significant correlation with *Baetis* density (experiment G). No significant relationship was observed with surface area.

These results suggest that chl *a* was a stronger predictor of *Baetis bicaudatus* density than ash-free dry weight, chl *a* : pheophytin ratio, velocity, or rock surface area. However, the physical variables examined had relatively small ranges which may have downplayed the importance of these variables (Table 1). The chl *a*–*Baetis* relationship was described by regression analysis for each among-rock experiment (Fig. 2).

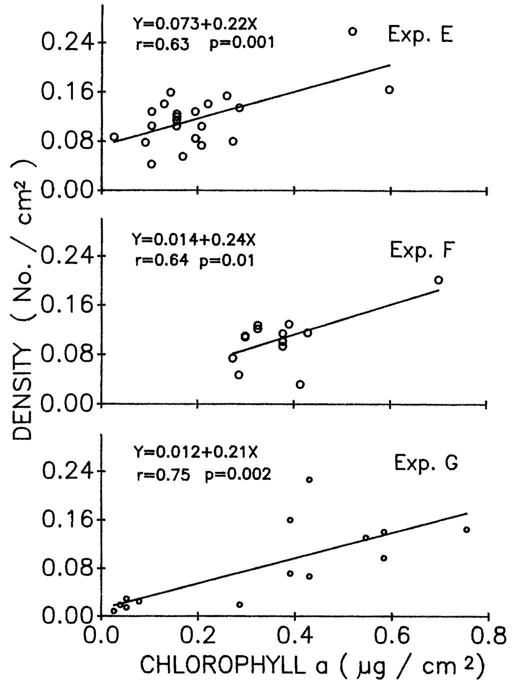

FIG. 2. *Baetis bicaudatus* density on rock surfaces versus chl *a* abundance in experiments E (June), F (July), and G (August).

Owing to the lack of intermediate chl *a* values in experiments E and F, these regressions should be treated with some caution. Regressions were compared by analysis of covariance (Sokal and Rohlf 1981). This procedure showed that there was no significant difference among the slopes of the three regression lines ($F = 0.043$, $p > 0.50$). There was, however, a significant difference among the origins of the regressions ($F = 11.58$, $p < 0.001$). The common slope of the regressions was 0.2174. These data show that the functional relationship between *Baetis bicaudatus* density and chl *a* was consistent through the summer in spite of variations in absolute densities.

Immigration

Immigration rate (number/100 cm^2/hr) was highest in experiment E and lowest in experiment G (Table 2). Over 50% of the immigrants in each experiment were from the drift. The remainder crawled onto the brick surface from adjacent areas. These immigration rates demonstrate that the *Baetis* densities observed in the

TABLE 1. Mean, range, and correlation coefficient with *Baetis bicaudatus* density of variables examined in experiments E, F, and G.

Variable	Experiment E (June), $n = 22$			Experiment F (July), $n = 13$			Experiment G (August), $n = 13$		
	Mean	Range	r	Mean	Range	r	Mean	Range	r
Ash-free dry weight (mg/cm^2)	0.89	0.1-1.8	0.46[a]	1.1	0.1-2.6	0.07	0.4	0.01-1.2	0.42[a]
Chl *a* (μg/cm^2)	0.20	0.03-0.60	0.63[a]	0.37	0.27-0.70	0.65[a]	0.33	0.03-0.75	0.75[a]
Chl *a*/pheophytin	959.6	0.5-17,900	−0.09	5.6	1.52-25.0	0.14	227.8	0.18-1755	0.25
Pheophytin (μg/cm^2)	0.07	0.01-0.18	0.22	0.12	0.1-0.26	0.29	0.12	0.01-0.42	0.05
Velocity (cm/s)	86.8	37.3-129.9	−0.13	75.5	49.6-112.0	0.05	72.8	34.0-102.0	0.45[a]
Upper surface area (cm^2)	167.3	93.7-268.7	0.12	156.7	81.2-231.2	0.01	110.7	31.2-175.0	−0.10

[a] Significant at $p < 0.05$.

among-rock experiments could develop rapidly. Assuming no emigration from the rocks, <12 hr would be required to reach even the highest observed densities.

Discussion

Periphyton abundance had a significant effect on *Baetis bicaudatus* distribution in Spring Run when observed on two spatial scales. Greater densities of *B. bicaudatus* accumulated on substrates with high periphyton densities than on substrates with lower periphyton densities. These relationships developed within a short period of time. This information suggests that newly arriving nymphs recognize relative periphyton abundance and modify their behavior to increase the amount of time spent in high food resource areas. Clearly, in Spring Run under the conditions tested, periphyton abundance had more influence on *B. bicaudatus* distribution than did patch size or water velocity.

Differential densities along periphyton abundance gradients likely are due to a combination of events that occur after a nymph arrives on substrate and not before contact with the surface. Although the swimming ability of this genus is well noted (Ciborowski 1983, Elliott 1971a, Minshall and Winger 1968), the effectiveness of this ability is greatest in slow water regions near the shores (Ciborowski 1987). All experiments in this study were conducted in high velocity water where the possibility of continuously monitoring substrate and food abundance conditions while drifting in the water column are reduced. There was little difference in substrate roughness or texture among rocks that might give microhydraulic clues to food abundance or provide enhanced opportunity for settling. Immigration from the drift to substrate patches in high velocity areas is most likely a random process in which the rate of immigration is proportional to the abundance of nymphs in the drift. Although differential immigration from the drift to high resource areas was not examined in this study, there is no published evidence to suggest it exists.

After arriving on a rock, area restricted search (Krebs 1978) is a sufficient mechanism to produce greater densities in patches of high food abundance. Kohler (1984, 1985) and Richards (1986) have described this form of food-related directional movement with *Baetis tricaudatus* Dodds and *Baetis bicaudatus.* Once on a substrate, nymphs have the ability to assess food abundance with mouthparts and other sensory structures and can respond accordingly. In high resource patches, movement velocity decreases while rate of turning increases, effectively concentrating foraging in high resource areas. This behavior should be effective among patches of any size. However, when patches are large and search time (and presumably energy expenditure) within and among patches is greater, other behaviors such as active drift may be invoked. Since a large portion of immigrants to vacant bricks in this study were judged to have crawled onto the bricks from adjacent areas, it can be assumed that area restricted search does have a role in distribution when the observation scale is rocks within a small section of stream. Benthic movements of several meters per day have been documented with *Baetis rhodani* (Pictet) and other mayflies (Elliott 1971b). Movements of such scale would be sufficient to search a number of rock surfaces within a day for resource rich areas.

TABLE 2. Immigration rate of *Baetis bicaudatus* (number/100 cm^2/hr), percentage of total immigrants that arrived from the drift, and chl *a* abundance (μg/cm^2) on brick surfaces during experiments E, F, and G. n = number of observations of a brick surface.

Experiment	n	Mean ± 1 SE	% from Drift	Chl *a*
E (June)	8	5.84 ± 0.78	52	0.305
F (July)	5	4.00 ± 0.55	62	0.156
G (August)	5	2.31 ± 0.31	59	0.545

The short amount of time required for *B. bicaudatus* to adjust its abundance relative to periphyton abundance gradients and the high rates of immigration observed indicate that emigration from habitat patches must be directly related to periphyton abundance. This relationship probably resembles the common slope observed in the regression analyses. A large proportion of newly arriving immigrants would have to emigrate through either crawling or drift in order to maintain the densities observed in this study even within a few hours of rock placement.

Actual immigration to and emigration from individual substrates has rarely been assessed in streams owing to difficulties inherent in observing stream substrates. Immigration rates for

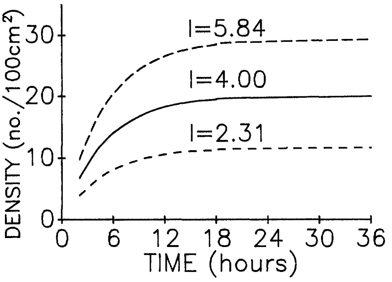

FIG. 3. Theoretical colonization rates from the equation $N = I/m(1-e^{-mt})$, where I = immigration rate, m = proportion emigrating per unit time, t = time, and e = base of Napierian logarithms (Sheldon 1984). Immigration rates are those observed in immigration experiments.

Baetis obtained in this investigation are considerably higher than those reported in other studies, although there are few studies with which to compare. Wiley and Kohler (1981) reported an immigration rate of 26 *Baetis* per 100 cm^2 in a 48-hr period. The turnover (proportion emigrating) in this period was 84%. Resource abundance was not reported. Their estimates were also based upon time-lapse photography, but may have been somewhat low due to the time between film exposures (30–60 s). The highest emigration values reported from sequential removal studies are those of Ciborowski and Clifford (1984) who calculated values of 22–69% leaving per 24 hr. Estimates of immigration based upon those values and observed densities would range from 14 to 44 individuals per 100 cm^2 per 24 hr. The immigration rates observed in our study (55–140 per 100 cm^2 per day) are considerably higher than either of these other studies. If the number of *B. bicaudatus* on a rock at the end of a 24-hr period had been used as an actual immigration rate similar to that used in a sequential removal study, values at least an order of magnitude lower would have been derived. Comparisons with existing colonization studies are further complicated by potential differences in the turnover rates on single large substrates and the baskets or trays that are typically used in such studies. These trays contain numerous small particles. Small individual particles may exhibit greater turnover rates because of their greater relative border area. Such an effect may influence observed turnover rate.

Even these estimates of immigration and emigration may be low when compared with those that occur after sunset. *Baetis* typically exhibits drift peaks during evening hours (Hynes 1970, Waters 1965). Assuming that drift is related to immigration on rock surfaces, the numbers of individuals arriving on a rock after dark would be greater than during daylight hours. The effect of this on densities, however, might be negated by increased emigration rates. At least one investigator (Kohler 1984) has observed greater movement velocities on substrates at night. The net effect of these two phenomena might be to increase the turnover of individuals after dark.

The differences in *Baetis bicaudatus* density observed at similar periphyton densities among months may be caused by differing immigration rates among the months. Relatively small differences in immigration rates can cause significant changes in what would be observed as equilibrium density, assuming emigration remained constant (Sheldon 1984). This situation is illustrated in Figure 3. The elevation of regression lines observed in this study is in general agreement with this prediction. *Baetis bicaudatus* densities were greatest when immigration rates were highest. Although field experiments in our study were not designed to assess equilibrium density, significant differences can be observed long before equilibrium is achieved.

The results of this study show that colonization studies in streams must consider the potential immigration rates of species and the rate at which reaction to environmental conditions occurs in the selection of census intervals. For species such as highly mobile grazers, careful attention also must be paid to algal abundance since emigration rates are strongly influenced by this factor. If substrates used in colonization studies are initially sterile, the equilibrium density achievable at any point in time may be driven more by the growth and accumulation of food resources than by immigration rate. The relatively long periods implied in the colonization curves depicted for *Baetis* by Ciborowski and Clifford (1984) and Sheldon (1977) may have been influenced by this factor.

This study strengthens the view that grazers in streams are acutely aware of and respond rapidly to algal abundance. Furthermore, responses can be observed at food abundance levels that occur naturally within a stream. The relationship between grazers and their food resource may be even more dynamic than previously thought.

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