

The effects of river fertilization on mayfly (*Baetis* sp.) drift patterns and population density in an arctic river

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Abstract

The life history, drift behavior, and benthic density of *Baetis* (Ephemeroptera) were examined in the arctic Kuparuk River in conjunction with a whole river fertilization experiment to determine if river fertilization affected *Baetis* drift and life history parameters. Drift was significantly higher in the control section of the river than in the fertilized, which suggested that the control section was a less suitable habitat than the fertilized section. There was no strong linear or exponential relationship between drift and benthic density, suggesting neither of these models are adequate to describe density independence versus density dependence. However, drift patterns in the control and fertilized sections suggest that drift is more of a function of absolute food supply than space or density of individuals. Drift was also sampled along a river transect at 6-hour intervals over a diel cycle. No diel periodicity in arctic summer drift was observed. The number of adults, number of eggs/female, and egg volume were calculated for adult *Baetis* collected in drift samples. There was no clear linear relationship between *Baetis* female dry mass and the number of eggs produced per female. However, a strong linear relationship was observed between individual egg volume and *Baetis* female dry mass, suggesting that larger females tended to produce larger eggs rather than more eggs.

Introduction

The mechanisms initiating and influencing stream invertebrate drift have received considerable attention from stream ecologists (e.g., review papers by Waters, 1972; Muller, 1982) resulting in many different hypotheses and considerable debate. Waters (1965) defined drift as being composed of three major components: behavioral drift, catastrophic drift, and constant drift. Behavioral drift is the result of some behavioral characteristic of the animal, such as a response to changes in light intensity, which causes diel periodicity in mayfly drift (Tanaka, 1960; Waters, 1962). Catastrophic drift is that which occurs as a result of floods or other physical disturbances,

whereas constant drift is composed of occasional individuals of all species that for various reasons lose their hold on the bottom and drift (Waters, 1965). This study is concerned with behavioral drift of *Baetis* in the Kuparuk River in arctic Alaska. Sampling was not conducted during any physical disturbances so as not to obtain catastrophic drift effects; the effect of constant drift was assumed to be consistent throughout the experimental conditions in the river.

The influence of population density on behavioral drift has recently been studied in an attempt to determine whether population regulation in streams is a function of population density. Although density-dependent drift has been shown for some stream invertebrates (Walton *et al.*,

1977; Wiley, 1981), it has not been shown for *Baetis* and other Ephemeroptera which dominate stream drift (Bohle, 1978; Corkum, 1978; Wiley & Kohler, 1984; Kohler, 1985).

Several hypotheses concerning stream drift suggest density-dependent population regulation. Muller (1954, 1982) proposed the colonization cycle hypothesis which suggests that as larvae grow, competition for space results in increased drift and colonization of suitable downstream habitats. Muller (1954, 1978) also proposed that adult aquatic insects compensate for the gradual downstream movements of their larvae by flying upstream to oviposit, thus upstream reaches would not be depleted of drifting species. Waters (1966) proposed the excess production hypothesis where, as an insect population density approaches carrying capacity, increasing competition results in increased drift as a means of removal and population control. Both the hypotheses of Muller (1954, 1982) and Waters (1966) suggest that drift is a density dependent agent of population regulation, with the means of regulation being competition between individuals for space, food or both (Hildebrand, 1974).

Food distribution and abundance appear to affect *Baetis* drift rates, at constant population density. Abundant food supply resulted in high local concentrations of *Baetis rhodani* and lack of drift, but depletion of food resulted in a more uniform distribution followed by increased drift (Bohle, 1978). Increased activity in searching for food at low food levels may result in increased drift (Hildebrand, 1974), and individuals may abandon habitats when their estimate of habitat quality falls to some threshold level (Kohler, 1985).

Diel periodicity of drift has been widely documented in many parts of the world (e.g. Tanaka, 1960; Waters, 1962). In arctic Alaska, Miller & Stout (1986) showed diel periodicity for stoneflies and chironomids in September once there were definite periods of darkness, but no periodicity during the summer period of continuous light. Since the mechanisms producing diel variation in drift are poorly understood (review by Wiley & Kohler, 1984), it is important that this aspect of

Baetis behavior in the arctic summer be documented. This is not only important in understanding *Baetis* drift and feeding behavior, but also important in understanding how photoperiod affects life-history (review by Sweeney, 1984).

Study area

The study area is the Kuparuk River, located on the North Slope of the Alaskan Brooks Range (68° 38' N, 149° 24' W). This fourth order stream flows northward into the Arctic Ocean, draining rolling tundra. The Kuparuk, with its substratum of boulders and cobbles, is frozen solid until late May or early June, when discharge is typically high due to snowmelt. In the year of this study, discharge was also high in early August due to substantial rainfall. The Kuparuk is characterized by a series of pools and riffles. The specific area of study was comprised of eight riffles separated by pools. The study area is intersected by the Trans-Alaskan Pipeline and the Dalton Highway which allowed easy access.

From 1 July to 15 August in 1983–1989, a section of the Kuparuk River was fertilized with phosphoric acid as part of a multi-investigator ecosystem level experiment (see Peterson *et al.*, 1985). Approximately $10 \mu\text{g l}^{-1}$ of phosphorus was added to the river at the same site (0 meters) during the first two summers of the fertilization. The phosphorus addition site was then moved to a location approximately 600 meters downstream in order to evaluate carry-over effects on the ecosystem. Epilithic algal biomass has significantly increased in the fertilized vs. the control section of the river since the start of the fertilization in 1983. Details and results of the enrichment are presented in Peterson *et al.* (1985), Hershey *et al.* (1988) and Hershey & Hiltner (1988).

Baetis, univoltine in the Kuparuk, is a major component in the drift and grazer community and the overwhelmingly dominant mayfly (Hershey, unpublished). It is also a major source of food for arctic grayling (*Thamallus articus*) (Hershey, unpublished), the only fish species in the river (B. J. Peterson, pers. comm.).

Methods

Response of Baetis drift patterns to river fertilization

On June 30, July 13, July 24 and Aug. 12, 1988, drift samples were taken at four riffles in the fertilized section (1000 m, 1400 m, 2000 m, 2500 m from 1983–1984 fertilization site) and at four riffles in the control section (–100 m, –400 m, –500 m, –1000 m) of the Kuparuk River. At each site two fifteen minute drift samples were taken above and two below the riffle with standard drift nets (0.14 m², 350 μ m mesh). Current readings were taken at the middle of the net opening with a Marsh McBirney current meter. Current readings were corrected for percent of net area submerged in order to calculate the number per m³ (no./m³) of *Baetis* nymphs in the drift. Drift samples were concentrated through a 150 μ m mesh net and preserved in 95% ethanol.

Baetis benthic density was sampled on June 30, July 8, July 24, and Aug. 8, 1988 at approximately the same river sites by scrubbing four rocks into a plastic basin for an estimated upper rock area of 363 ± 18 cm². The contents were sieved through the 150 μ m mesh net and preserved in 95% ethanol (Hershey & Hiltner, 1988). Using count data and the area sampled, benthic density in no./m² was estimated.

To obtain count data, drift and benthic samples were sorted in a glass pan over a light table. Samples estimated to contain greater than 50 *Baetis* were split with a Folsom sample splitter until a sample size of about 50 *Baetis* was obtained. *Baetis* were then sorted from the resulting sample fraction. The samples or fractions were then examined using a dissecting microscope to make sure all *Baetis* were removed. Lengths of *Baetis* were measured using a camera lucida on a dissecting microscope to project an image onto a digitizing pad.

A two-way analysis of variance was used to compare *Baetis* drift density between control and fertilized sections and between sampling dates. All drift estimates were log_e transformed to correct for heterogeneity of variances. Net drift across riffles was calculated as the mean drift of

the two nets below each riffle minus the mean drift of the two nets above each riffle. Net drift in the control versus fertilized sections on each sampling date was compared using a two-way ANOVA on log_e transformed data to test the hypothesis that *Baetis* had a greater propensity to leave riffles in the control section due to lower abundance of food. A two-way ANOVA was also used to determine the effect of date and treatment on benthic density. Linear and exponential models were used to describe the relationship between drift and benthic density to determine if drift was density independent versus density dependent (Hildebrand, 1974):

Linear: Drift density = $\beta_0 + \beta_1$ (Benthic density);

Exponential: log_e (Drift density) = $\beta_0 + \beta_1$ (Benthic density).

Baetis diel drift

From 0955 hrs. on July 23 to 1350 hrs. on July 24, 1988 drift samples were taken at six-hour intervals to determine diel periodicity of *Baetis* drift. Drift was sampled at two fertilized riffles (1000 m, 1400 m) and at two control riffles (–100 m, –400 m). As in the seasonal survey, two fifteen minute drift samples were taken above and two below each riffle with standard drift nets. Five river transects were completed over the two dates. The time of each sample and weather conditions present at each site were recorded.

Current readings, sample processing, and analyses were completed using the same procedures described in the preceding section on the response of *Baetis* drift patterns to river fertilization. A two-way ANOVA was used to make comparisons between drift in control and fertilized sections and time of day. The dependent variable used was the mean no./m³ *Baetis* drifting during each sampling period.

Life history parameters for Baetis

Adult *Baetis* were collected in the drift samples described above. Total number/m³ of adult *Baetis*

sampled was used as an estimate of numbers ovipositing. Oviposition can be distinguished from emergence because mayflies emerge as subimagos and then go through a final molt before egg laying occurs (e.g., Borror *et al.*, 1981). Adult *Baetis* lengths were measured using a camera lucida, dissecting microscope, and digitizing pad. Female *Baetis* dry mass was estimated from body length measurements using the predictive equation:

$$\ln W = -5.714 + 3.2 \ln L,$$

where W = dry mass, L = length (Smock, 1980).

Gravid females were gently split open and the number of eggs per female was counted. A ran-

dom subsample of five eggs was taken; egg lengths were measured using the camera lucida and digitizing pad. The widths of sixteen eggs were also measured to determine length/width ratios for eggs. The average of the sixteen length/width ratios was used to back calculate widths for all eggs measured. Egg volume was calculated using the standard formula for the volume of an ellipsoid ($4ab^2/3$, where $2a$ = length and $2b$ = width).

Relationships of *Baetis* female dry mass to the number of eggs per female and egg volume were determined using regression analyses (Sweeney & Vannote, 1981).

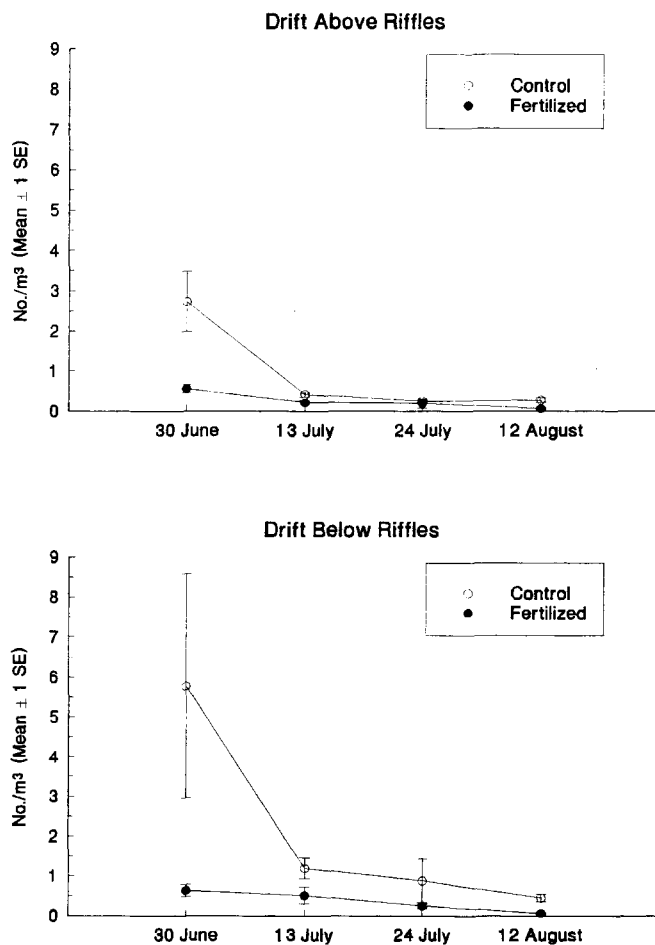


Fig. 1. *Baetis* drift density (no./m³) above (top panel) and below (bottom panel) riffles in the control and fertilized sections of the Kupaaruk River during 1988.

Results

Response of Baetis drift patterns to river fertilization

Drift was significantly higher in the control section of the river than in the fertilized section for samples taken both above ($F_{1,24} = 26.23$, $P < 0.0001$) and below each riffle ($F_{1,24} = 32.34$, $P < 0.0001$). This trend was especially evident early in the season when drift was high in the control section (Fig. 1). For both comparisons, date of sampling was significantly different (above $F_{3,24} = 19.01$, $P < 0.0001$; below, $F_{3,24}$, $P < 0.0001$). The date of sampling and treatment interaction was not significant for either comparison (up $F_{3,24} = 1.064$, $P > 0.05$; down $F_{3,24} = 1.39$, $P > 0.05$). Lack of a significant interaction term suggests that drift was consistently higher in the control than fertilized section of the river throughout the season in spite of significant seasonal changes in drift.

Net drift was significantly higher in the control section compared to the fertilized section ($F_{1,22} = 6.72$, $P < 0.05$) and date ($F_{3,22} = 1.54$,

$P > 0.05$) and date by treatment interaction ($F_{3,22} = 0.32$, $P > 0.05$) were not significant (Fig. 2). These results suggest that *Baetis* had a greater tendency to emigrate from the control riffles than from the fertilized riffles.

Baetis benthic density was significantly different between dates ($F_{3,24} = 98.45$, $P < 0.0001$). *Baetis* benthic density increased significantly from June 30 to July 8 and then significantly declined throughout the season (Fig. 3). The initial increase was probably due either to hatching of nymphs or to inadequate sampling of early instars, and the subsequent decline was probably due to drift, emergence, and mortality. In the early season (June 30 and July 8) density appeared more abundant in the control section (Fig. 3). In the late season (July 27) density appeared more abundant in the fertilized section (Fig. 3). By Aug. 8, most emergence was completed, thus density comparison between sections is not relevant. There was, however, no overall significant treatment effect for density and no significant date by treatment interaction (Treatment $F_{3,24} = 1.76$, $P > 0.05$; Treatment \times date $F_{3,24} = 2.5$, $P = 0.8$).

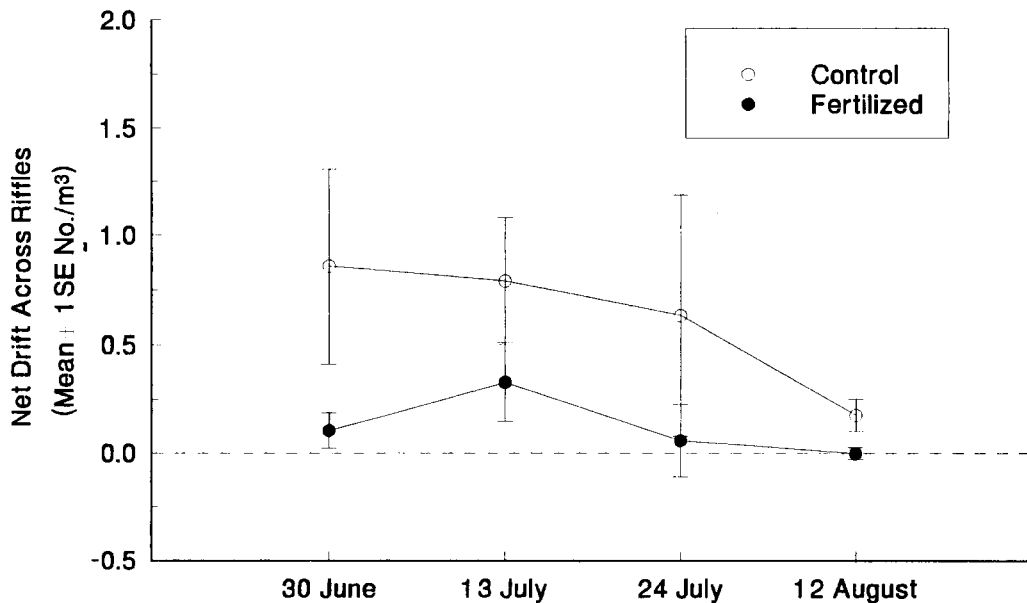


Fig. 2. Net drift across riffles (below-above) in the control and fertilized sections of the Kuparuk River. The figure shows that *Baetis* net drift was higher in the control section indicating that nymphs tended to leave these riffles compared to fertilized riffles.

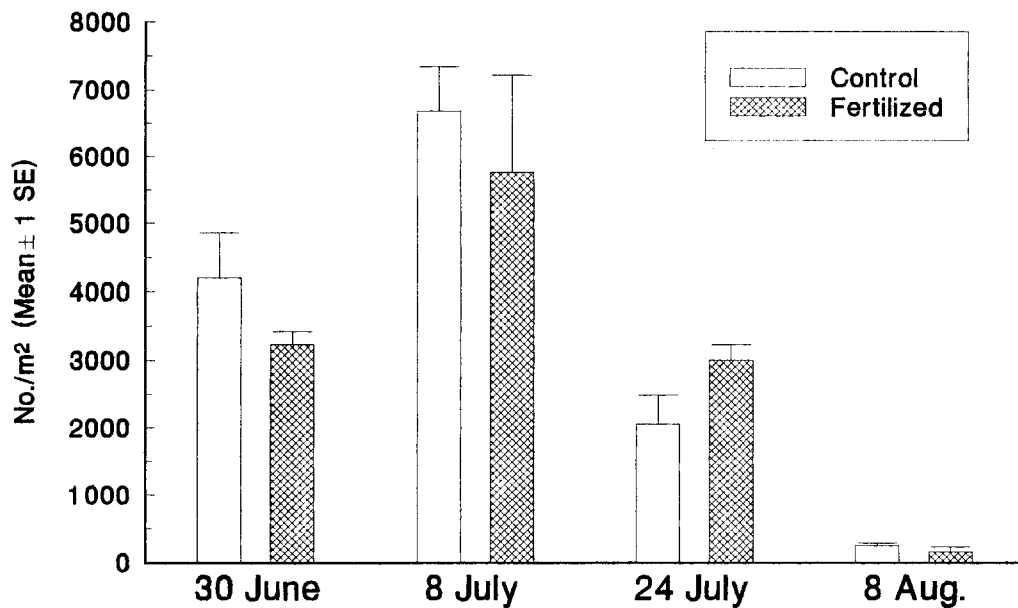


Fig. 3. *Baetis* benthic densities in the control and fertilized sections of the Kuparuk River during 1988.

An exponential regression model was slightly more satisfactory for describing the relationship of drift to benthic density than the linear model, but neither were very satisfactory (Table 1, Fig. 4). In the control section, the exponential model was significant and the lack of fit test indicated that this model was adequate, however, only 23% of the variation in drift was due to benthic density. In the fertilized section, the exponential model gave a significant lack of fit. The linear model was not significant in either the fertilized or the control section (Table 1).

Baetis diel drift pattern

Drift was not significantly different between the five sampling times for samples taken above ($F_{4,10} = 2.14$, $P = 0.15$) and below ($F_{4,10} = 0.27$, $P = 0.89$) each riffle suggesting no diel periodicity in the arctic summer drift patterns (Fig. 5). Treatment effect was also non-significant above riffles ($F_{1,10} = 3.12$, $P = 0.11$), but was significant below riffles ($F_{1,10} = 9.7$, $P = 0.01$). Despite the overall non-significant treatment effect above riffles, *a priori* comparisons indicated a significant treatment

Table 1. Results of regression analysis used to describe the relationship between *Baetis* drift density (no./m³) and *Baetis* benthic density (no./m²). Linear model: $D = B_0 + B_1$ (Density). Exponential model: $\text{Log}_e D = B_0 + B_1$ (Density).

Model	n	Sig. of Reg. F(p)	R ²	Lack of Fit F(p)
Control:				
$D = 0.51 + 0.0001$ (Density)	24	2.66 (0.12)	0.11	1.05 (> 0.05)
$\text{Log}_e D = -1.02 + 0.0002$ (Density)	24	6.75 (0.02)	0.23	1.40 (> 0.05)
Fertilized:				
$D = 0.17 + 0.00004$ (Density)	24	2.56 (0.12)	0.10	7.04 (< 0.01)
$\text{Log}_e D = -2.64 + 0.0003$ (Density)	24	12.48 (0.002)	0.37	4.67 (< 0.05)

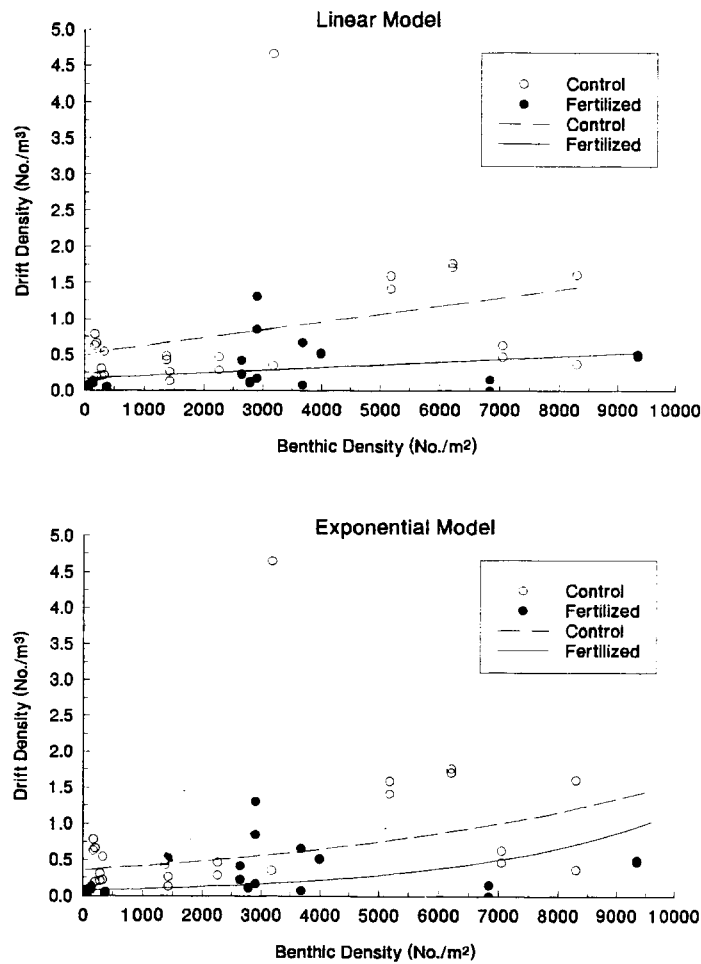


Fig. 4. Linear and exponential fits of *Baetis* drift density as a function of benthic density in control and fertilized sections of the Kuparuk River. Neither model gave a satisfactory fit to the data.

effect in the first sampling period for samples taken above each riffle (Fig. 5). Multiple comparisons also showed a significant treatment effect from the fourth sampling period for samples taken below each riffle ($P < 0.05$, Fig. 5). In all the below riffles; drift appeared higher in the control than in the fertilized section. These results are consistent with the generally higher drift observed in the control section of the river (Fig. 1). The transect run and treatment interaction was not significant for samples taken above or below riffles, suggesting that the effect of fertilization on drift did not vary with time of day.

Life history parameters for Baetis in arctic Alaska

The no./m³ of adults collected as a measure of oviposition was not significantly different between the control and fertilized sections of the river. In general, the number of adults collected was not significantly different on different sampling dates except that on June 30 no adults were found. The date of sampling and treatment interaction was not significant. This result indicates that the adult density was not significantly different between the control and fertilized sections of the river throughout the season and supports the conclu-

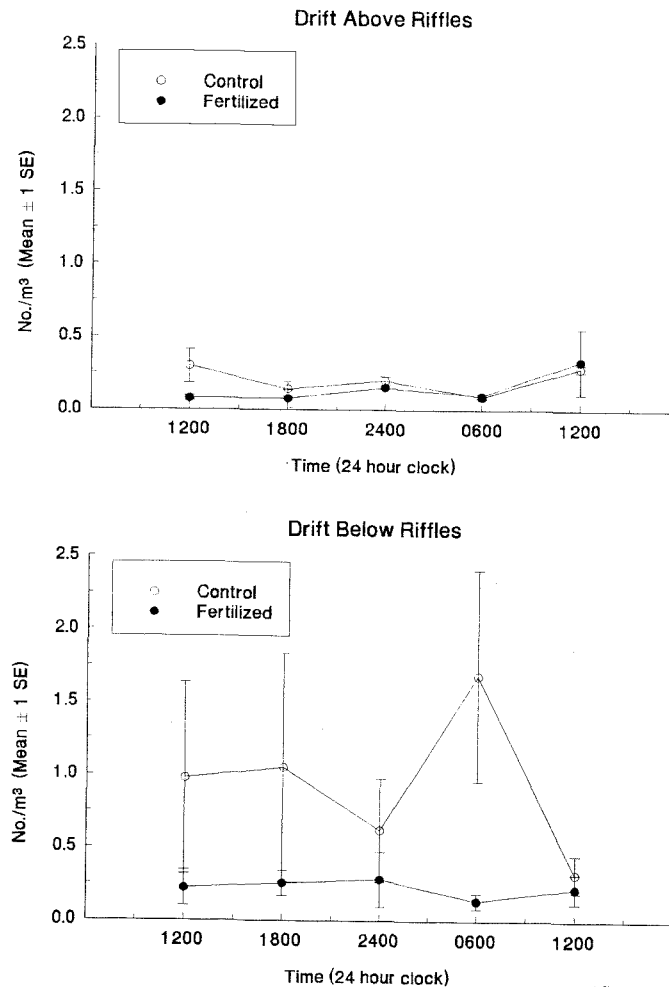


Fig. 5. Diel drift of *baetis* nymphs above (top panel) and below (bottom panel) riffles. The figure shows no strong diel drift pattern during this 24-light diel period of the arctic summer.

sion that these were ovipositing adults and had not necessarily emerged from the section of the river where they were collected. An average egg length/width ratio of 1.471 ± 0.144 was computed to back calculate individual egg widths for egg volume estimates. One data point, determined to be an extreme outlier at 13.5 times the interquartile range, was excluded (Devore & Peck, 1986).

The number of eggs per female was positively correlated with adult mass up to about 2.0 mg. Females larger than 2.0 mg tended to produce fewer eggs; therefore, there was no linear relationship ($r^2 = 0.085$) between female dry mass and

the number of eggs per female. To get a better estimate of this relationship a quadratic equation was used:

$$Y = 64.5 + 112.7x - 226.7x^2.$$

The quadratic gave a slightly better fit ($r^2 = 0.212$), although neither model fit the data well. There was, however, a strong linear relationship ($r^2 = 0.746$) between egg volume and female dry mass (Fig. 6) suggesting that larger females tended to produce larger eggs rather than more eggs.

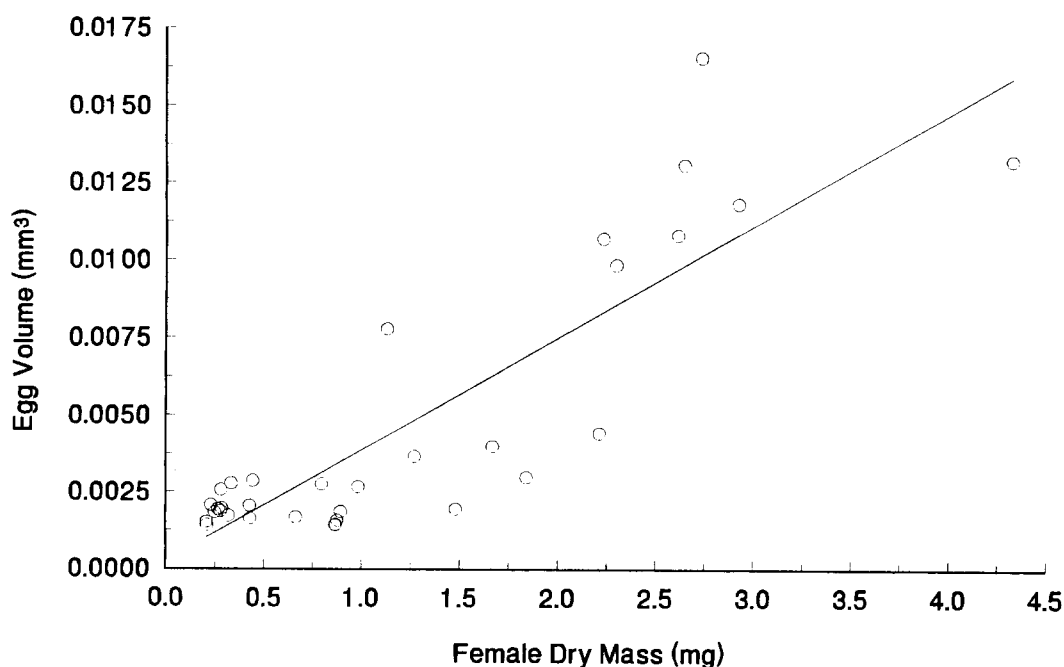


Fig. 6. *Baetis* egg volume (mm^3) as a function of female dry mass, indicating that egg volume increases linearly with female dry mass.

Discussion

Response of Baetis drift patterns to river fertilization

The results of this study show that drift density was significantly higher both upstream and downstream of control riffles than fertilized riffles, and that net drift out of riffles was higher in the control section. This suggests that nymphs were emigrating from the control riffles more than the fertilized riffles. Since epilithic algal biomass has increased significantly in the fertilized section of the river since the start of the fertilization in 1983 (Peterson *et al.*, 1985; Peterson, personal communication) the significantly higher drift of *Baetis* in the control section of the Kuparuk indicates a strong relationship between food abundance and drift.

The generally poor relationship between drift and benthic density suggests that using linear and exponential models to describe density independent versus density dependent drift is not adequate for these data. However, the comparisons of drift in control and fertilized sections of the

river are more consistent with the conclusion that drift is a function of per capita food supply rather than interference or density of individuals. That conclusion is consistent with the findings of Hildebrand (1974), Bohle (1978) and Kohler (1984, 1985) in artificial streams. They found that drift was largely active, and density independent. Hildebrand (1974) concluded that increases in drift behavior result from increased activity in searching for food at low food levels, and Kohler (1985) concluded that individuals tend to abandon habitats when their estimate of habitat quality falls below some threshold level. Thus, a density-independent factor was the major force regulating drift in this population; the hypothesis that drift is a density dependent agent of population regulation (Muller, 1954, 1982; Waters, 1966) is not supported for this *Baetis* population. Dudley *et al.* (1986) and Richards & Minshall (1988) found higher *Baetis* densities in the presence of macroalgae and abundant periphyton. The late season trend toward higher *Baetis* density in the fertilized section is consistent with their findings.

The patterns of *Baetis* drift and benthic density are consistent with Muller's hypothesis (1954, 1982) that adult aquatic insects compensate for the gradual downstream movements of the larvae by flying upstream to oviposit. The significantly higher no./m³ *Baetis* drifting in the control section in the early season (June 30) may be due not only to low food abundance but also to strong recruitment upstream the previous year. Allan (1989) found that small *Baetis* drift farther than large *Baetis* and that they drift farther at higher current velocity. In the Kuparuk, early season discharge and current velocity was high and *Baetis* were smaller than in the late season. This combined with the low per capita food abundance in the control section might account for the higher *Baetis* drift density in the control section early in the season. Small size and high current were clearly not the overriding factors, however, since early season drift in the fertilized section was not elevated. In the late season when *Baetis* was more abundant in the fertilized section, drift in the fertilized section did not increase. Some other factor was influencing drift more than density; our results suggest that the other factor is food abundance.

Baetis diel drift pattern

The results of this study indicate that there is no diel periodicity in arctic summer drift. Drift was consistent throughout the sampling period with no optimal time at which drift occurred. It is of interest to point out that during the third sampling period (2400 hours) the sky was cloudy, overcast and darker yet drift was not significantly different from any other time of the day. This may suggest that short-term changes in light availability are not enough to significantly influence drift patterns. These results support those of Elliot (1968) who found that over 24 hours of continuous light in an artificial stream the activity level of *Baetis* nymphs did not change. Activity increased, however, the first night after the light was turned off. In the arctic, once there are definite periods of darkness in the fall, *Baetis* nocturnal drift may increase. In

Imnavait Creek, near the Kuparuk, marked diurnal drift of stoneflies and nocturnal drift of chironomids has been observed, but only in September, once there were definite periods of darkness (Miller & Stout, 1986).

Kohler (1985) suggested that selection directly influences drift behavior and that the minimization of day drift may be adaptive. It has been suggested that nocturnal drift is an adaptation to minimize mortality due to fish predation (Allan, 1984) or invertebrate predation (Corkum & Pointing, 1979). Turcotte & Harper (1982) examined drift in a fishless mountain stream and found no evidence for consistent diel periodicities with nocturnal maxima. Prolonged summer photoperiod at high latitudes might partially compensate for the reduced feeding rates associated with the low temperatures of more northern habitats because an increase in daylength increases the feeding period for day-active species (Sweeney, 1984). This would also suggest that there are no optimal times for *Baetis* feeding in the arctic summer since the threats from predation would be continuous.

Life history parameters for Baetis in the Kuparuk River

In the Kuparuk, there was no linear relationship between *Baetis* female dry mass and the number of eggs/female. This result is in contrast to the linear relationships previously found between fecundity and adult dry weight for other Ephemeroptera species (Sweeney & Vannote, 1981, review by Sweeney, 1984). There was, however, a strong linear relationship between egg volume and female dry mass suggesting that larger females tend to produce larger eggs rather than more eggs. As these results show, larger adult female *Baetis* produce larger and presumably better quality eggs (Richards & Kolderie, 1957); egg volume may be a better indicator of reproductive fitness than egg number. This is interesting because Hershey (unpublished data) for the years 1984 to 1986 found that there were significantly larger *Baetis* nymphs in the fertilized section of the river than in the control. Since the fertilization

resulted in larger nymphs which presumably became larger adults, these adults should have had a higher reproductive success.

Summary

Environmental factors have been shown to affect many specific life-history parameters in aquatic insects. It has been shown that fertilization, which resulted in increased food abundance, influences drift density and reproductive fitness of an arctic *Baetis* population. *Baetis* had a significantly greater tendency to emigrate from the control riffles and drift was generally higher under control than fertilized conditions. Drift was a function of food supply and not dependent on the density of individuals.

Baetis diel drift behavior in the arctic summer showed no diel periodicity with no optimal time at which drift occurs. This would suggest that there are no optimal times for feeding since the threats from predation should be continuous.

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