Nymphal development of *Baetis vagans* McDunnough (Ephemeroptera: Baetidae) and drift habits of large nymphs

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Nymphal development of *Baetis vagans* McDunnough was studied at the Forks of the Credit River, Peel County, Ontario. Here, *B. vagans* is a bivoltine species inhabiting fast water; one generation occurs in the stream from November until late May and a second generation of smaller nymphs from July until mid-October. Nymphs continued to grow over winter although growth was slower than in the summer generation.

In laboratory drift studies, the presence of a stonefly predator, *Paragnetina media* (Walker), significantly increased the drift of large *Baetis vagans* nymphs during dark periods. By drifting at night, mayfly nymphs may be less susceptible to predation by both invertebrates and fish.

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Le développement larvoire de *Baetis vagans* McDunnough a été étudié à Forks of the Credit, Comté de Peel, Ontario. A cet endroit, *B. vagans* est une espèce bivoltine habitant des eaux rapides; il y a une première génération de novembre à la fin de mai, puis une seconde génération de plus petites larves de juillet à la mi-october. Les larves croissent durant tout l'hiver, bien que leur croissance soit plus lente que celle de la génération d'été.

Des études de dérive ont été entreprises en laboratoire; la présence d'un plécoptère prédateur, *Paragnetina media* (Walker), augmente significativement la dérive des larves de grande taille de *Baetis vagans* durant les heures d'obscurité. La dérive nocturne rend probablement les larves de *Baetis* moins vulnérables à la prédation par les invertébrés et les poissons.

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Introduction

Baetis vagans McDunnough is a common inhabitant of running waters in eastern and central North America (Edmunds et al. 1976) and is frequently present in the drift fauna (Hynes 1970; Waters 1972; Adamus and Gaufin 1976). Many workers have commented on the life history patterns of this species (Murphy 1922; Ide 1935; Waters 1966; Coleman and Hynes 1970; Bergman and Hilsenhoff 1978*a*). This study gives a detailed account of the nymphal development of *B. vagans*.

Some workers have reported that small mayfly nymphs are prevalent in the daytime drift (Anderson and Lehmkuhl 1968; Steine 1972; Devonport and Winterbourn 1976; Allan 1978), yet others suggest that the tendency to drift increases prior to emergence (Müller 1966; Waters 1966; Elliott 1967*a*, 1967*b*). Waters (1969) and recently Ciborowski (1979) have proposed that preemergent drift may serve to relocate some species to more suitable emergent sites such as slow-water areas. We conducted a distribution study of large *B. vagans* nymphs at the Credit River, Ontario, to describe the sites that this typically fast-water species occupied just prior to emergence.

The preponderance of either small or large nymphs in the drift fauna at any one time may be dependent on several factors: life history patterns, behavioural responses to fluctuating physical or chemical parameters, and perhaps, the presence of pelagic or benthic predators. Bishop and Hynes (1969) attributed the scarcity of large drifting invertebrates to fish predation. They suggested that predation by invertebrates, Perlidae, and Rhyacophilidae might also reduce the numbers of larger drifting fauna. Utilizing an artificial stream, we investigated the drift of large *B. vagans* nymphs in the presence of the stonefly predator, *Paragnetina media* (Walker).

Materials and Methods

Nymphal Development

Baetis vagans nymphs were collected for life history studies from the Forks of the Credit River, Peel County, Ontario (43°48′ N, 79°59′ W). From April to October, 100 nymphs were collected weekly, when available. From November to March, when nymphal growth was slower, samples were taken biweekly. The sampling schedule extended from 12 August 1974 until the end of August 1975. Nymphs were picked by hand from a variety of substrates including rocks, logs, fallen branches, and vegetation. Nymphs were also gathered from the stream bed

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using a modified Hess (1941) and Waters and Knapp (1961) bottom sampler (mesh size: 0.423 mm).

Initially, three growth parameters (wing pad length, ratio of wing pad length to seventh abdominal segment width, and head capsule width) were measured for each specimen. The coefficient of variation of the three parameters was used to determine which one had the least intrasample variability over a 10-week sampling period. Head capsule width (HCW) measurements were the least variable and this parameter was subsequently used to determine size distributions. All nymphs were assigned to one of four developmental stages or categories (after Clifford 1970) and sexed when possible. Large nymphs were returned to the laboratory and reared. In this study, 'large' *B. vagans* nymphs are those whose mesothoracic wing pad lengths are greater than the distance between them (categories III and IV). Category IV nymphs also possess darkened mesothoracic wing pads.

Distribution of Large Nymphs

To determine the distribution of large *B. vagans* nymphs on the stream bed, 10 randomly selected grid sites were examined within a 100-m^2 section of the East Credit River, 200 m upstream from the Forks. Each square grid (0.44 m^2) was divided into quadrants providing 40 sites. After recording the water depth, both mean current velocity within the water column and flow 3 cm from the bottom (limited by propeller radius) were measured at each site with an Ott C-1 current meter (Kempten, West Germany). A rock, enclosed in a dip net to prevent loss of organisms, was removed from each quadrant. *Baetis* nymphs associated with each rock were immediately preserved in 70% ethanol. The maximum length and width of each rock was measured and the product used as an index of surface area. Later, a correlation matrix was calculated to determine if any relationship existed between the physical factors (substrate surface area, current velocity, and water depth) and the numbers of nymphs. Samples were collected on 23–24 May 1974: water temperatures at midday were 18 and 19°C respectively.

Laboratory Drift Studies

Laboratory drift studies were conducted during May 1977 to determine the influence of predation by *P. media*, food (prepared instant oatmeal), and cover (artificial turf) on the drift of category III *B. vagans* nymphs in both light and dark conditions. Experiments were conducted in an artificial stream which was housed in a temperature-controlled environmental room. Dechlorinated water was continually circulated along an elliptical channel (1.25 m in length) by a motor-driven paddle wheel. Two aluminum trays, each 28 cm × 17.5 cm × 2.5 cm, were filled with stones (16–22.6 mm in diameter), with or without food and (or) cover, and positioned in the stream channel. Current velocity was 10 cm/s; water depth was 15 cm; water temperature was 15°C.

Either 100 nymphs of *B. vagans* alone or 100 *B. vagans* and 10 *P. media* (starved for 24 h) were poured through a funnel upstream from the substrate trays. After a settling period of 45 min, a drift net with changeable catchment jar was positioned immediately downstream from the trays. Drift was monitored at ½-h intervals for 3 h of light followed by 3 h of dark. Each trial was performed three times for all combinations of substrate types.

Results and Discussion

Nymphal Development

The 31 samples collected during 1974–1975 yielded a total of 2838 nymphs of *B. vagans*. Two generations occurred (Fig. 1). Based on HCW measurements, the fast-growing individuals of the summer generation are smaller in all developmental categories than those of the winter generation. Water temperatures ranged from 16 to 19.5°C in July and August, then gradually decreased to 8–9°C in late September (Fig. 1). Despite decreasing temperatures, nymphal size of the summer generation steadily increased with time. Nymphs continued to grow over winter although growth was slower than in the summer generation. Because of their double-compound eyes, the HCW of males was larger than that of females for any particular sample date giving the impression that male nymphs are larger. Although HCW increased from one developmental category to another, there was considerable overlap among the four developmental categories in both generations (Corkum 1976).

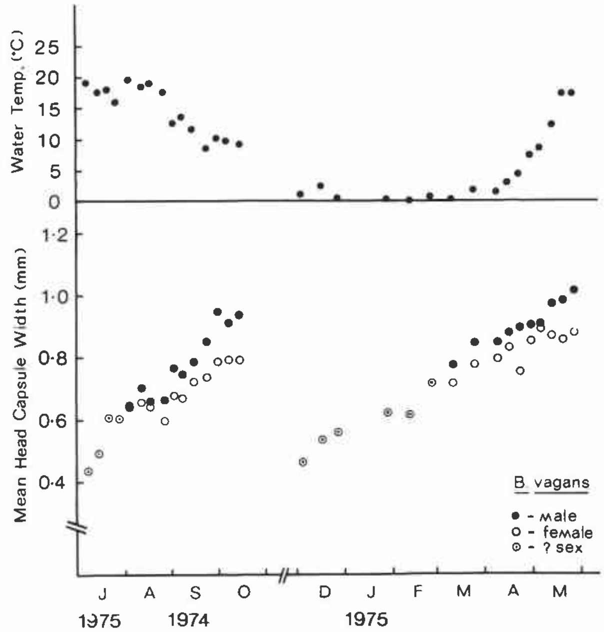

FIG. 1. Water temperatures recorded at the sample site and head capsule widths of *B. vagans* nymphs collected from the sample site during 1974 and 1975.

Figure 2 illustrates the growth of the winter generation of nymphs from December 1974 until the end of May, peak emergence time. Although first-instar nymphs (gills absent) were present in early December, many nymphs did possess gills indicating that eggs hatched at the site in November. By early March, it was possible to distinguish sexes in all individuals. The maximum HCW of 1.27 mm appeared on April 29, thereafter fully developed nymphs were smaller. Emergence at the sample site began on 10 May 1975 and continued until early June.

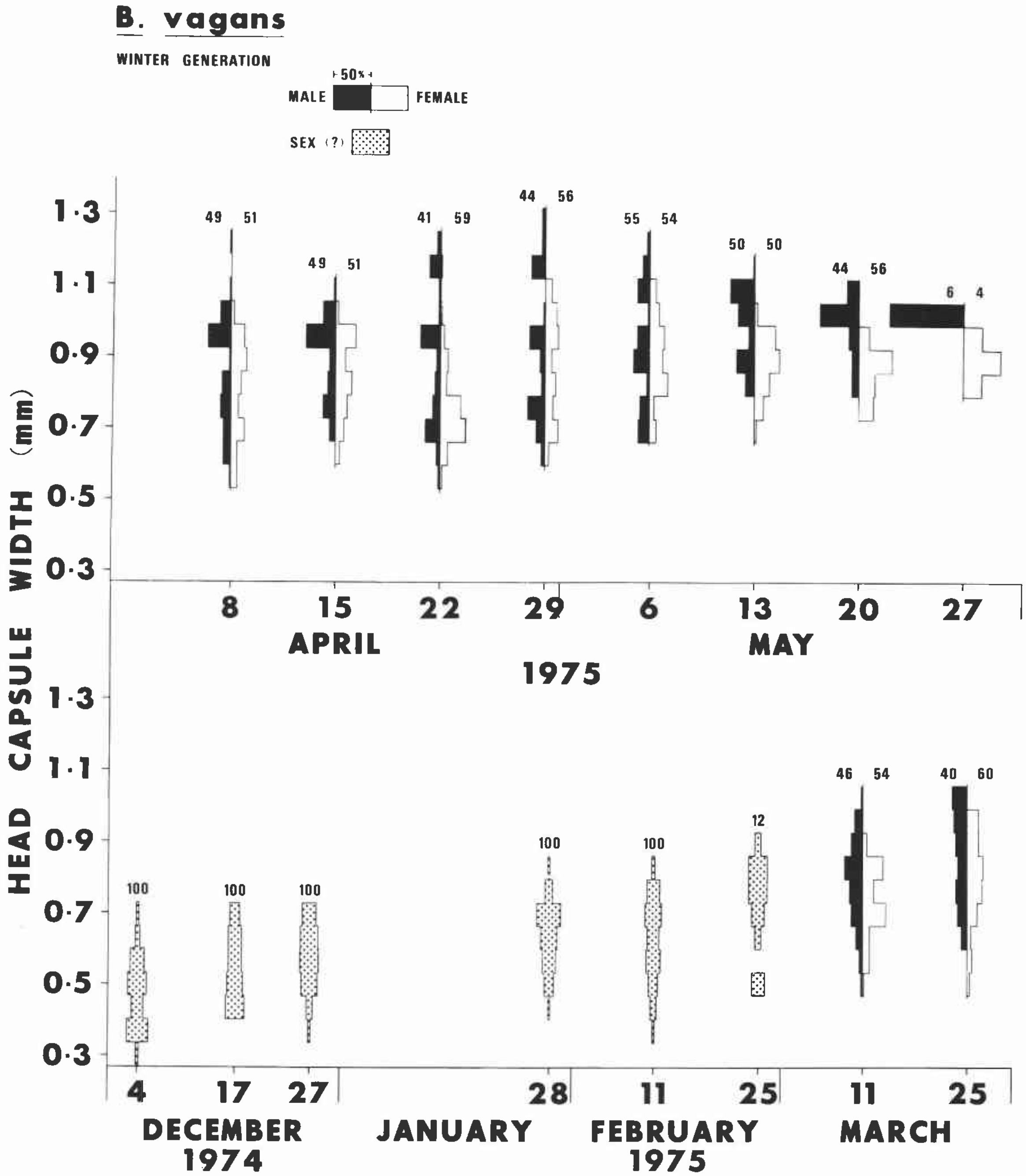

FIG. 2. Growth of nymphs based on head capsule widths of samples from the winter generation of *B. vagans* at the Forks of the Credit. Numbers indicate sample size.

Nymphs of the second generation were collected at the site about 5 weeks after peak emergence of the winter generation. Again, many nymphs possessed gills indicating that eggs likely hatched in late June. Three and one-half months of rapid growth occurred from July to mid-October (Fig. 3). Nymphs collected in August 1974 did not differ in size from nymphs collected in August 1975. Nymphs with a maximum HCW of 1.08 mm appeared on September 30 and in October. Male subimagos appearing in the field were first observed on 7 October 1974 (1330–1430 h). On 10 October 1974, a female imago was observed under an exposed rock by the stream at 1000 hours.

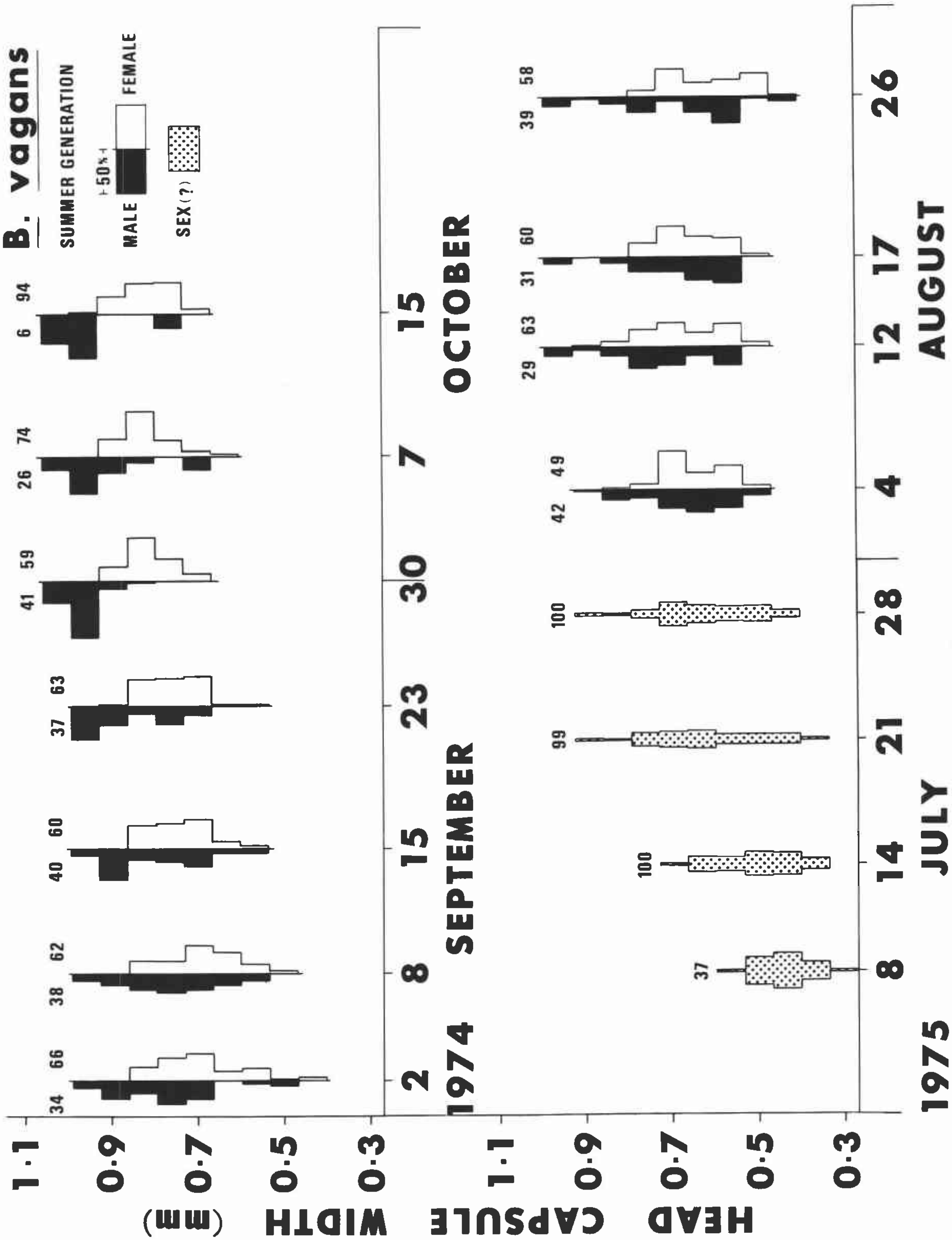

FIG. 3. Growth of nymphs based on head capsule widths of samples from the summer generation of *B. vagans* at the Forks of the Credit. Numbers indicate sample size.

TABLE 1. Generations per year of *B. vagans*

Location	Number of generations per year	Emergence period(s)	Reference
Ithaca, New York	1.5	October August May	Murphy 1922
Pine Creek, Ontario:			
station 1, T max: 11°C	1	May – early August	Ide 1935
station 2, T max: 20°C	2	Early spring – late June Mid-August	
station 3, T max: 21°C	2	Early spring – June Mid-July throughout summer	
Valley Creek, Minnesota	3–4	Early July September March–April May–June (atypical)	Waters 1966
Speed River, Ontario	2	—	Coleman and Hynes 1970
Wisconsin (various localities)	2	April–May Late June – mid-October	Bergman and Hilsenhoff 1978*a*
Credit River, Ontario	2	May–June October	This study

Baetis species typically emerge during daylight hours (Edmunds et al. 1976). Numerous individuals of both generations were observed emerging from the rapid water areas at the Credit Forks about 1400 hours on sunny days.

The proportion of female nymphs in the winter generation was 0.54 ($n = 919$) whereas the proportion of females in the summer generation was 0.66 ($n = 1071$). The hypothesis that equal numbers of males and females existed in both generations was rejected ($p < 0.05$, G-statistic, goodness of fit test). Apparently, there was a strong tendency towards more females in the summer than in the winter generation.

McCafferty and Morihara (1979) have hypothesized that parthenogenesis in certain *Baetis* species (*B. macdunnoughi* and *B. hageni*) is associated with cold adaptation. One might infer that the proportion of females in populations of *Baetis* species would be greater in cooler waters. However, in our study with *B. vagans*, the proportion of females was greater in the warmer summer months than in the winter generation. It should be emphasized that *B. vagans* is not known to be parthenogenic (Bergman and Hilsenhoff 1978*b*).

The estimated number of generations for *B. vagans* from several studies, all within the cold-temperate region of North America, is summarized in Table 1. Generation estimates vary from 1 per year (Ide 1935) to 3–4 per year (Waters 1966). Changes in voltinism may vary with temperature regime along a course of a river (Ide 1935). There appears to be no association between numbers of generations per year and latitude, range about 42–44°15′ N. The maximum estimate is for the westernmost site, Valley Creek in east-central Minnesota (Waters 1966). Two generations per year seem to be typical for *B. vagans* in the temperate streams of N.E. North America, if nymphs are collected well downstream from a river's source (see Ide 1935).

Distribution of Large Nymphs

The distribution study of large *B. vagans* nymphs was conducted in late May, near the latter part of the spring emergence period for this species. Both linear and logarithmic transformations of the numbers of nymphs were positively correlated with linear ($r = 0.42$, $p < 0.01$) and logarithmic transformations ($r = 0.49$, $p < 0.01$) of the current velocity 3 cm from the stream bed. The untransformed index of surface area and the logarithmic transformed data of mean current velocity were both positively correlated with the linear and logarithmic transformed numbers of *B. vagans* ($p < 0.05$). Water depth had no relation to nymphal numbers on the stream bed.

Corkum et al. (1977), utilizing a laboratory stream, showed that category III nymphs of *B.*

vagans were found most often on organic substrates (branches) and infrequently on inorganic substrates. In our study, by chance, only inorganic substrates were retrieved from the stream bottom. Corkum et al. (1977) also found more category III *B. vagans* nymphs on the laboratory stream bed in moderately flowing water (30–50 cm/s) than in slower areas (0–20 cm/s).

Our field distribution study showed that last-instar nymphs (those with black wing pads) still occupied fast-water areas. Subimagos were seen emerging from rapid-water areas as well. Apparently, preemergent drift in *B. vagans* does not redistribute nymphs to areas with differing current regimes.

Laboratory Drift Studies

A three-way analysis of variance was used to test the influence of food, cover, and predators on the drift of category III *B. vagans* nymphs under both light and dark conditions. A difference of means test showed that significantly more *B. vagans* nymphs drifted in the dark than under light conditions ($p < 0.001$). None of the variables nor their interactions significantly influenced nymphal drift under lighted conditions. In the dark, the presence of the stonefly predator, *Paragnetina media*, was the only factor which significantly increased the drift of the mayfly nymphs ($p < 0.001$).

Bishop and Hynes (1969) suggested that invertebrate predation by stoneflies (Perlidae) and caddisflies (Rhyacophilidae) might eliminate the larger invertebrate larvae and thus reduce the numbers of large forms entering the water column. In our laboratory studies, however, we demonstrated that the influence of the perlid, *P. media*, increased the drift of large *B. vagans* during dark periods. Evidently, *B. vagans*, which is well adapted for swimming, drifts at night and avoids invertebrate predation at a time when it would also be less susceptible to fish.

In a drift study on the Speed River, Ontario, Bishop and Hynes (1969) showed that of all drifting Baetinae, only 64 of 7379 individuals were greater than 5.0 mm in length. They suggested that some of the larger-drifting forms were eliminated from the water column by fish predation. Allan (1978) has recently shown that the risk of predation on *Baetis bicaudatus* Dodds, by brook trout, *Salvelinus fontinalis* (Mitchill), increases as the nymphs increase in size. At present, Corkum and Clifford (in press) are studying the influence of stonefly predators on the settling and drift of both small and large *Baetis* nymphs.

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