

and in each instance the hosts were collected during March.

The occurrence of *B. cuspidatus* in *D. cepedianum* is not inexplicable since the intermediate host is a cyclopoid copepod. *Dorosoma cepedianum* are planktophagic fish (Jester and Jensen 1972) and readily consume cladocerans, copepods, rotifers, and numerous other zooplankton (Bodola 1965).

The results of this study, therefore, provide a new host record for *B. cuspidatus* and also represent the first adult tapeworms ever recorded from

*D. cepedianum*. Larval *Proteocephalus* tapeworms are the only other tapeworms of *D. cepedianum* (Hoffman 1967).

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## Is benthic activity of stream invertebrates related to behavioural drift?

LYNDA D. CORKUM<sup>1</sup>

Department of Zoology, Erindale College, University of Toronto, Mississauga, Ont., Canada L5L 1C6

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Although benthic activity and drift have been found to occur within the same light phase, the correlation between these variables is poor. It is hypothesized that the ratio of mean activity among stream invertebrates in the dark to that in the light is inversely related to seasonally increased photoperiods.

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L'activité benthique et la dérive se produisent durant la même phase lumineuse, mais il y a peu de corrélation entre ces deux variables. Il semble que le rapport activité moyenne des invertébrés d'eaux courantes à l'obscurité : activité moyenne à la lumière soit inversement proportionnel aux augmentations saisonnières de la photopériode.

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### Introduction

Müller (1966) and Elliott (1967a) postulated a close relationship between downstream transport (drift) of invertebrates in running water and their activity in the benthos. Rhythms in mayfly activity throughout a 24-h period have been previously reported (Harker 1953) and related to drift (Chaston 1968; Elliott 1968). Mayfly nymphs appear to be photonegative in running water; the nymphs occur beneath rocks during the day but crawl to the upper surfaces at night (Elliott 1968). Increased activity at night as well as proximity to the water column probably increases the likelihood of a nymph entering the drift (Waters 1972). Since there is an increase in both activity and drift at night, the two have been thought to be related. I hope to demonstrate that benthic activity does not necessarily

initiate drift and that the two should be considered as separate phenomena.

### Methods

Harker (1953) and Elliott (1968) studied activity patterns of mayfly nymphs in the laboratory and both utilized activity units as a measure of nymphal movement. Harker recorded an activity unit as movement by a nymph in a 2-s period. Observations of samples of five nymphs were made for 10 min at hourly intervals. Luminous paint on the thorax of nymphs aided in nighttime observations. Elliott (1968) recorded an activity unit as movement by a nymph for 10 s or less. Observations were recorded for 10-min intervals each 0.5 h. Nighttime observations on samples of 10 nymphs were made with a dull red light bulb, which was shown not to affect nymphal activity.

I have utilized these authors' data to calculate mean activity per observation in the dark (D) and light (L) and then determine the activity ratio, D/L.

### Results and Discussion

Harker's (1953) and Elliott's (1968) activity values were utilized to study the relationship between the activity ratio (D/L) and photoperiod (day-

<sup>1</sup>Present address: Department of Zoology, University of Alberta, Edmonton, Alta., Canada T6G 2E9.

TABLE 1. Mean activity counts in the dark and light for several mayfly species obtained from the literature

Species	Size, mean modal length, mm	Date examined	Photoperiod, hours of dark:light	Mean activity per observation		Activity ratio, D/L
				Dark	Light	
Elliott (1968)						
<i>Baetis rhodani</i>	7.5	Early July 1966	9:15	14.5	—	—
	7.5	Middle " "	9:15	5.6	2.7	2.07
	7.5	Late " "	9:15	15.9	—	—
	5.5	January 1967	16:8	16.4	1.7	9.65
	7.5	March 1967	15:9	16:4	1.8	9.11
<i>Ecdyonurus venosus</i>	7.0	January 1967	16:8	13.1	1.5	8.73
<i>Ephemerella ignita</i>	6.0	July 1966	9:15	18.8	2.9	6.48
<i>Heptagenia lateralis</i>	7.0	March 1967	15:9	17.1	1.6	10.69
<i>Rhithrogena semicolorata</i>	8.0	July 1966	9:15	10.9	1.2	9.08
	6.0	January 1967	16:8	11.3	0.4	28.25
	7.0	March 1967	15:9	12.1	0.6	20.17
Harker (1953)						
<i>Baetis rhodani</i>	—	—	10:14	6.0	5.8	1.03
<i>Ecdyonurus torrentis</i>	XV <sup>a</sup>	February	12:12	6.1	2.8	2.18
	XV	May	7:17	6.4	6.1	1.05
	X	November	11:13	5.8	3.4	1.70
<i>Heptagenia lateralis</i>	—	—	10:14	5.3	7.0	0.76

<sup>a</sup>To determine nymphal size, Harker (1953) followed Rawlinson's (1939) staging scheme: XIV-XVII, large nymphs with fully developed gills, metathoracic wing pads hidden by the mesothoracic pair; IX-XIV, small nymphs, includes nymphs without gill pads.

length) (Table 1). The activity ratio is inversely related to seasonally increased daylengths (Fig. 1). This relationship exists whether the species was a swimmer, *Baetis rhodani*, or a clinger, *Ecdyonurus*, *Ephemerella*, *Heptagenia*, and *Rhithrogena*. This association may be due to each variable being correlated with other variables, such as water temperature, a wider range of nymphal sizes, or feeding habits. It seems likely that as an insect increases in size with longer photoperiods and higher temperatures, it will spend more time actively searching for food within the benthos or may move to new habitats to prepare for emergence.

Almost any species found in the stream benthos may eventually be found in the drift (Bishop and Hynes 1969; Waters 1972). Invertebrates may be passively swept into the water column by increased current velocities (catastrophic drift) or may actively leave the stream bottom and enter the water column (behavioural drift). Corkum (1978) observed that *Paraleptophlebia mollis* nymphs leaving the substrate were not necessarily those that had previously been most active. Elliott (1968) demonstrated that nymphal activity and drift had about the same nocturnal periodicities, but that the variance in the drift rate was far greater than variance in activity. Chaston (1968) showed that both drift and activity were greater during the night than day, but that the peak activity period for *Ephemerella* sp. nymphs occurred at 0300 hours whereas peak drift periods occurred 2 h after sunset (i.e. at 1800, 2000, and 2300 hours in the winter,

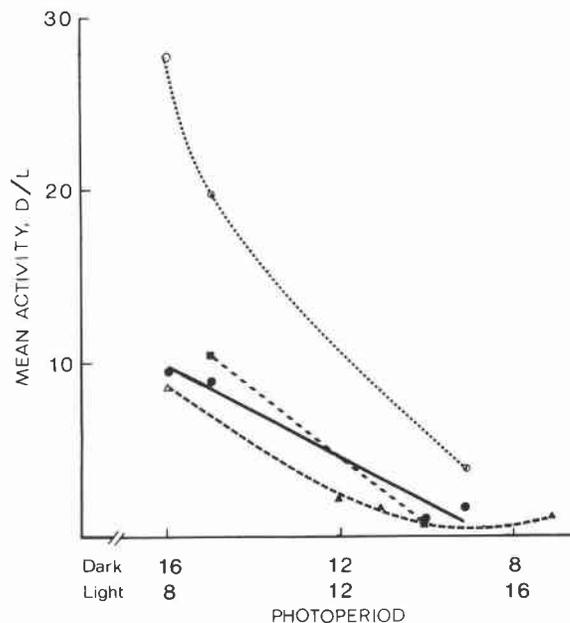


FIG. 1. The ratio of mean nymphal activity in the dark (D) to light (L) in relation to photoperiod length for representative mayfly species. ○---○, *Rhithrogena semicolorata*; ■---■, *Heptagenia lateralis*; ●—●, *Baetis rhodani*; △, *Ecdyonurus venosus*; ▲---▲, *E. torrentis*. (Curves fitted by eye.)

autumn, and summer, respectively). Evidently, invertebrate drift is not an immediate response to benthic activity.

Many workers have observed changes in nymphal behaviour with increasing nymphal size or

photoperiod. Moon (1935) showed that nymphal activity increased as nymphs matured and suggested that movement might be related to feeding (Moon 1940). Bishop (1969) postulated a direct relationship between foraging among stream insects and their drift peaks. Solem (1973) suggested that the presence of *Leptophlebia marginata* and *L. vespertina* nymphs within the water column of a lake reflected their activity on the lake bottom, just as other workers had inferred activity in the benthos from drift in stream channels. Solem described a shift in nymphal activity from nocturnal in March and April to diurnal in May and June, just before emergence. Increasing behavioural drift levels have been generally associated with preemergence or periods of rapid growth of invertebrates (Elliott 1967a, 1967b). Hayden and Clifford (1974) described a diurnal upstream migration by mature nymphs of *Leptophlebia cupida* after ice breakup in the spring. Thus, many insects appear to become diurnally active at later nymphal stages.

Whereas benthic activity steadily increases during the day with longer photoperiods, nocturnal activity remains constant (Fig. 1). Thus, nighttime activity does not change with the seasons. In contrast, many workers have reported nighttime drift to be greater during the spring and summer months (Elliott and Corlett 1972; Clifford 1972a, 1972b; and others). If benthic activity is a precursor of drift, it is difficult to explain this lack of correlation between seasonal drift rates and activity.

Ciborowski (1978) demonstrated that the number of *Ephemerella subvaria* nymphs drifting during darkness was a linear function of the preceding photoperiod. Thus, with longer daylengths, a higher concentration of drift occurs within the progressively shorter nights. Earlier, Müller (1965) showed that the nocturnal drift pattern of *Baetis rhodani* nymphs was directly related to the length of the dark period.

From this interpretation of the literature, it appears that, with increasing photoperiod, activity may no longer be concentrated at night, but continue throughout a 24-h period. If this proves true, benthic activity and drift should be treated as two distinct entities with photoperiod being a good predictor of both.

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