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THE ROLE OF DRIFT DISPERSAL IN PRODUCTION ECOLOGY OF A STREAM MAYFLY[1]

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Abstract. The role of drift behavior in the production ecology of the mayfly *Tricorythodes atratus* McDunnough was investigated in a headwater reach of the Mississippi River in northern Minnesota, USA. Comparison of drift and bottom samples revealed that larger nymphs exhibited a greater propensity to drift; in bottom samples, small immatures (1–2 mm) were predominant in a study riffle, whereas larger nymphs (>2 mm) were relatively more abundant in a downstream pool. Annual production was 8.56 $g \cdot m^{-2} \cdot yr^{-1}$ (dry mass) and the annual turnover ratio (annual production/annual mean biomass) was 26; the species was bivoltine. Errors in production rate estimation resulting from sampling a single habitat were substantial when differential size dispersal of nymphs occurred.

Key words: drift dispersal, Ephemeroptera, mayfly, Minnesota, P/B̄ ratio, secondary production, standing stock, Tricorythidae.

INTRODUCTION

The dispersal of stream insects by drifting has been well documented and recently reviewed (Waters 1972, Muller 1974). Several investigations have indicated that in the case of some species, drifting immatures are larger relative to those collected in benthic samples. Anderson (1966) found that an increase in drift of Ephemeroptera, Plecoptera, and Simuliidae during the night was primarily due to an increase in number of animals in larger size classes. Similar observations were reported for other Ephemeroptera (Elliott 1967, Steine 1972, Allen 1978) and Plecoptera (Elliott 1967). Such differences have been thought to be related to the life history and behavior of the species in question (Lehmkuhl and Anderson 1972, Waters 1972), but the role that this differential size dispersal plays in production ecology, or in the estimation of production, has not been explored.

The present study revealed that drifting nymphs of the stream mayfly *Tricorythodes atratus* McDunnough were likewise relatively larger than those in bottom samples. Production was estimated in both a riffle and an adjoining pool, where larger nymphs drifting from the riffle became aggregated. The purpose of this report is to demonstrate possible errors in production rate estimation due to the differential in nymph size between drifters and those samples from the bottom.

STUDY AREA

Investigations were conducted in a headwater reach of the Mississippi River, where it is a small, warm-water stream in Itasca State Park, Clearwater County,

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Minnesota. The stream rises as an overflow from the northern arm of Lake Itasca and meanders north through a mixed deciduous-coniferous forest.

Sections of the Mississippi used in this study were located at the crossing of Wilderness Trail Road (Fig. 1). The study riffle immediately upstream from the road measured 62.6 m long and 5.5 m wide; mean depth was 0.25 m. The study pool was located just below the road and measured 34.5 m long and 27.6 m wide; maximum depth was 0.9 m. The streambed was composed of fine sand, silt, gravel, and small stones with a few large rocks scattered throughout. Mean annual current velocity in the riffle and pool was 0.51 and 0.21 m/s, respectively, and mean annual discharge in the riffle was 0.7 m³/s. During summer, water temperature varied from ≈16° to 25°C. Although water temperatures in winter were near 0°C, the study sections were never ice covered. The pH of the water ranged from 7.2 to 8.2, dissolved oxygen from ≈8 to 12 mg/l, and alkalinity from 120 to 260 mg/l in summer and winter, respectively.

METHODS

Collecting methods for drift and benthos samples generally followed those described previously (Hall et al. 1975). During collection periods water velocity, mean depth, water temperature, and air temperature were routinely recorded. Both drift and benthic samples were taken monthly during January, February, and March and twice a month for the remainder of the study years. Drift collections were made from June 1971 to June 1972, while bottom collections were taken from June 1971 to January 1973. Drift samples were collected hourly during 24-h periods with 253-μm mesh nets. The bottom sampler was patterned after one used by Waters and Knapp (1961) and enclosed 0.1 m²; mesh size of the Nitex netting was 253 μm. Ten bottom sampling sites per sampling date were

chosen from a stratified random design. Counts of numbers of individuals from both habitats were transformed to $\log_{10}x$ or $(x + 1)$ in order to obtain 95% confidence intervals. Samples were sorted with the aid of a dissecting microscope to insure that eggs and small-instar nymphs were not overlooked.

Standing stock in biomass was estimated by computing the ratio of fresh mass to dry mass of immatures collected at various times during the study and comparing it to the ratio of preserved mass to dry mass. The mean dry mass of preserved organisms was 85% of the mean dry mass of unpreserved organisms. By incorporating this factor, estimates of biomass were corrected and thus based essentially on fresh dry mass and are expressed throughout as dry mass.

Production rate of *T. atratus* was estimated by using the formula $P = G\bar{B}$, where P = production in milligrams per square metre for a specific time interval, G = instantaneous rate of growth during that time, and $\bar{B}$ = mean standing stock in milligrams per square metre for the same time period (Ricker 1946, Allen 1949). Cohort instantaneous growth rate was calculated as the natural logarithm of the ratio of mean individual dry mass prior to emergence to mean individual dry mass of first-instar nymphs. The result was divided by the total number of days in the cohort period to obtain a mean G value for 1 d. Computation of G by this procedure was preferred over the original method of Ricker and Allen because, if continuous egg hatching occurs, an underestimation of growth rate will be obtained (Macan 1957). This G value was then multiplied by the estimated mean standing stock in biomass calculated for each sampling date to obtain an average production on a particular sampling day. These daily estimates were graphed separately for each habitat (riffle and pool) for bottom samples taken from May through November 1972, and areas under the curves were measured planimetrically to provide total cohort production.

Mean annual standing stock was similarly determined by plotting monthly or semimonthly estimates over the yearly period, measuring planimetrically the area under the curve, and dividing the area by the abscissal scale (i.e., 366 d in 1972).

RESULTS

The life cycle of *T. atratus* in the warmwater Mississippi Headwaters is as follows. Overwintering eggs start hatching during the month of May, and nymphs grow very rapidly at the high temperatures found in that stream. Adults begin emerging ≈7 wk from the initial onset of hatching. Thus, duration of the cohort is estimated at 7 wk. Eggs hatch continuously, probably for about 5 wk since numbers in the benthos drop to very low levels by mid-August. Benthic numbers then begin to rise again, indicating the start of the second generation.
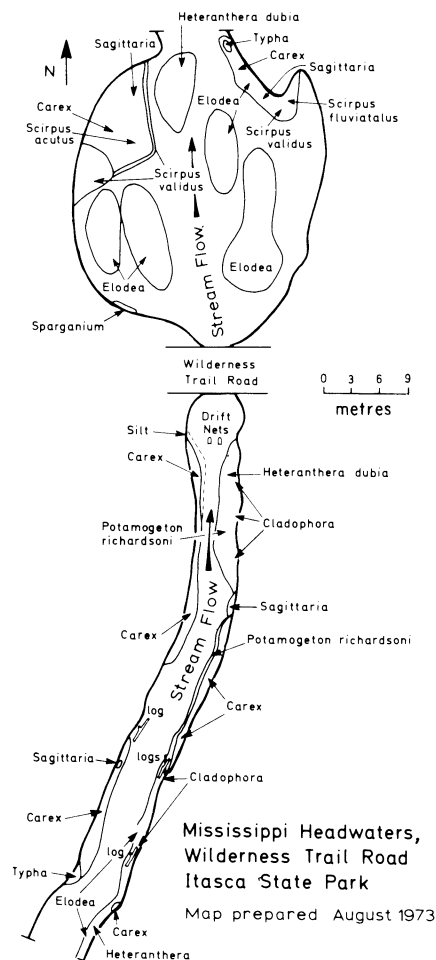

FIG. 1. Map of riffle and pool area studied, Mississippi River, Itasca State Park.

A greater percentage of individuals in the first two size classes was found in the riffle benthos relative to the drift sample, while a larger percentage of the 2–6 mm sizes was found in the drift (Table 1). Thus, individuals in the drift appeared, on the average, larger than those in the benthos. A Kolmogorov-Smirnov two-sample test confirmed this observation ($P <$ .001). To eliminate the possibility that silt may have clogged the mesh openings of the benthic sampler and that a proportionately greater number of smallest instars were taken relative to the drift collection, a second Kolmogorov-Smirnov test was conducted with the exclusion of the smallest size class. The same result was obtained.

The differential dispersal of larger nymphs led us to question what effect this behavior would have on production estimates of this species if only a riffle was sampled, since that habitat would lose a particular segment of its population. A subsequent drift study carried out on the downstream edge of the adjacent pool
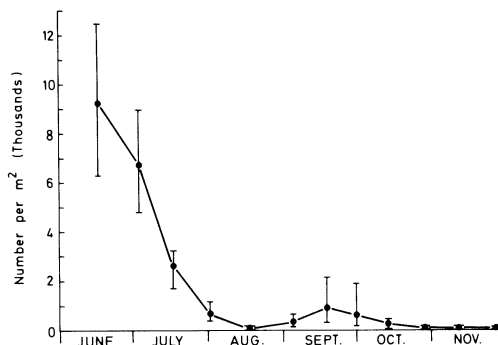
TABLE 1. Mean size class distribution of *Trycorythodes atratus* nymphs from benthic and drift samples (16 June 1972).

Size class (mm)	Benthos		Drift	
	N	%	N	%
0–1	278	9.1	4	0.6
1–2	1555	51.1	232	34.4
2–3	805	26.5	290	43.0
3–4	363	11.9	131	19.4
4–5	39	1.3	16	2.4
5–6	1	0.03	1	0.2
Total	3041		674	

FIG. 2. Density (with 95% confidence intervals) of *Tricorythodes atratus* nymphs, Mississippi River, 1972, pool and riffle combined.

revealed that organisms were not drifting out. The morphometry of this particular pool, quite unlike that described by Kovalak (1978*b*) from which *Tricorythodes* spp. nymphs did drift out, augmented the probability that nymphs would settle there. Water rushing into the pool area was channeled to both sides to deep basins where the velocity dropped almost to zero and circular motions were set up. Water spilled through the outlet at a very slow rate compared to the input. Thus, individuals, particularly larger ones, drifted to the pool and remained there. This latter conclusion leads to the supposition that eggs hatch predominantly in the riffle, a contention supported by observations that (1) females were seen depositing eggs in the riffle and (2) egg densities were much higher in riffle than pool reaches (Hall 1975). Eggs have been found attached to aquatic plants in drift samples from riffle sites (Hall et al. 1975), a phenomenon that may account for low egg densities in the pool.

Density of nymphs collected in the riffle and pool during 1972 showed variation through time (Fig. 2). The nymphs appeared first in the June samples, at which time the highest number (9231/m²) was observed. Numbers declined precipitously until the end of July, remained low in August, started to increase until mid-September, and finally decreased in October. No nymphs were found in the benthos after late November.

Mean individual dry mass varied between riffle and pool samples (Fig. 3). Initially, individual dry masses from both areas did not differ. However, by mid-July a substantial difference was apparent, 0.27 and 0.15 mg/m² in the pool and riffle, respectively. Values in mid-August and early September do not reflect this trend because they are based on small numbers of larger individuals found in the riffle (e.g., three individuals were found in the riffle samples on 17 August). Greater values in the pool persisted throughout the second cohort, indicating that larger organisms were consistently found there. The larger mean individual dry mass in the pool must be due, in part, to the demonstrated drifting of larger individuals into this habitat. However, differential growth in the pool cannot be discounted.

Two generations with different daily production rates were discerned during summer and autumn of 1972 in both the riffle and pool (Fig. 4). During the first generation greater biomass was produced relative to the second one. Nymphs were first collected in the 16 June samples and thus probably hatched shortly after the previous sampling period (27 May), at which time no nymphs were present. Hence that date (27 May) was designated as the beginning of the first cohort.

Cohort duration was estimated by determining the time interval between first appearance of organisms in the bottom samples and first collection of subadults in drift nets. This period was estimated at 50 d; it was not possible to determine whether cohort life was different between riffle and pool. Separation into two cohorts was further aided by data on number of eggs found in the benthos throughout the year and on mean individual dry mass in 1972 (Hall 1975).

Production rate estimates (daily values) were calculated for the period of May through November 1972. Mean standing stock in biomass, annual production, and P/B̄ (turnover) ratios are presented in Table 2. Production was calculated separately for each generation, and annual production was obtained by summing the two. Mean standing stock was 1.3 and 0.15
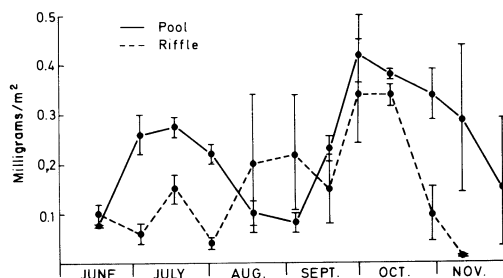
FIG. 3. x̄ ± SE of individual dry mass in milligrams/m² of *Tricorythodes atratus* nymphs taken from the pool and riffle, Mississippi River, 1972 (N = 5).

g/m^2 for the first and second cohort, respectively, and mean annual standing stock was 0.33 g/m^2. Cohort production rates were 7.52 for the first and 1.04 g·m^{-2}·yr^{-1} for the second; annual production was 8.56 g·m^{-2}·yr^{-1}.

P/$\bar{B}$ ratios for the first and second cohorts were 5.8 and 6.9, respectively, while the annual P/$\bar{B}$ ratio was 26. This latter ratio (annual production/annual mean biomass) is larger than the cohort ratios because annual mean biomass is small, being calculated over an entire year and including samples from the 5 mo (December through April) in which nymphs were not present. The cohort P/$\bar{B}$ ratios (cohort production/mean cohort biomass) are lower, being calculated only over that segment of the year in which nymphs are present.

If the instantaneous growth formula (P = G$\bar{B}$) is compared to that of the P/$\bar{B}$ ratio, it is obvious that the cohort instantaneous rate of growth (G) is equal to the P/$\bar{B}$ ratio, since G = P/$\bar{B}$. In this study, cohort G was estimated by taking the natural logarithm of the ratio of mean dry mass prior to emergence (1.28 mg; mean of males and females) to mean dry mass of first instars (0.7314 μg). The value obtained was 7.49. Cohort P/$\bar{B}$ ratio values calculated from samples collected in the field were 5.8 and 6.9 for the first and second cohorts, respectively. Waters (1969) stated that observed cohort G values generally run a little higher than calculated P/$\bar{B}$ ratios for insects.

A comparison was made of production estimates for the riffle and pool alone and for both combined (Table 2). Sampling the riffle only during the first cohort gave an underestimation of 45% compared to the value obtained for the riffle and pool combined, while sampling the pool only gave an overestimation of 22%. During the second cohort these percentages increased substantially. A 96% underestimate in the riffle and a 48% overestimate in the pool were obtained.

DISCUSSION

Production estimates

The annual production calculated for *T. atratus* (8.56 g/m^2 dry mass) is considerably higher than reported values for other mayfly species (0.12–4.45 g/m^2, Waters 1977). Higher production may be attributed to an abundance of organic food material derived from the lake located immediately above the study area and to high temperature during the growing season. Cushing (1963) also found a species of *Tricorythodes* occurring in larger densities below lake outflows relative to similar habitats above the lakes in the Montreal River, Saskatchewan, Canada. Similarly, *Tricorythodes minutus* was collected from a large boreal forest river just below the outflow of an oligotrophic lake in central Alberta (Clifford et al. 1973). In a later study McCullough et al. (1979) also found *T. minutus* to be fast growing with two to four generations per year and a cohort turnover ratio similar to that of *T. atratus*.
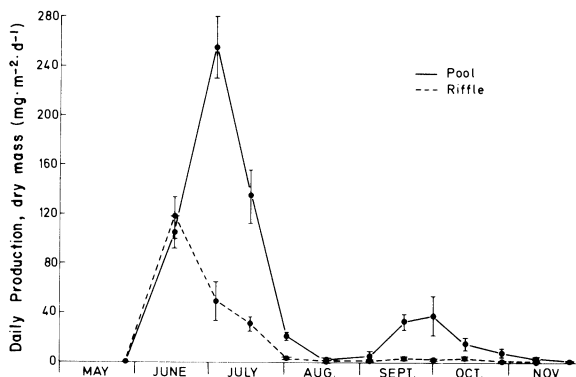

FIG. 4. Daily production curves used to calculate cohort and annual production rate estimates of *Tricorythodes atratus* nymphs collected from the Mississippi River. Vertical bars are ±SE of the mean.

In addition, food quality may have affected growth rates. McCullough (1975) reported a higher assimilation efficiency when *T. minutus* was fed a diet of diatoms instead of detritus. During the 3-yr study of the fast-growing *T. atratus* proportionately more diatoms than detritus were found in the digestive tract from early June to September (Hall et al. 1975).

P/$\bar{B}$ ratios

Waters (1977) concluded that cohort P/$\bar{B}$ ratios reported by various investigators have a mode of ≈5.0. *Tricorythodes atratus*, however, had cohort P/$\bar{B}$ ratios of 5.8 and 6.9. These higher ratios relative to the mode may have resulted from adults emerging at widely different sizes, thus decreasing the final population density relative to the initial, which would increase the cohort P/$\bar{B}$ ratio (Waters 1969). In both sexes of *T. atratus* emergence takes place any time after an organism attains a length of 4.5 mm (Fig. 3), but most males and females grow as large as 5.5 and 6.5 mm, respectively. Corresponding individual masses would also vary widely.

The P/$\bar{B}$ ratios for the first and second cohorts (5.8 and 6.9) were lower than the calculated G value (7.49). This difference is due to the assumption in the math-

TABLE 2. Estimates of cohort and annual mean standing stocks ($\bar{B}$), production rates (P), and P/$\bar{B}$ ratios for *Tricorythodes atratus* in the Mississippi River, 1972. Combined production rates were weighted according to area differences in the riffle and pool. All units are in dry mass.

	$\bar{B}$ (g/m^2)	Production rate (g/m^2)			P/$\bar{B}$ ratio
		Riffle	Pool	Combined	
First cohort	1.3	4.5	9.18	7.52	5.8
Second cohort	0.15	0.04	1.54	1.04	6.9
Annual	0.33	4.19	10.72	8.56	26

ematical model ($G = P/\bar{B}$) that the final population is zero at that point in time (i.e., all insects have emerged). However, the final size is generally >0 because organisms of different sizes are present. This fact produces a larger $\bar{B}$ for an extended period of time, resulting in smaller cohort $P/\bar{B}$ ratios relative to the calculated G value.

Drift dispersal and production

Differential distribution of nymph size classes on the stream bottom is not a new phenomenon. Other investigators have reported that larger immature individuals were most frequently taken downstream or at edges of streams in slower moving water (Macan 1957, Minshall 1967, Lehmkuhl and Anderson 1970, 1972). Thorpe (1973) found that the mean size of *Baetis rhodani* increased downstream; Macan (1957) found 63% of larger nymphs of this same species at the lowermost stations.

Differential drift rates of nymph size classes, likewise, are not new phenomena. Winterbourn (1974) reported that drift of the mayfly *Deleatidium* possibly had a large effect on production rate estimates in a riffle area due to the greater propensity of larger individuals to drift. He suggested that larger organisms drifting onto the study area from regions of quieter water upstream may have given an overestimation of production. Waters (1966) speculated that overestimation in production rates of *Baetis vagans* also may have resulted from larger organisms drifting down from upper reaches of the stream. This activity is not unique to mayflies. Studies by investigators on blackflies (Thorpe 1974), midges (Ward and Cummins 1978), stoneflies (Elwood and Cushman 1975, Siegfried and Knight 1978), and caddisflies (Resh 1977) have shown differential size dispersal.

Such spatial dispersion through time of different nymph size classes can have a pronounced effect on benthic production estimates. Species with a high propensity to drift can obscure the actual amount of biomass produced in an area and thus lead to inaccurate estimates of production, particularly since it is assumed that immigration and emigration balance each other. Bailey (1966) and Waters (1966) demonstrated the error in this assumption when they showed that drift of invertebrates off a riffle was greater than that drifting onto it and that fewer came out of a pool than drifted into it. Similarly, Dendy (1944) observed that pools serve as catching basins for stream drift. However, all studies published to date concerning production rate estimates of mayfly species in lotic environments have dealt with either a riffle (Waters 1966, Pearson and Kramer 1972, Waters and Crawford 1973, Zelinka 1973, Winterbourn 1974) or a pool (Tsuda 1972) but not with both during the same investigation. Quantitative data from this study show the importance of knowing life history and behavioral characteristics and of sampling more than one habitat.

Half-grown and larger immatures of *T. atratus* were present in the benthos and drift throughout most of the summer and thus accounted for continual movement to the pool. For species with synchronized egg hatching and emergence, drift dispersal may occur over a shorter period, e.g., during pre-emergence and emergence time or during density-independent flooding (Resh 1977, Siegfried and Knight 1978). For these synchronized emergents, movement of larger individuals nonetheless may interfere significantly with production estimates, but biomass loss will be easier to detect. For the majority of stream insects, however, extended recruitment of young is the rule rather than the exception (Hynes 1970).

A major ecological question relates to the function of drift of larger individuals. At high population densities size segregation may result from competition for habitat or food resources. Wilson (1975) speculated that larger animals can better utilize variable resources than smaller ones. For example, smaller immatures of *T. atratus* may have adequate food and protection in the riffle. However, larger nymphs increase at a faster rate than smaller ones (Hall 1975) and may forage more extensively during this growth period and drift to pools where there are greater detritus accumulations. Hildebrand (1974) speculated that *Tricorythodes* is a detritivore since it did not drift when offered a nondetrital food source in seminatural streams. Kovalak (1978a) felt that the occurrence of larger individuals in faster currents is probably due to differential habitat selection controlled by oxygen requirements, while the occurrence of larger individuals in slower currents is most likely due to differential growth. Cummins (1972) stated that organisms located in slower current regimes can channel more energy into growth because less energy is expended in maintaining position in the stream. In addition, the drifting of larger immatures may be linked to pre-emergence activity. As nymphs mature, they may actively seek regions of quieter water in which, presumably, emergence may take place more easily. Also it cannot be denied that both foraging and pre-emergence activity may be important.

From the results of this study an important point is apparent. To obtain accurate production estimates the investigation needs to take into account the life history and behavioral characteristics of the species to be studied. What is the distribution of the species? Does it prefer certain habitats over others within a stream? Does the species drift? If so, are different size classes predominant in the drift? Is the assumption valid that losses to and from an area equal each other, or does the species drift to certain microhabitats and aggregate there? Levin (1976) stated that the spatial aspect of the environment provides opportunities for movement

and habitat diversification which in turn allow the otherwise impossible coexistence of species. In some instances such opportunities are also available on an intraspecific level.

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