

The relation of drift to benthos density and food level in an artificial stream¹

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Abstract

The relationship between drift rates, benthos density, and food level for select taxa of stream invertebrates was studied in an artificial stream system to determine if drift is independent of or dependent on population density, and if food level affects drift rates. Two taxa were introduced in a range of densities at a single level of periphyton food, and the drift from each density was measured. Four taxa were introduced in a range of densities at low and high food levels, and the drift from each density at each food level was measured. The drift of all taxa, examined by simple linear regression analysis, at each food level was judged a density independent response to increasing population density. The drift of three taxa at a given density was significantly greater at the lower food level; it is suggested that increased activity in searching for food at the lower food level resulted in increased drift.

Drift, the downstream displacement of animals normally inhabiting eroding substrates, is a widespread and naturally occurring process in streams throughout the world. Waters (1972) provided an excellent review of published information on drift of stream insects, beginning with investigations of Needham (1928) and continuing through recent studies by Elliott (1971). My study was designed to determine the role of benthos density and food level as a step in clarifying the function of drift in the life cycle of stream invertebrates.

Müller (1954) suggested a general hypothesis concerning the function of drift in invertebrate population dynamics, which he called the "colonization cycle." As small larvae grow, competition for space results in increased drift and colonization of suitable downstream habitats. Drift in this sense then functions as a density dependent agent of population regulation. Upstream areas would not be depleted be-

cause at low densities drift would also be low. Müller also suggested upstream flight and oviposition of adults to compensate for downstream drift.

Waters (1966) extended the colonization cycle hypothesis and suggested that at the beginning of a given generation of insects, when carrying capacity of the stream bottom has not been reached, density and production of benthos may increase without competition. As population density approaches carrying capacity, increased competition results in increased drift as a means of population control. Drift may then be a function of production rate at or above the point where carrying capacity is reached, or a function of the degree to which the carrying capacity is exceeded.

Both hypotheses imply that drift is a density dependent agent of population regulation. The means of regulation is competition for space, food, or both. The relationship of drift to benthic density is not well understood. Waters (1972) stated that with few exceptions there is no direct relation of drift to benthic density; however, direct relationships between drift rate and density have been observed (Dimond 1967; Pearson and Franklin 1968; Pearson and Kramer 1972; Reisen and Prins 1972; Lehmkuhl and Anderson 1972). Hughes (1970) is the only investigator who reported a direct relationship between drift and food supply: in an artificial

¹This research was supported by the Office of Water Resources Research, Project A-040-Mich., administered by Michigan State University, East Lansing. The study is part of a thesis submitted to the Horace H. Rackham School of Graduate Studies, University of Michigan, in partial fulfillment of the requirements of the degree of Doctor of Philosophy.

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Fig. 1. Artificial stream system located on the grounds of the Pigeon River Trout Research Station, Michigan Department of Natural Resources, Otsego County, Michigan.

stream system drift of an amphipod was reduced when an artificial food source was added to the system. Since there are conflicting views regarding the relation of drift to density, my study was designed to examine this relation.

J. W. Elwood and L. D. Eyman reviewed the manuscript. F. F. Hooper, J. T. McCadden, J. W. Leonard, and F. C. Evans reviewed an earlier version. The use of the facilities at the Pigeon River Trout Research Station, Michigan Department of Natural Resources, is acknowledged.

Methods

An artificial stream system (Fig. 1) consisting of four channels each 14.4 m long by 0.30 m wide was built of plywood. Each channel had six equal sections joined by plywood plates and was supported by horses and jackscrews to allow manipulation of elevation. Two inlet boxes were

constructed such that two channels were fed by each inlet box. The inside of the channels and inlet boxes were coated with nontoxic polyester resin. Water from the Pigeon River was supplied to the channels by two electric pumps, one for each inlet box. Water entering each inlet box was screened with No. 471 Nitex. Gate valves were used to control the volume of water entering the inlet boxes. Each channel was adjusted to maintain an average current speed of 43 cm sec^{-1} and a depth of 15 cm. The Pigeon River, a moderately productive trout stream, originates in Otsego County, Michigan, and flows north about 104 km before emptying indirectly into Lake Huron through Mullet Lake. Benson (1953) and Hildebrand (1973) provide a more complete description of the Pigeon River.

Substrate holding boxes, with a surface area of 0.03 m^2 , were filled with rubble

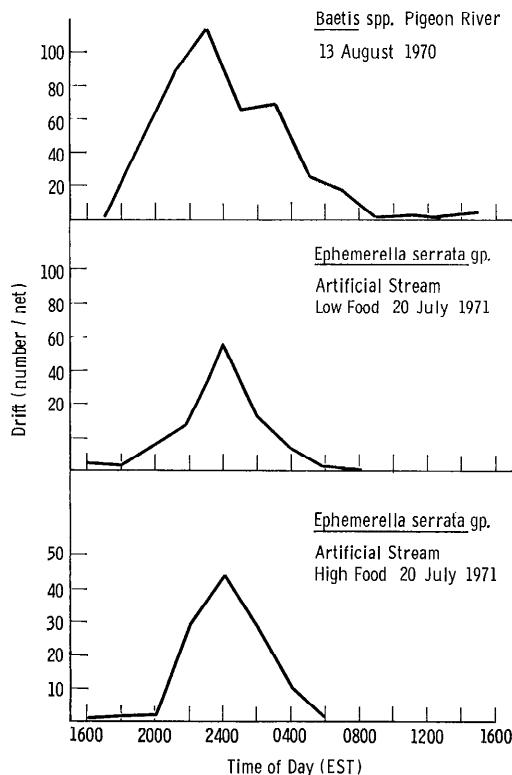


Fig. 2. Comparison of diel patterns of drift in the Pigeon River and artificial stream system (low and high food level) at comparable times of year.

substrate from the Pigeon River (average gravel diameter about 10.2 cm) and spaced evenly throughout the channels. The drift nets used had a rectangular opening of 930 cm², a bag length of 46 cm, and a mesh size small enough to retain the animals under study.

The first experiments investigated the relation between drift and density at a single level of periphyton food. Substrates denuded of invertebrates but with normal stream levels of periphyton were placed in the holding boxes. Animals were collected from the Pigeon River either by placing gravel containing invertebrates in a holding channel or by hand picking select taxa from the substrate and transporting them in insulated ice chests to the holding channel. An experimental run consisted of introducing a range of densities for select

Table 1. Summary of regression equations and statistics for regression of drift on density for artificial stream experiments at different food level regimes.

Taxon	Drift Equation	n	R ²	Sig
One food level experiments				
Simuliidae	D = 13.45 + 0.056 density	8	0.902	0.001
Two food level experiments				
Hydropsychidae	D = 0.28 density	6	0.903	0.001
Ephemerella serrata gp.	Low food D = 0.54 density High food D = 0.29 density	12	0.802 0.878	0.001 0.000
Ephemerella needhami	Low food D = 0.51 density High food D = 0.29 density	8	0.984 0.950	0.001 0.001
Hydropsychidae	Low food D = 0.36 density High food D = 0.22 density	8	0.997 0.960	0.001 0.001
Tricorythodes sp.	Low food D = 0.13 density High food D = 0.13 density	12	0.803 0.802	0.001 0.001

individual taxa in a series of substrate boxes and measuring the drift from each. Animals were introduced during the day, and drift was measured every 15 min until the animals became established in the substrate. Density in the substrate was calculated as the difference between the number of organisms introduced and the number drifting from the substrate during establishment. No drift recorded after 15 min indicated establishment. An experiment consisted of measuring the drift every hour from each substrate box during the night immediately following the introduction and establishment of animals.

A second class of experiments investigated the relation between density and drift at each of two periphyton food levels. A low food level was established by placing dried substrates in holding boxes in one channel and allowing about 3 days for periphyton colonization. A high periphyton food level was established by placing dried substrates in holding boxes in a second channel enriched with 500 ppb total nitrogen and 100 ppb total phosphorus, and allowing about 3 weeks for colonization and growth. Stock nutrient solutions were prepared from commercial agricultural fertilizers. The procedure for collection and distribution of animals was

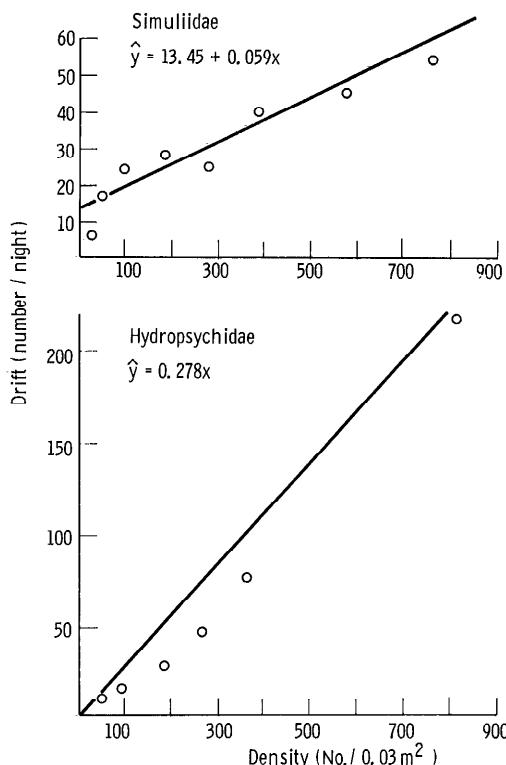


Fig. 3. Regressions of drift on density at a single food level for Hydropsychidae and Simuliidae, artificial stream studies.

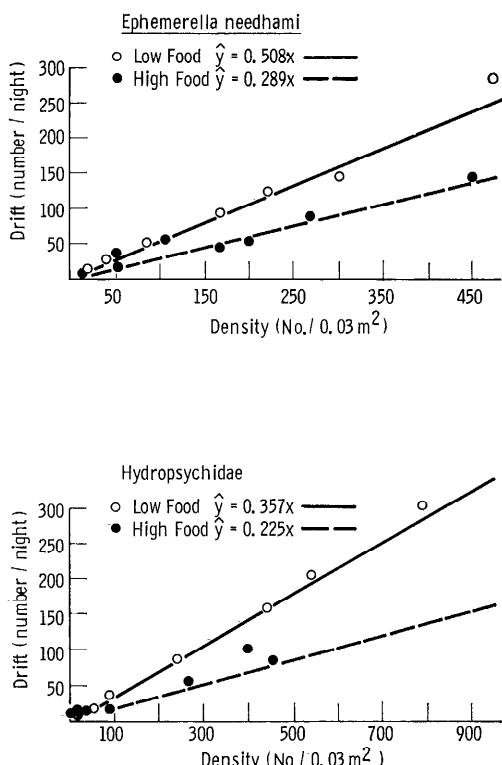


Fig. 4. Regressions of drift on density at low and high food level for *Ephemeral needhami* and Hydropsychidae, artificial stream studies.

the same. An experiment consisted of introducing animals in a range of densities at each food level and measuring the drift for the night immediately following introduction.

In the single food level experiments, the black fly (Simuliidae) and the caddis fly (Hydropsychidae) were used. In the two food level experiments, the relation of density and drift was investigated for the mayflies *Ephemeral needhami*, *Ephemeral serrata* gp., *Tricorythodes* sp., and the caddis fly. The stream channel experiments were conducted in fall and summer 1971 and summer 1972.

Two simple linear regression analyses were performed for all experiments. The first regression used drift rate (No. night⁻¹) as the dependent variable and substrate density (No. 0.03 m⁻²) as the independent variable. The second regression used log-

drift (No. night⁻¹) as the dependent variable. The best fit, linear or exponential, was determined on the basis of the highest R^2 . The intercepts for a regression were tested to determine if they were significantly different from zero. Statistical tests for observed differences in R^2 were not performed. In the two food level experiments, regressions were compared at each food level through analysis of covariance.

Drift was considered a density dependent agent of population regulation if the percentage of standing crop lost as drift increases with increasing standing crop. Drift is considered density independent and not a regulating mechanism if the percentage of standing crop lost as drift remains constant with increasing standing crop. Thus in this analysis, if the best fit of the regression of drift on density is linear, drift is acting in a density inde-

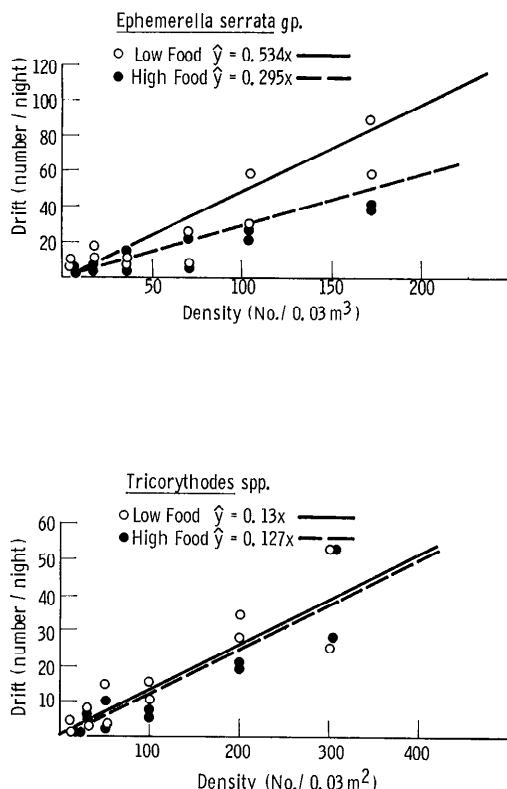


Fig. 5. Regressions of drift on density at low and high food level for *Ephemera serrata* gp. and *Tricorythodes* spp., artificial stream studies.

pendent fashion. If the best fit is exponential, drift is acting in a density dependent fashion.

Results

To determine whether animals used in the artificial stream experiments were drifting in diel patterns similar to those in the natural system, I extended the two food level experiment for *E. serrata* gp. over 24 hr and compared the diel pattern with a diel pattern of *Baetis* spp. observed in the Pigeon River at a similar time of year (Hildebrand 1973). A direct comparison of diel patterns for *E. serrata* gp. in the river and the artificial stream was not possible because this species emerged before the August drift sample in the Pigeon River. At both low and high food levels, *E. serrata* gp. exhibited a night active pat-

Table 2. F-statistic and level of significance for comparison of regressions of drift on density at low and high food levels, artificial stream experiments.

Taxon	Equality of regressions		
	F	n	Sig
<i>Ephemera serrata</i> sp.	7.11	24	0.010
<i>Tricorythodes</i> sp.	0.54	24	0.590
<i>Ephemera needhami</i>	32.67	16	0.001
<i>Hydropsychidae</i>	50.85	15	0.001

tern with a single peak between 2200 and 2400 hours. *Baetis* spp. exhibited a night active pattern with a major peak between 2200 and 2400 and a minor peak of 0400 (Fig. 2). With the exception of the minor peak at 0400 for *Baetis* spp., the diel patterns for the natural and artificial systems were similar. It was thus assumed that all animals in the channel experiments showed behavior patterns of activity similar to those in the natural system. Sampling only at night was judged adequate since more than 90% of the 24-hr drift occurred at night.

In the single food level experiments, the drift of Simuliidae and Hydropsychidae was judged a linear function of population density (Table 1; Fig. 3). The calculated regression lines for these taxa were significant at the 0.01 level (Table 1).

In the experiments with two food levels, drift of *E. serrata* gp., *Tricorythodes* spp., *E. needhami*, and *Hydropsychidae* was judged a linear function of population density at both low and high food levels (Table 1; Figs. 4 and 5). The calculated linear regression for each of these taxa at low and high food levels was significant at the 0.01 level (Table 1). For *E. serrata* gp., *E. needhami*, and *Hydropsychidae* the regressions of drift on density at low and high food levels were significantly different at the 0.01 level. At a given density, the drift for these taxa was greater at the lower food level (Table 2). For *Tricorythodes* spp. the regressions of drift on density at the low and high food levels were

not significantly different at the 0.05 level (Table 2). At a given density for this taxon, drift at the low and high food level was not significantly different.

Discussion

Under the controlled conditions in the artificial stream system, the drift of all taxa examined was a linear function of population density. Drift was judged density independent (Table 1; Figs. 3-5) over a range of densities that reached or exceeded the intraspecific densities of these taxa in the Pigeon River (Hildebrand 1973). The linear relation of drift to density observed suggests that intraspecific competition for space is not a mechanism resulting in increased drift and population regulation for the taxa examined. Drift appeared to be a function of probability of dislodgment from the substrate, which was not affected by density.

The drift of *E. serrata* gp., *E. needhami*, and Hydropsychidae was significantly greater at the low than at the high food level (Table 2; Figs. 4 and 5). This suggests that increased activity in foraging for food at the low food level results in increased drift and conforms to the suggestions of Elliott (1967) and the findings of Hughes (1970) for *Gammarus* sp. The food habits of *E. serrata* gp., *E. needhami*, and Hydropsychidae were not determined; however, *Ephemerella aestiva*, *Ephemerella dorthea*, *Ephemerella subvaria*, and *Ephemerella* spp. feed on algae (Coffman 1967; Minckley 1963; Chapman and Demory 1963). I have assumed that the two *Ephemerella* taxa examined in this study use periphyton directly as a food source. Hydropsychidae in nature are primarily filter feeders on various types of algae (Minckley 1963; Chapman and Demory 1963). At least one species has been reported to be largely carnivorous (Coffman et al. 1971). During the short duration of my experimental runs, Hydropsychidae did not establish the nets that they use in filter feeding; I have assumed that they feed directly on periphyton in the absence of nets.

The drift of *Tricorythodes* sp. was not

influenced by food level (Table 1; Fig. 5). The explanation for this may be that *Tricorythodes* sp. is primarily a detritivore and does not use periphyton directly as a food source. Koslucher and Minshall (1973) report that during summer up to 85% of the gut contents of *Tricorythodes minutus* consists of detritus.

The relation observed between drift and food level suggests that intraspecific competition for food may be a mechanism resulting in increased drift and population regulation. Since only two food levels were tested, it was not possible to determine if drift was related to food level in a density dependent or density independent fashion. If the carrying capacity of a stream system for benthic invertebrates is related to available food, the observed response of drift to food level supports the hypothesis of Waters (1966) that drift is a function of the degree to which carrying capacity is exceeded.

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Submitted: 20 March 1974

Accepted: 10 June 1974