

SOME ECOLOGICAL RELATIONSHIPS OF THE INVERTEBRATE DRIFT IN PRATERS CREEK, PICKENS COUNTY, SOUTH CAROLINA¹

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Abstract. The role of organic drift in the ecology of a southern, upper Piedmont stream was evaluated from September 1967 to August 1968. By sampling for a 24-hr period each month, data on the diel and monthly fluctuations of the drift were obtained. Chemical and physical analyses of the water were made to evaluate the role of selected abiotic variables in the ecology of the drifters.

Community biomass could not be estimated by drift because fluctuations in the standing crop were not significantly correlated with fluctuations in the drift rate. With the exception of *Ephemera* sp. the drifters did not respond in a density-dependent fashion to benthic population increases. Drift seemed to be initiated by pupation or emergence activity.

The diel drift for the majority of the benthos examined was decidedly negatively phototactic. Pronounced crepuscular activity was observed for most of the hemimetabolous forms with a consistent midnight depression of activity.

INTRODUCTION

The downstream drift of lotic invertebrates has recently received much attention by stream biologists and has been well reviewed by Bishop and Hynes (1969) and Waters (1969, 1972). Two major theories have arisen quantitatively relating drift to benthic density: (1) Invertebrate drift is density dependent where benthic densities must exceed a certain threshold level (i.e., carrying capacity) before behavioral drift is initiated. Thus by monitoring the volume of drift, secondary lotic productivity may be estimated (Waters 1961, 1962a, 1965, 1966, 1969, Dimond 1967, Pearson and Franklin 1968). (2) Invertebrate drift is density independent related to growth and life history phenomenon where drift rates are highest prior to pupation and emergence (Logan 1963, Hughes 1966a, 1966b, Elliott 1967a, 1967b, 1968, 1971, Elliott and Minshall 1968).

Certain abiotic parameters have been shown to influence drift rates. Increasing or decreasing discharge and increasing water temperatures have been positively correlated with drift. Most drifters demonstrate a marked nocturnal periodicity; however, Müller (1963) and Waters (1968) have shown that temperature may alter expected drift patterns. These effects have been reviewed by Waters (1972).

To date, few investigations concerning drift have been reported for warm-water areas such as the southern Appalachians, and only a few studies have considered variations in the drift rates of the entire

community for a year-long period. The main objective of this study was to evaluate the role of drift in the bionomics and standing crop of the dominant invertebrates of a South Carolina Piedmont stream.

THE STUDY AREA

Praters Creek is a typical southern Piedmont epirhithron located in southwest Pickens County, South Carolina. The study area consisted of a 50-m portion of the creek composed of a series of solid granite outcrops interspaced with pools and rocky riffles. This portion of Praters Creek drains an area of mixed pastureland and deciduous vegetation; however, livestock were not pastured for 200 m upstream from the study area, so organic pollution and "cattle-induced" drifting were assumed to be negligible. The sunlit portions of the stream bottom were covered with dense mats of *Podostemon ceratophyllum* Mitch. The aquatic microphytic vegetation has been presented previously by Reisen and Spencer (1970).

To further describe the study area, chemical and physical analyses of the water were conducted. Praters Creek was found to have a mean pH of 6.9 (6.6–7.3), an alkalinity (methyl orange) of 23.3 (12.0–32.0) mg/liter, a total nitrate concentration of 0.13 (0.10–0.16) mg/liter, and an orthophosphate concentration of 0.29 (0.05–0.50) mg/liter. The means for the physical parameters were: current velocity 0.805 (0.610–0.950) m/sec, and discharge 0.104 (0.850–0.120) m³/sec. The monthly fluctuations in rainfall, and air water temperatures, and dissolved oxygen concentrations are presented in Table 1.

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TABLE 1. The abiotic parameters of Praters Creek, Pickens County, South Carolina, September 1967–August 1968 (ranges in parentheses)

Date	Total monthly rainfall (cm)	Mean daily temperature (°C)		Mean daily dissolved oxygen (mg/liter)	Moon phase rating (0–3)	Total hours daylight
		Air	Water			
22 Sept 67	1.13	14 (7–26)	14 (11–17)	8.9 (8.5–9.5)	2.0	12.2
19 Oct 67	6.93	9 (3–17)	8 (5–10)	9.8 (9.3–10.5)	3.0	11.5
19 Nov 67	6.53	11 (6–17)	5 (4–6)	10.2 (9.8–10.5)	3.0	10.3
22 Dec 67	20.63	8 (2–14)	5 (2–7)	10.2 (9.9–10.6)	2.0	9.8
19 Jan 68	13.95	6 (–3 to 14)	3 (0–6)	10.3 (9.5–10.7)	2.5	10.2
18 Feb 68	2.54	7 (–1 to 14)	7 (5–9)	10.8 (10.3–11.4)	2.5	11.1
15 Mar 68	10.14	9 (7–12)	10 (10–11)	10.4 (10.2–11.0)	2.5	11.9
12 Apr 68	6.91	13 (3–26)	14 (11–17)	9.7 (9.3–9.9)	3.0	12.9
10 May 68	2.90	19 (16–23)	17 (17–18)	9.0 (8.9–9.1)	3.0	13.9
10 June 68	16.38	24 (18–29)	18 (17–19)	8.7 (8.5–8.9)	3.0	14.5
8 July 68	9.75	23 (20–26)	19 (18–20)	8.7 (8.4–9.0)	3.0	14.4
6 Aug 68	28.58	24 (21–31)	21 (19–23)	8.3 (7.9–8.6)	2.5	13.8

METHODS AND MATERIALS

Sampling periods were chosen at 4-week intervals from 22 September 1967 through 6 August 1968. Samples were obtained every 2 hr during a 24-hr period. Each 24-hr period was preceded by at least 2 days of fair weather to ensure that catastrophic drift had subsided (Waters 1964, 1965).

Drift samples were obtained with a portable modification of the sampler described by Waters (1962a). Nets were 30 cm square and 76 cm long and made of Nitex netting with nine meshes/cm. Duplicate nets were placed side-by-side on a flat portion of the granite outcrop covered with *P. ceratophyllum*. This segment of the stream was approximately 10 m wide with an average depth of 12 cm. Since the samplers were placed in the deepest portion of the stream, about one-half the total discharge passed through the nets. Because the stream never exceeded a depth of 18 cm during the sampling periods, the entire water column was always sampled. Water and air temperatures were measured and samples for dissolved oxygen (alkali-azide modification of the Winkler method) were collected near the drift nets every 2 hr. Other measurements included total rainfall between samples (used as an index of discharge fluctuation as described by Anderson and Lehmkühl (1968)), moon phase (rated 0–3 with 0 being a new moon and 3 being a full moon), and total hours of daylight between sunrise and sunset. Average 24-hr values for these variables are summarized in Table 1. Rainfall data were obtained from the Clemson University Agricultural Experiment Station located at Clemson, South Carolina, about 13 km south of the study area (Kish and Landers 1968).

Biomass/m² (standing crop) on the outcrop was estimated monthly by duplicate Surber samples using a sampler 30.5 cm on a side with a netting size of seven meshes/cm. By counting the numbers of individuals per species, these samples were also used as

estimates of the benthic density and were expressed as numbers/m².

Drift and Surber samples were fixed in the field with 5% formalin and then taken back to the laboratory for processing. Here samples were hand-sorted using a NaCl modification of the flotation method described by Anderson (1960). Specimens were preserved in 80% ethyl alcohol and later identified, counted, air-dried, and weighed.

Duplicate bottom samples along the banks and in the riffles were taken with a seine (eight meshes/cm) using a modification of the "kick" method described by Hynes (1961). Owing to the error inherent in this method, samples were sorted in the field, combined, and expressed as a relative abundance (total specimens collected in four "kick" samples along the banks and in the riffles). These areas were sampled primarily to ascertain the presence of fauna collected in the drift but not found on the outcrop.

Drift rates were expressed as numbers of grams of invertebrates per taxon collected in the entire water column passing by the width of stream bottom sampled (standardized to a meter base) per specified time increment in hours. Since the entire water column was sampled and since discharge was not measured for each 2-hr sample, drift rates were not expressed as numbers or biomass per volume of water per time increment. Benthic density was expressed as numbers or biomass of invertebrates/m² of bottom sampled.

Least-square, stepwise, multiple regression analyses were used to objectively and statistically select the best set of significant variables (Draper and Smith 1966). Inherent in this technique was the rejection of certain independent variables exhibiting significant multicollinearity. Since many biological systems respond in a density-dependent fashion, log₁₀ transformations of the dependent variables were used to improve the overall fit as well as to control the variance

TABLE 2. Variations in the total drift, autochthonous drift, and standing crop in Praters Creek, Pickens County, South Carolina, September 1967–August 1968

Date	Total drift (g/m per 24 hr)	Autoch. drift (g/m per 24 hr)	Standing crop (g/m ²)
22 Sept 1967	0.186	0.057	4.969
19 Oct 1967	0.289	0.128	19.340
19 Nov 1967	0.179	0.110	10.424
22 Dec 1967	0.273	0.173	5.540
19 Jan 1968	0.087	0.065	3.054
18 Feb 1968	0.124	0.037	7.191
15 Mar 1968	0.302	0.274	3.175
12 Apr 1968	0.262	0.060	15.742
10 May 1968	0.407	0.159	22.894
10 June 1968	0.261	0.128	27.713
8 July 1968	0.215	0.089	15.165
6 Aug 1968	0.326	0.171	18.447

and fulfill the basic assumption of linearity (Draper and Smith 1966, Pearson and Franklin 1968). If the \log_{10} transformation did not improve the overall fit, the relationship was considered arithmetic and thus density independent. As defined by Odum (1959), density-dependent factors are those factors whose effects vary with increasing density while density-independent factors are those which exhibit a constant effect regardless of the density. In this paper density-dependent factors will be those which elicit a curvilinear or geometric response while density-independent factors will elicit a straight-line or arithmetic response. Thus it will be possible for drift rates to fluctuate in a density-independent or a density-dependent fashion with increasing benthic density. The level of significance used in all analyses was 0.05.

RESULTS AND DISCUSSION

A regression analysis of the total by-weight 24-hr drift (combined autochthonous and allochthonous components) was performed with standing crop, relative abundance, air temperature, water temperature, rainfall, and moon phase designated as the independent variables (Tables 1 and 2). No significant regression was found. A similar analysis was conducted using the total by-weight 24-hr autochthonous drift as the dependent variables, but again the regression was nonsignificant. By inspection, it appeared that intergeneric differences in seasonal activity periods and drift patterns yielded the nonsignificant regression. Since the regression of autochthonous drift on standing crop was nonsignificant, drift could not be used to estimate the standing crop of the benthos in Praters Creek.

Since the regression of total aquatic drift was not significant, each taxon was considered separately. The results of these analyses are summarized in Table 3. Regression analyses of individual taxa were performed where drift by taxon (expressed as numbers/m per 24 hr) was the dependent variable and drifting

adults, benthic density, relative abundance, rainfall, water temperature, moon phase, and total hours daylight were the independent variables (Table 3). Significant multicollinearity among temperature, total hours daylight ($r = 0.907$), and dissolved oxygen ($r = -0.080$) prevented these variables from being included in any of the regression expressions where temperature was significant. Moon phase never exhibited a significant effect. From past studies (Tanaka 1960, Waters 1962b, Anderson 1966, Elliott 1967b, Holt and Waters 1967, Elliott and Minshall 1968, and others) light intensity appears to be significant. A more accurate measure of light may have improved the correlation of this variable, adding it to the subset of significant variables. In addition, 2-hr light intensities may have shown a significant negative regression with the diel drift patterns. By comparing total day length, dissolved oxygen, and water temperature on a month-to-month basis with the dependent variables, temperature more frequently improved the fit of the regression expression.

Chironomidae (Diptera) larval drift rates showed a significant positive arithmetic response to increases in the drift rates of the imagoes (Fig. 1I, Table 3). This suggested that the drift rate of the immatures increased as pupation activity progressed. A short pupation period would allow both the late pupating larvae and the early emerging adults to be collected simultaneously (Reisen and Fox 1970). The diel periodicity of the larval drift for the months of March, April, and May are presented in Fig. 2A. Since larval drift was highest, these months were presented as "best" examples for with increased numbers of specimens collected, point estimates would be more accurate. It would appear that the immature chironomids were crepuscular drifters just as the adults are characteristically crepuscular fliers. This rhythm did not appear to be strongly fixed because the March pattern was dissimilar to the April and May patterns. Perhaps this was because the chironomid population was composed of the younger instars, since fewer adults were collected in March; or it might have been due to the presence of more than one taxon in the drift, each having a different drifting behavior.

Simuliidae (Diptera) larvae showed a significant positive logarithmic regression with increasing water temperature (Fig. 1B and 1C, Table 3). The low multiple correlation coefficient ($r = 0.577$) was due primarily to the population decline in May. Apparently, most of the larvae emerged in April, reducing the larval density, and thus the numbers of larvae in the drift. A second emergence occurred in August (Reisen and Fox 1970). April and August were chosen to represent the diel periodicity of simuliid drift due to the larger numbers of larvae drifting during those months. Simuliidae did not display a

TABLE 3. A summary of the stepwise multiple regression analysis for each of the dominant drifters in Praters Creek, Pickens County, South Carolina. (Only the slope values for the significant variables are presented.)

Taxa	Transformation dependent variable	Intercept	Adult drift rate (no./m per 24 hr)	Benthic density (no./m ²)	Relative abundance (no. insects)	Total rainfall (cm/month)	Mean water temp (°C)	Multiple correlation coefficient
Diptera								
Chironomidae	none	93.478	0.0992	—	—	—	—	0.81268
Simuliidae	log ₁₀	24.180	—	—	—	—	0.0679	0.57785
<i>Antocha</i> sp.	log ₁₀	83.630	—	—	—	—	-0.0751	0.68124
Ephemeroptera								
<i>Baetis</i> spp.	none	-75.636	2.0573	—	6.9352	—	—	0.90101
<i>Ephemerella</i> sp.	log ₁₀	6.567	—	0.0009	—	—	—	0.59452
<i>Stenonema</i> sp.	log ₁₀	10.120	—	—	—	0.0290	—	0.60452
Plecoptera								
<i>Nemoura</i> sp.	none	7.253	—	1.5058	—	—	—	0.98526
<i>Leuctra</i> spp.	none	19.412	1.1664	—	—	—	—	0.63545
Capniinae	none	0.664	—	—	2.2684	—	—	0.99469
Trichoptera								
<i>Hydropsyche</i> spp.	none	-51.369	—	—	0.0831	2.8638	3.0873	0.85231

distinct diel periodicity for the sampling periods considered (Fig. 2B). The regression of larval drift on water temperature for specified 24-hr periods was nonsignificant in contrast to the findings of Pearson and Franklin (1968), who included water temperature in their subset of predictive variables.

Antocha (Diptera: Tipulidae) showed a significant negative geometric response to increasing water temperature (Fig. 1D, Table 3). High numbers of larvae drifting in the colder months were related to increased abundance prior to a probable March or early-April emergence. Adults were never collected in the drift, so this variable could not be critically evaluated. This type of cycle has been previously suggested by Hynes (1961) and Minshall (1967). Unlike the drift of the other two dipterans considered, *Antocha* exhibited a fairly well-defined nocturnal drift patterns with a peak drift period occurring between 11:30 PM and 3:30 AM (Fig. 2C). No midnight depression during increased moonlight was observed, which contradicts the findings of Anderson (1966) but supports those of Elliott and Minshall (1968).

Hydropsyche (Trichoptera: Hydropsychidae) exhibited a significant positive arithmetic regression with relative abundance, rainfall, and water temperature (Fig. 1A, 1B, and 1G, Table 3). In part, drift may have been related to larval movements prior to pupation, as was indicated by the significance of the relative abundance variable (samples taken near the stream banks have more pupal cases than samples taken in the riffle areas). The significance of rainfall apparently was related to habitat disturbance during the periods of greater discharge prior to the sampling periods. Increasing temperatures were accompanied by increases in the drift. The diel drift peak occurred between 9:30 PM and 11:30 AM during the month of October (Fig. 2D).

A regression analysis performed on the drift rates of *Baetis* (Ephemeroptera: Baetidae) suggested that

the best set of predictive variables were the adult drift rate and the relative abundance of naiads along the banks and in the riffles (Fig. 1F, Table 3). Benthic density and relative abundance were not correlated ($r = 0.114$), so that the lack of significant benthic density was not due to multicollinearity, but rather to the microhabitat selection by the naiads. These naiads are negatively phototactic and positively thigmotactic and seem to prefer the rock riffles and the undercut banks of the stream to the more exposed outcrops.

Baetis naiads moved to the shallows prior to emergence and this may have increased their numbers in the drift. *Baetis* responded to increasing relative abundance in a density-independent fashion; consequently, the productivity of this species could not be predicted by drift as suggested by Dimond (1967) and Waters (1966). For accurate prediction of *Baetis* productivity, drift would have to respond in a density-dependent fashion where the drift rate increased geometrically after the carrying capacity of the stream was exceeded. The drift pattern of *Baetis* in Praters Creek seemed contradictory to the findings of Waters (1962a, 1966) who related baetid drift with benthic density and Pearson and Franklin (1968) who included dissolved oxygen, water temperature, and current velocity in their set of predictive variables. The synchronization of the drifting naiads and adults seemed to substantiate the findings of Elliott (1967b) and Hughes (1966a, 1966b); they suggested that only the older naiads drift since they have greater dorsal-ventral orientation difficulty due to a progressively increasing impregnation of the ocelli with chitin and mineral salts. During October and March, diel *Baetis* drift showed both crepuscular and nocturnal peaks (Fig. 2F). This two-peak pattern was similar to the findings of Holt and Waters (1967); however, they found that the highest peak occurred just after sunset while in this study the

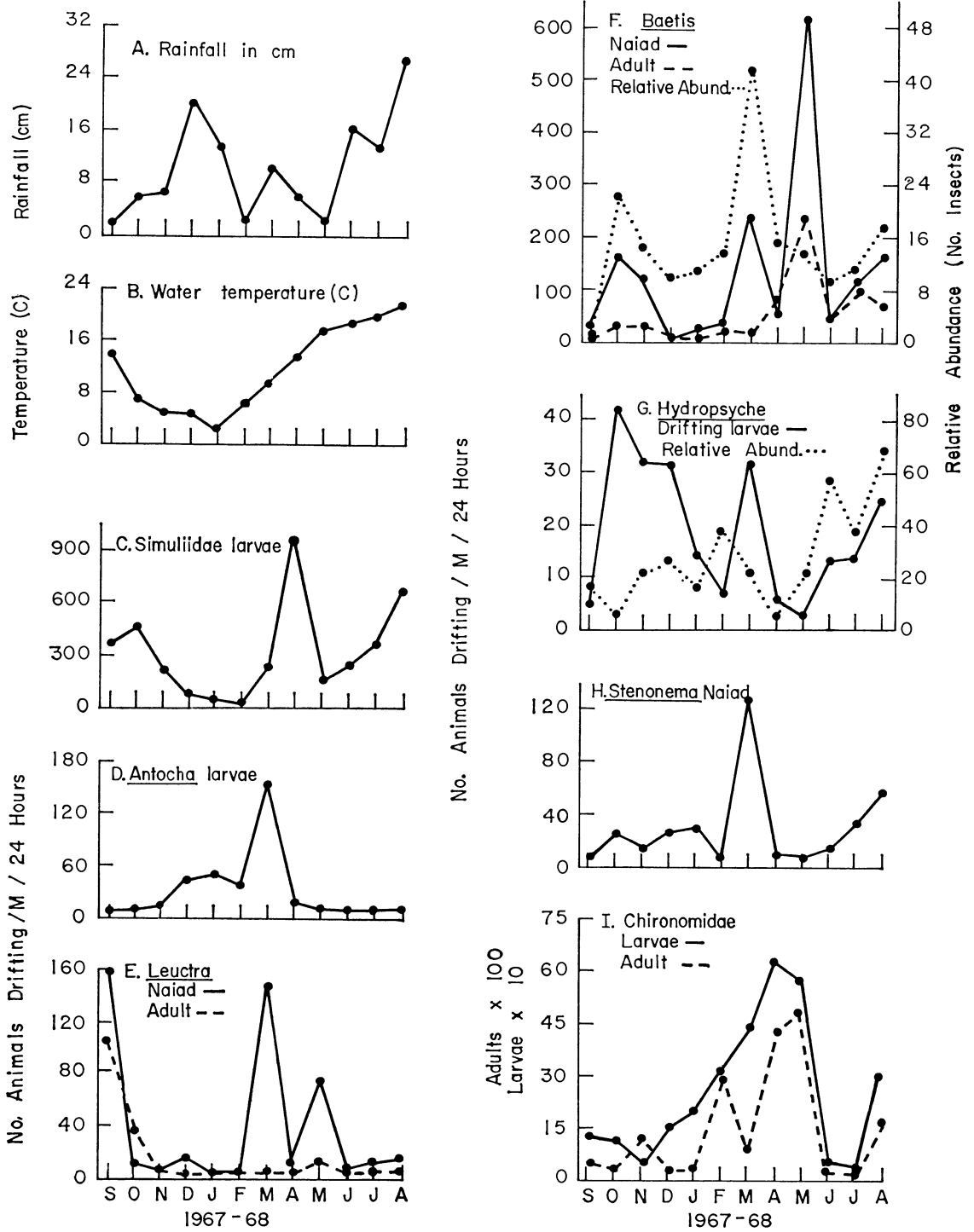


FIG. 1. The monthly fluctuations of rainfall (cm), water temperature (°C), and the drift rates of lotic insects (no. animals/m per 24 hr) in Praters Creek, Pickens County, South Carolina, September 1967–August 1968.

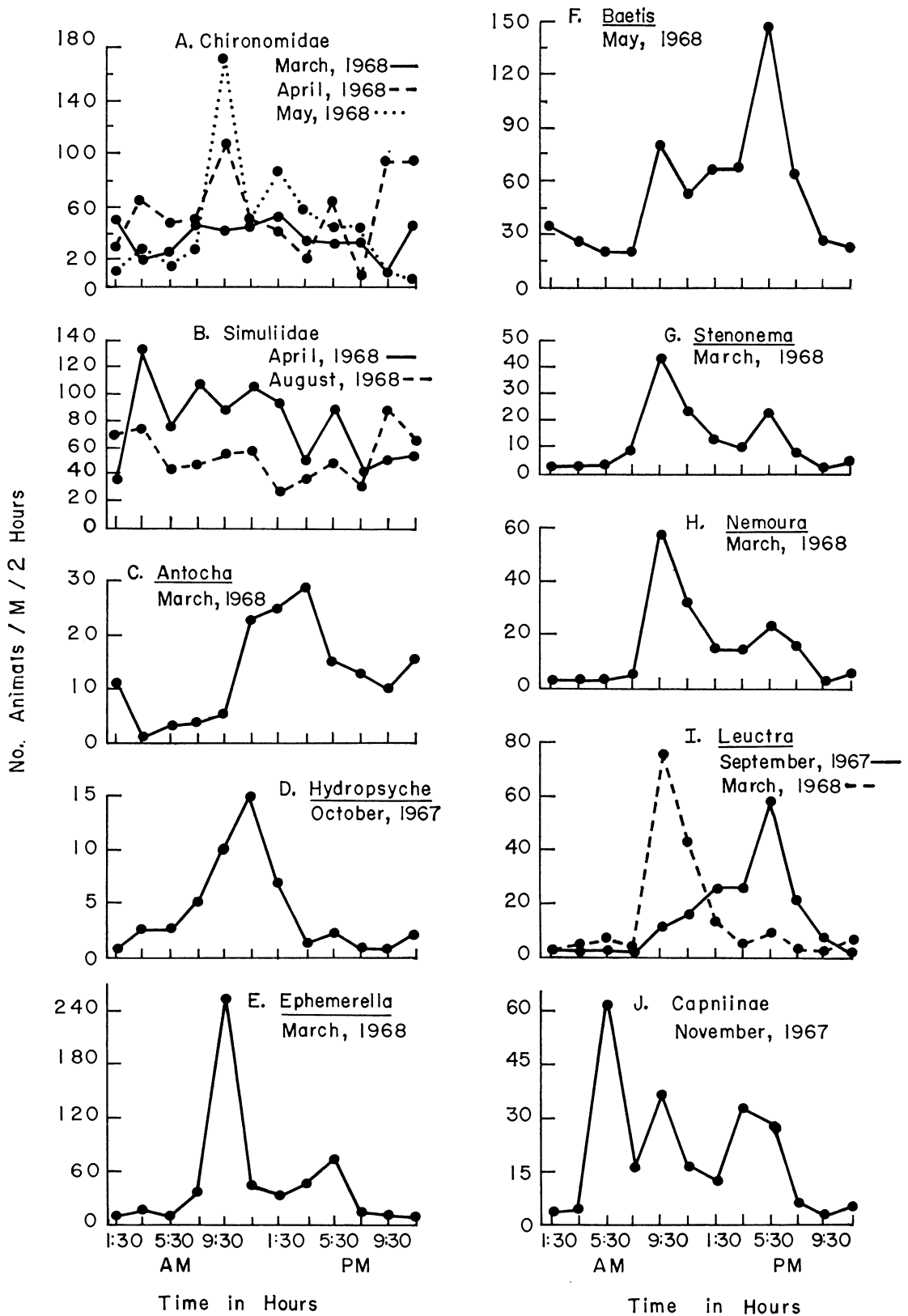


FIG. 2. The hourly fluctuations of the drift rates of lotic insects (no. animals/m per 2 hr) during selected periods, September 1967–August 1968.

greatest drifting occurred between 1:30 AM and 3:30 AM.

Ephemerella (Ephemeroptera: Ephemerellidae) exhibited a positive logarithmic response to increasing benthic density which substantiated the findings of Waters (1962a, 1966) and Dimond (1967), but was different from those of Elliott (1967a, b) and Elliott and Minshall (1968) (Fig. 3C, Table 3). Benthic density and thus productivity (as defined by Dimond 1967) could be predicted by drift. The lag between the drift rate and the benthic density (e.g., March–April) may have been due to the colonization of the outcrop by drift. Waters (1964) reported that experimentally denuded stream sections were recolonized by ephemeropteran drift. The diel drift pattern for *Ephemerella* was almost identical to the *Baetis* patterns described by Holt and Waters (1967); the greatest drift came after sunset (between 7:30 PM and 9:30 PM) and immediately before dawn (between 3:30 AM and 5:30 AM) with a midnight depression (Fig. 2E).

Stenonema (Ephemeroptera: Heptageniidae) exhibited a positive logarithmic response to increasing rainfall between sampling periods (Fig. 1A and 1H, Table 3), which indirectly reflected the influence of increased discharge and corresponding habitat disturbance. Since samples were never taken during spates or in the rain, the direct effect of rain storms, and thus discharge increases, was not ascertained. Increased drift rates in March and August suggested pre-emergence activity patterns similar to those of *Baetis*. The diel periodicity of *Stenonema* (Fig. 2G) closely paralleled the drift pattern of *Ephemerella* (Fig. 2E).

Paraleptophlebia and *Habrophlebia* (Ephemeroptera: Leptophlebiidae) were collected in large numbers, but their drift patterns could not be statistically correlated to any of the biotic or abiotic variables considered.

For the Plecoptera, none of the abiotic variables considered exhibited a significant regression. *Nemoura* (Plecoptera: Nemouridae) showed a positive arithmetic response to increasing benthic density (Fig. 3A, Table 3). Relative abundance also showed a similar pattern and exhibited a high correlation with both drift ($r = 0.983$) and benthic density ($r = 0.997$). Significant multicollinearity between relative abundance and benthic density prevented relative abundance from being included in the overall regression expression; however, simple regression with the naiad drift was significant. These responses were all arithmetic, suggesting a density-independent response. It appeared that in Praters Creek *Nemoura* had one generation per year with an emergence in late March or early April. The diel periodicity of the drift of *Nemoura* for March (Fig. 2H) was similar to the *Ephemerella* pattern (Fig. 2E).

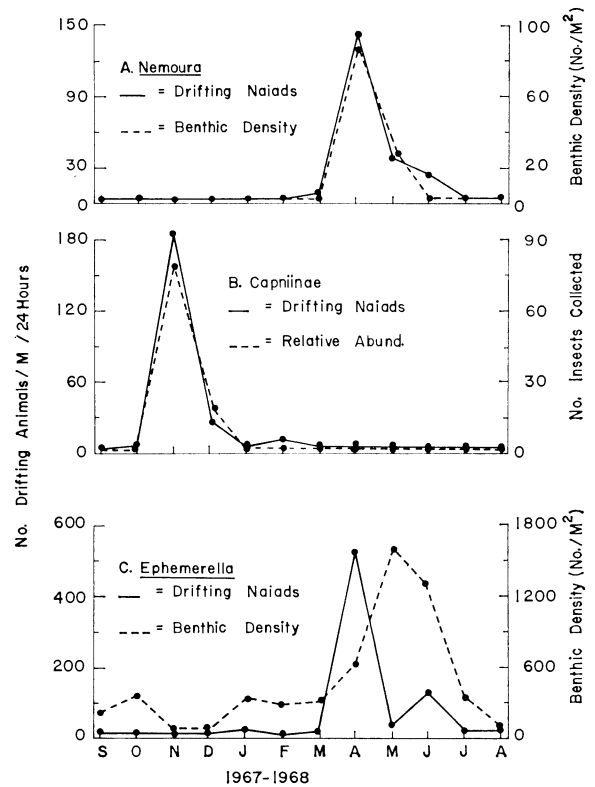


FIG. 3. The monthly fluctuations of the drift rates (no. animals/m per 24 hr), benthic densities (no. animals/m²) and relative abundance (no. insects collected) of the lotic insects of Praters Creek, Pickens County, South Carolina, September 1967–August 1968.

Leuctra (Plecoptera: Nemouridae) naiad drift showed a significant positive arithmetic regression with the imago drift, corresponding to the findings of Elliott (1967c) (Fig. 1E, Table 3). Due to the presence of more than one species of *Leuctra* in Praters Creek naiad drift showed three major increases during September, March, and May (McCaskill and Prins (1968) collected five species of *Leuctra* from this portion of South Carolina). These pulses paralleled emergence activity. The September diel pattern was similar to the *Baetis* pattern (Fig. 2F); however, in March the time of highest drift shifted from early evening to early morning (Fig. 2I).

Naiads of the genera *Allocapnia* and *Nemocapnia* (Plecoptera: Nemouridae) were taxonomically inseparable in the early instars and subsequently were pooled into the subfamily Capniinae. The drift of this group showed a density-independent response to increasing relative abundance (Fig. 3B, Table 3). Members of this group were rarely collected on the outcrop, but at times were abundant along the banks and in the riffles. The diel drift pattern of November was similar to *Ephemerella* except for an unexplained depression at 7:30 PM (Fig. 2J).

The drift of *Isogenus* and *Isoperla* (Plecoptera:

Perlodidae) was not significantly correlated with any of the biotic or abiotic variables considered although they were repeatedly taken in the drift.

Fluctuations in the overall standing crop of Praters Creek could not be predicted using organic drift, where drift was considered to be the biomass produced exceeding the carrying capacity of the stream segment considered. Fluctuations in the total and the autochthonous drift were not correlated with fluctuations in the standing crop. The benthic density of *Ephemere* sp. could be accurately predicted from a log₁₀ transformation of the drift rate and was thus considered density dependent. For the rest of the benthos considered, drift seemed more closely correlated to emergence or pupation activity than to benthic density. High drift rates of the immature forms were often followed by decreases in the benthic densities, or relative abundance of the same species, or both during the next monthly sampling period. This, coupled with a frequently observed high incidence of drifting imagoes, seemed to indicate a relationship between drift and emergence or pupation. Since different variables seemed more important in the drifting of the different genera, no generalization concerning the entire benthic community could be postulated.

Diel periodicity of the holometabolous insects was generally less pronounced than that of the hemimetabolous insects. Hemimetabola drift seemed to correspond to the diel *Baetis* pattern described by Holt and Waters (1967), although the amplitude of the evening and morning peaks seemed to vary. At least in one instance, *Leuctra*, peak diel activity periods shifted from evening to morning during different seasons. Although the moon phase variable was consistently nonsignificant from month to month, a midnight depression in drifting activity was observed for most of the naiads. More accurate measurement of available moonlight may have increased the importance of this variable.

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