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SOME FACTORS AFFECTING DRIFT RATES OF *BAETIS* AND SIMULIIDAE IN A LARGE RIVER

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Abstract. Effects of eight factors on the drift rates of *Baetis* nymphs and Simuliidae larvae were tested with multiple regression analyses. Illumination, population density of all other organisms and temperature had significant influences on drift rates of both organisms. Turbidity and water-level fluctuations were related to changes in drift rates indirectly through influence upon light penetration and population density, respectively. Dissolved-oxygen concentration, calendar date, and depth of water at the sample site did not clearly affect drift rates of either organism. In areas where population densities were high, the eight factors tested accounted for 65% to 81% of the variability observed in drift rates. Maximum drift rates were 170×10^6 *Baetis* sp. nymphs (63.2 kg) and 10.9×10^6 Simuliidae larvae (5.4 kg) per day.

Introduction

Recent investigations have emphasized the magnitude of invertebrate drift in streams and its interaction with population density (Müller 1954; Waters 1961, 1966). Waters (1965) divided total observed drift into three classes: 1) "catastrophic" drift due to an unusually severe physical disturbance of the environment such as flooding, 2) "constant" drift due to ordinary accidental dislodgement, and 3) "behavioral" drift due to an active response by the individual organism. Behavioral drift is influenced by light intensity in several organisms (Tanaka 1960; Waters 1962; Müller 1963). Waters (1966) has also suggested that behavioral drift is directly related to production in excess of the carrying capacity of the stream bed.

Müller (1966) found that drift rates of *Gammarus* varied directly with temperature, and that drift rates of *Baetis* and Simuliidae increased following preemergence and prepupation activities, respectively.

The objectives of this study were: 1) to measure simultaneously the drift of two organisms, an unidentified species of *Baetis* (Ephemeroptera) and Simuliidae larvae (Diptera) and several environmental factors known or suspected to influence drift rates, and 2) to determine how much of the variability observed in the drift rates of these two organisms could be accounted for by the factors tested. It was necessary that we have an idea of how much of the variability could be accounted for to carry out effectively future drift-rate and production studies.

Methods

The study was conducted on the Green River, Utah and Colorado, immediately below Flaming Gorge Dam during the summers of 1964 and 1965. Sampling stations (I–IV) were established at Little Hole (11.7 km below Flaming Gorge Dam = 11.7 kmBD), Carr Ranch (68.7 kmBD), Echo Park (103.9 kmBD), and Island Park (125.5 kmBD; Fig. 1). This section of the Green River was a rather warm and turbid stream before installation of the dam in 1962. Since impoundment the first 50–60 km of river below the dam has become a clear, cold trout stream. With increasing distance from the dam, atmospheric influences and the addition of tributary waters combine to return the river toward a semblance of its preimpoundment state. The river environment was greatly altered at station I following impoundment. At station II the environment

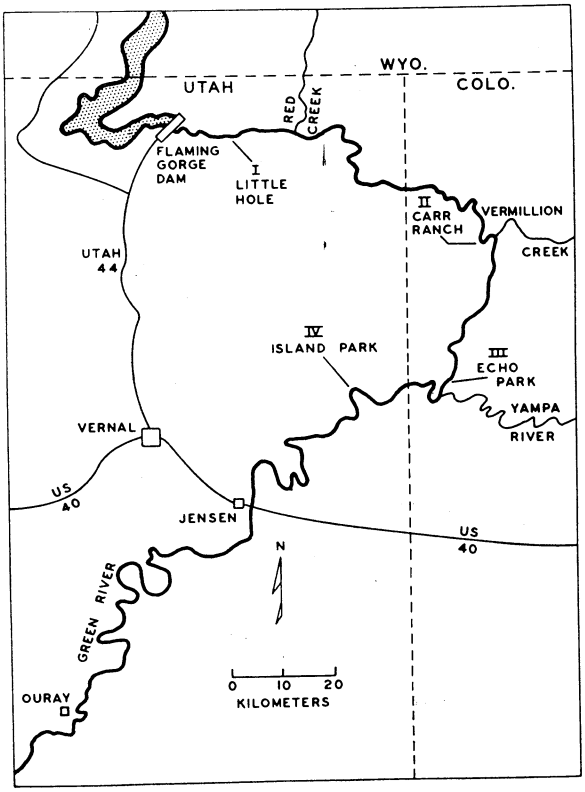

Fig. 1. Location of sampling stations on the Green River, Utah-Colorado.

showed signs of transition to the preimpoundment state, and stations III and IV appeared to be much the same in 1964 and 1965 as they were in preimpoundment years. The Green is a large river and mean monthly flows during the summers of 1964 and 1965 ranged between 11 and 77 m^3/sec.

Drift sampling was done on an exploratory basis only in 1964 under no uniform schedule. Regular sampling began on May 16, 1965 and ended on September 20, 1965. Each of the four stations was visited once every 3 weeks for 3 days on a continuous rotation, with every fourth day set aside for travel between stations. A 3-day station visit consisted of two 24-hr drift series of eight drift samples (5-min samples taken every 3 hr beginning at 0600 hr) separated by 1 day of bottom-fauna sampling. At station III only one 24-hr drift series was collected during a visit.

Benthic invertebrates on hard substrates were sampled with a wire-mesh device similar to those described by Hess (1941) and Waters and Knapp (1961). Ninety-five and 87 samples were collected in 1964 and 1965 respectively. Organisms on soft bottoms were sampled with a 15.2-cm Ekman dredge mounted on a 2-m-long, 1.8-cm-diameter metal rod. Sixteen and 36 samples were collected with the dredge in 1964 and 1965 respectively. Bottom-fauna densities were expressed as the sum of the products of the number of organisms per meter^2 of area for each type of substrate and the estimated percentage of the substrate present immediately above the sampling station. Density of all organisms, therefore, was estimated in terms of an "average" meter^2 of substrate for each station.

Drift organisms were sampled with a conical nylon-mesh net (Nitex #423 material) mounted on a hoop 29.2 cm in diameter. The drift net was staked down with its rim resting on the substrate in water 35–70 cm deep. A 15.2-cm-diameter flow meter with attached counter was installed in the mouth of the net. Sets were made for 5 min and the mean number of meter revolutions recorded for this time period was 353. Drift-net catches were converted to a "standard sample" which was the number of organisms which would have been taken with a flow-meter reading of 300 revolutions in 5 min. The formula used was:

No. of organisms at 300 revolutions = 300 $\times$ no. of organisms in the sample/no. of revolutions recorded for the sample.

The above conversion assumes that a linear relationship exists between number of meter revolutions and current velocity. The actual relationship was slightly curvilinear, and the above formula embodies a slight error (4% or less). Average velocity of water through the drift net was estimated from a calibration curve to be 0.23 m/sec at 300 revolutions in 5 min. The volume of water filtered for the "standard sample," therefore, was 4.59 m^3. Sixty-nine and 281 drift samples were collected in 1964 and 1965 respectively.

Incident light, water temperature, turbidity, water level, dissolved oxygen, and water depth at the sample site were all recorded at the beginning of each 5-min sample period. Eight arbitrary levels of illumination were established for use in the multiple regression analyses: bright sunlight, partly cloudy day, heavy overcast day, dusk or dawn, night with full moon, ¾ to ¼ moon, ¼ moon, and night with no moon. Water temperature was measured with a mercury-glass thermometer. Turbidity and dissolved oxygen were determined with a Jackson candle turbidimeter and the Winkler method respectively. Water levels were obtained from permanent staff gages installed at each station.

Results

Bottom fauna density

Densities of *Baetis* sp. and Simuliidae were by far the highest at station I. Numbers of both

TABLE 1. Drift of aquatic invertebrates in the Green River, summer 1965, expressed as total numbers taken in two diurnal series each of which consisted of eight 5-min samples taken every 3 hr beginning at 0600 hr

Location and date	*Baetis* sp.	Simuliidae	Other aquatic invertebrates
Station I			
June 11, 14	58	3	43
July 8, 10	340	183	365
Aug. 5, 7	7,850	628	442
Aug. 25, 27	4,398	700	356
Sept. 17, 19	13	44	167
Station II			
June 5, 8	1,104	3	95
July 3, 5	280	88	29
July 31, Aug. 2	2,168	399	354
Aug. 21, 23	3,280	129	211
Sept. 5, 7	365	143	174
Station III[a]			
May 29	1,186	18	54
June 27	146	102	104
July 20	54	22	40
Aug. 15	14	2	20
Sept. 11	2	2	10
Station IV			
May 23, 25	49	12	65
June 18, 21	19	15	63
July 14, 16	86	11	136
Aug. 10, 12	27	7	120
Aug. 31, Sept. 2	6	0	50

[a]Only one diurnal series was taken during each visit to station III, so the figures from this station were multiplied by two for comparative purposes.

organisms were low early in the summer, increased markedly in early August following the summer generation hatch, and declined slowly into September. *Baetis* sp. had two generations per year in the Green River while the Simuliidae had two or more generations per year. *Baetis* sp. density ranged from 506 per m^2 on July 7 to 26,200 per m^2 on August 6. Simuliidae density ranged from 0 to 14,800 organisms per m^2 on the same dates. Numbers of all other aquatic invertebrates (mostly chironomids at this station) ranged from 8,480 to 45,400 per m^2.

Densities of *Baetis* sp. and Simuliidae were low at station II (less than 43 organisms per m^2) because of the low gradient and large areas of sand-silt substrate, neither of which are favorable for these two organisms. It is important to note, however, that the density of both organisms was often higher (431–538 per m^2) in the vicinity of debris snags at this station. The density of all other aquatic invertebrates combined ranged from 86 to 3,090 organisms per m^2.

Stations III and IV were both in areas of rubble substrate and high gradient, but the river was usually turbid and algal growths were much reduced. *Baetis* sp. and Simuliidae densities were very low at both stations (less than 172 and 54 organisms per m^2 respectively), as was the combined density of all other aquatic invertebrates (344–840 per m^2).

Abundance of drift organisms

Drift rates for both *Baetis* sp. and Simuliidae were highest at stations I and II near the dam, and decreased markedly at stations III and IV (Table 1). In general, numbers of both organisms were low early in the summer at stations I and II, rose sharply in late July following hatch of the summer generation, and declined steadily into September. The most abundant organisms in the "other" category at all stations were chironomid larvae.

Maximum drift rates were encountered at station I on August 7, 1965. At a mean discharge of 11.4 m^3/sec, we estimated that 170×10^6 *Baetis* nymphs (63.2 kg) and 10.9×10^6 Simuliidae larvae (5.4 kg) drifted past the sampling station on August 7, 1965. For this date, the 24-hr ratio of *Baetis* nymphs drifting over a square meter of stream bottom to the standing crop of nymphs on that area was 161:1. For Simuliidae larvae the same ratio was 35:1. These ratios are much higher than those obtained by Waters (1964) for *Baetis* in a small stream in Minnesota.

Regression analysis of factors affecting drift

Multiple regression analysis was used to determine the unique contribution of eight factors to drift rates of *Baetis* sp. nymphs and Simuliidae larvae. All analyses were carried out on the IBM 1620 computer of the Department of Applied Statistics and Computer Science at Utah State University. Only the 1965 data were analyzed. The eight independent variables were:

X_1 = water temperature (°C)
X_2 = dissolved-oxygen content (ppm)
X_3 = turbidity (JTU)
X_4 = water depth at the sample site (cm)
X_5 = illumination (8 arbitrary levels)
X_6 = calendar date (Julian)
X_7 = density of all other benthic invertebrates upstream (no./m^2)
X_8 = water level (cm)

The dependent variables were:

$Y_1 = \log_{10}$ no. *Baetis* sp. nymphs + 1 in each 5-min standardized drift sample
$Y_2 = \log_{10}$ no. Simuliidae larvae + 1 in each 5-min standardized drift sample

Numbers of *Baetis* sp. and Simuliidae in the standardized drift sample were converted to logarithms to meet the assumption of linearity for regression analysis. In addition, simple correlation coefficients between all pairs of X and Y variables were calculated to help define interactions. Data from stations I and II were analyzed separately, but data from stations III and IV were combined for analysis.

The R^2 multiple correlation values obtained indicated that 76%, 81% and 32% of the variability observed in the drift rates of *Baetis* sp. nymphs was accounted for by the eight factors tested at stations I, II, and III-IV respectively. The percentages obtained for Simuliidae larvae were 72%, 65%, and 13% respectively. (Mimeographed copies of the six analyses are available from the author upon request.)

Illumination.—Diurnal periodicity of drifting *Baetis* nymphs has been reported by Tanaka (1960), Waters (1962), and Müller (1963). In our study, numbers of drifting *Baetis* sp. nymphs and Simuliidae larvae increased dramatically after sunset at stations I and II. Postsunset increases were less frequently observed at stations III and IV. In the multiple-regression analyses illumination was one of the most important individual contributors to variation in numbers of drifting *Baetis* sp. nymphs at station I, and the most important contributor at station II as interpreted by the unit-free standard partial-regression coefficients (b'; Snedecor 1956). Illumination also accounted for a significant (.05 level) amount of variability in drift rates of Simuliidae larvae at stations I and II.

Bottom-fauna density.—For the multiple regression analyses, numbers of *Baetis* sp. and Simuliidae were subtracted from the combined bottom-fauna densities used in the analysis of drift rates of these two organisms respectively to avoid autocorrelation. For example, the figure for bottom-fauna density put into the multiple regression analysis for *Baetis* sp. drift at station I on June 11 and 14 was the sum of the densities of Simuliidae and all other aquatic invertebrates obtained from bottom samples taken on June 13. Therefore, the regression "density" refers to interspecific density.

Both *Baetis* sp. and Simuliidae drift rates were correlated with the combined density of all other bottom fauna at station I ($r = .68$ and .65 respectively; $P < .01$), and bottom-fauna density upstream accounted for a significant amount of the variability observed in the multiple regression analysis as well (density yielded the highest b' in the *Baetis* sp. analysis and the second highest b' in the Simuliidae analysis at this station). Bottom-fauna density at station II showed nonsignificant correlations with drift rates of both *Baetis* sp. and Simuliidae, but the multiple regression mean squares were significant and the

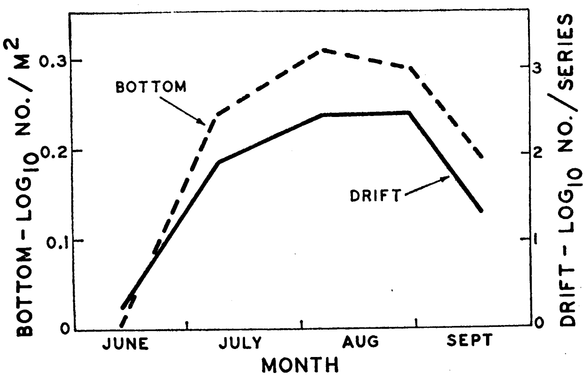

FIG. 2. Density of *Baetis* sp. nymphs on the bottom and drifting, station I, Green River, 1965.

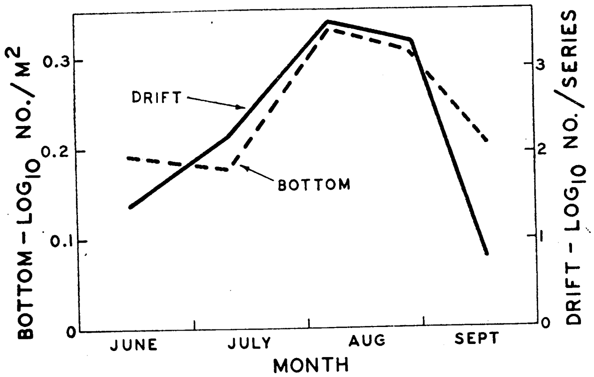

FIG. 3. Density of Simuliidae larvae on the bottom and drifting, station I, Green River, 1965.

partial regression coefficients were negative. The density of bottom fauna at station II was heavily influenced by a late-season increase in the numbers of another species of *Baetis* (sp. IV) and numbers of chironomid larvae, both of which are adapted for life on silt and sand substrates, whereas *Baetis* sp. nymphs and Simuliidae larvae require rubble or debris for support. Therefore, while the bottom-fauna density fluctuated widely at station II the fluctuation occurred on areas not heavily populated by *Baetis* sp. and Simuliidae and had little effect on the drift rates of these two organisms. In the analysis for stations III and IV, mean squares for combined bottom-fauna density were not significant.

A high positive correlation was found between 24-hr series drift catches of both *Baetis* sp. and Simuliidae and their own respective (intraspecific) densities at station I ($r = .82$ and .98; $P < .01$; Figures 2 and 3). Drift rates of both organisms were less closely correlated with their respective densities at station II ($r = .40$, $P < .10$ and .73, $P < .05$), but drift rates were much higher relative to densities on the bottom than at station I. No such intraspecific correlation was found at stations III and IV.

Temperature.—Temperature was the most important factor in explaining variability in drift rates of Simuliidae, and the secondmost important factor in explaining variability in drift rates of *Baetis* sp. at station I, as interpreted by the *b'* values. At station II temperature again provided significant *b* values but the signs were negative for both organisms. Temperature was correlated significantly with dissolved oxygen and date at all stations, and with depth and bottom-fauna density at station I. Müller (1966) reported that drift rates of *Gammarus* increased with a rise in water temperature and that very low temperatures disrupted the diurnal drift pattern of *Baetis*.

Turbidity.—Turbidity was a significant contributor to variability in the multiple regression analyses only at station II for *Baetis* sp., but under certain conditions it seemed certain that turbidity also affected drift rates of other organisms and at other stations. Early in the afternoon of September 5, 1965 local rains at station II caused a sudden increase in turbidity (from 25 to 700 ppm) which was immediately accompanied by a rise in drift rate of *Baetis* sp. nymphs (Fig. 4). No change in water level occurred and drift continued to rise after sunset. Two days later, turbidity was again less than 25 ppm, and *Baetis* sp. drift followed the normal pattern of increase beginning shortly after sunset. Simuliidae drift during the turbidity fluctuations followed essentially the same pattern as that described for *Baetis* sp. On the afternoon of June 27, 1965 turbidity increased from 113 to 1,350 ppm at station III but no increase in drift rates was observed. Both *Baetis* sp. and Simuliidae densities upstream were probably too low to induce behavioral drifting on this occasion, since no postsunset increase was observed either.

Water-level fluctuations.—Observations were made on permanent staff gages at half-hour intervals during all diurnal drift series; the difference between maximum and minimum readings in the 3 hr before sampling time was coded in 10-cm intervals and used as a measure of water-level fluctuation for the regression analyses. Varying power demands on Flaming Gorge Dam often caused extreme daily fluctuations in flow. Fluctuations were most pronounced near the dam and were dampened progressively downstream. Maximum water-level fluctuations observed for a 24-hr period in 1965 were 65 cm at station I, 45 cm at station II, 24 cm at station III, and 10 cm at station IV.

Changes in water level accounted for none of the variation observed in drift rates of *Baetis* sp. and Simuliidae (no *b* values significant). Water-level change was not significantly correlated with

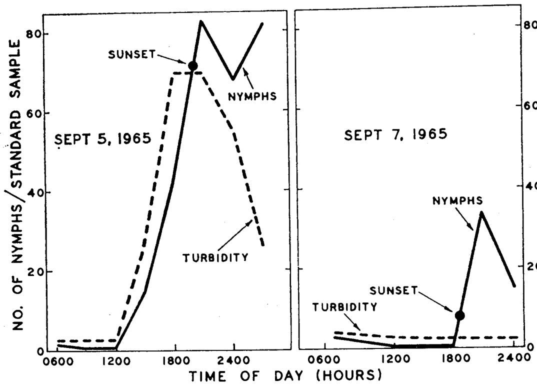

FIG. 4. Turbidity and drift rates of *Baetis* sp. nymphs, station II, Green River, September 5 and 7, 1965.

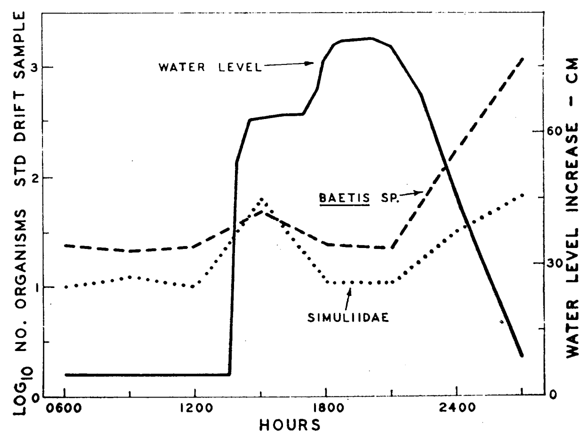

FIG. 5. Increased drift of *Baetis* sp. and Simuliidae following a sudden increase in flow, station I, Green River, August 5, 1965.

any other factor in the analyses. The failure to find statistical significance, however, may have been due to choice of the 3-hr-long recording period. Sudden increases in flow caused rapid rises in the catastrophic drift of *Baetis* sp. and Simuliidae at station I, but only for the first 40–90 min after the initial rise in water level. On August 5, 1965, a sudden 58-cm rise in water level at station I resulted in only temporary increases in daytime drift rates of both organisms (Fig. 5). This same temporary increase in catastrophic drift was also observed in oligochaetes and chironomids.

On September 7, 1964 flow was drastically reduced at station IV by hydrological studies being conducted at Flaming Gorge Dam. An estimated 25% of the streambed, which had been submerged for at least the previous 5 months was exposed beginning on the morning of September 7. In the afternoon drift rates were not different from those observed earlier in the summer. After sunset, however, drift rates of *Baetis* sp., other may-

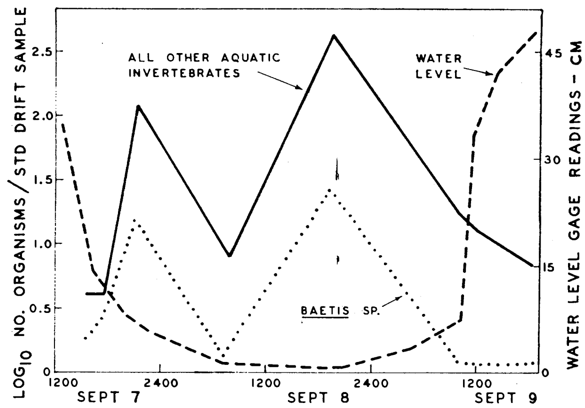

FIG. 6. Drift of *Baetis* sp. and other aquatic invertebrates during a 45-cm drop and rise in water level, station IV, Green River, September 7–9, 1964.

flies, caddisflies, and stoneflies reached the highest levels recorded at this station (Fig. 6). Simuliidae larvae increased only slightly in drift, probably because population density was very low at the time. The sudden reduction in flow occurred just before the fall emergence of many aquatic insects and at a time when total invertebrate density on the streambed was high. Water levels returned to normal on September 9, and drift rates of all aquatic organisms decreased sharply and exhibited no postsunset increase, with the exception of chironomid larvae, which increased. The high drift of chironomids accompanying the rise may have resulted from erosion of larvae-containing silt deposits laid down shortly before by the receding water.

Invertebrates were observed at the water's edge throughout the study while water levels were fluctuating. Little or no crawling activity of benthic invertebrates occurred during increases in flow. As levels fell, *Baetis* sp. nymphs moved towards deeper water, usually by crawling but occasionally by swimming. Simuliidae larvae attempted to move toward deeper water as levels fell, usually by swimming. Few *Baetis* sp. nymphs were stranded as the water line receded but stranded Simuliidae larvae (dead and alive) were commonly found under rocks and debris in the exposed area.

Date.—Calendar date, expressed as day number on the Julian calendar, accounted for more variability in drift rates of Simuliidae at station II than any of the other factors ($b' = .978$). Date also accounted for significant amounts of variability in drift rates of *Baetis* sp. at stations I and III-IV. Significance in these cases probably reflects the seasonal changes in abundance of the summer generations of these organisms since date correlated highly with densities of both *Baetis* sp. and Simuliidae.

Dissolved oxygen.—Dissolved-oxygen concentration accounted for a significant amount of variability only in the drift rate of Simuliidae at station II. Oxygen concentrations during the study were usually between 7 and 8 ppm, and were probably adequate for both organisms studied. Dissolved oxygen correlated highly significantly with temperature and illumination at stations I ($r = -.63$ and .48 respectively; $P < .01$) and II ($r = -.51$ and $-.38$ respectively; $P < .01$) and with temperature alone at stations III and IV ($r = -.78$; $P < .01$).

Depth.—Waters (1965) reported that drifting organisms were nearly evenly distributed vertically in a small stream, but that *Baetis* nymphs showed a slight tendency to concentrate in the upper strata of water. Depth of water over the upper rim of the drift net in the present study ranged from 0 to 38 cm at all stations and was significant only in the combined analysis for *Baetis* sp. at stations III-IV. Our sampling was restricted to the shallow, inshore areas and the vertical distribution of drift organisms in the main channel (maximum depth, 1.5–1.8 m) is unknown.

DISCUSSION

Total catches of invertebrates in the 24-hr series declined steadily with increasing distance from Flaming Gorge Dam. If behavioral drift (which made up the bulk of the total drift) is related to production in excess of carrying capacity (as suggested by Waters 1961, 1966) then this production was highest at station I and lowest at station IV. The small standing crop of organisms at station IV seemed to substantiate the conclusion that production was low at this station.

Although illumination and population density were the most important factors related to drift, temperature accounted for significant amounts of variability in the drift rates observed at stations I and II. The b values, however, were positive and negative respectively at these two stations. It may be that invertebrate activity (and the chance of being swept away by the current) increases as temperature increases. At station II drift catches of both organisms were higher than might have been expected from an area supporting a relatively small bottom-fauna population. Water released from the dam reached station II only 12 hr later. Drift organisms observed at station II may well have originated in the station I area where population densities were much higher, and they may have drifted through station II because of lack of suitable attachment points. There is no need to postulate that any of the organisms drifted the entire 57 km in 1 night since the trip could have been made in a saltatorial manner over a number of nights. If this were the case it would help explain why calendar date accounted for so much of the variability observed in drift rates of Simuliidae larvae at station II. Since calendar date and population density were highly correlated at station I, perhaps some of the variability assigned to date at station II should have been assigned to population density and perhaps other factors operating at station I.

Turbidity was a significant contributor to variability in the multiple regression analyses only at station II for *Baetis* sp. Data from station I provided almost no information on the effects of turbidity on drift because turbidity at this station never exceeded 62 ppm and rarely exceeded 25 ppm. If turbidity influences drift rates indirectly through its effect on light penetration, and light intensity triggers behavioral drift only at densities in excess of carrying capacity, then turbidity probably could not have affected drift rates at stations III and IV where population densities were low and diurnal periodicity in drift was rarely observed.

Field observations indicated that severe water-level fluctuations influenced drift rates of both organisms. No significant mean squares for water-level change, however, were obtained in the regression analyses. This failure to find significance apparently resulted from the method used to introduce water-level change into the analyses (difference between maximum and minimum staff-gage readings in the 3 hr before sampling). The 3-hr period was probably too long to catch the immediate effects of rising water on catastrophic drift. Timing of the fluctuation with respect to both time of day and population density must be considered when assessing the effects of water-level fluctuation on behavioral drift. The high drift rates observed at station IV during reduced flow may have been increased behavioral drift caused by a reduction in available living space.

The R^2 values of .76 and .81 obtained for *Baetis* sp. and the values of .72 and .65 obtained for Simuliidae at stations I and II, respectively, are rather high for data of this nature collected over such a wide area. On the basis of these results we feel that further investigations on the drift-rate production relationship can be successfully carried out at locations like stations I and II where populations are high enough to induce behavioral drifting.

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EVIDENCE FOR REPRODUCTIVE PERIODICITY IN THE DEEP SEA

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Abstract. Deep sea bottom samples taken at depths between 1,100 m and 3,800 m in the western North Atlantic during the summer months of 1964, 1965 and 1966 yielded large numbers of young of the brittlestars *Ophiura ljungmani* and *Ophiomusium lymani*, whereas proportionately fewer young were present in samples taken at approximately the same depths

[1] Woods Hole Oceanographic Institution Contribution No. 2067.