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IN A SOUTH CENTRAL OKLAHOMA STREAM

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Norman, Oklahoma

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THE ECOLOGY OF LARVAL BLACKFLIES (DIPTERA: SIMULIIDAE)
IN A SOUTH CENTRAL OKLAHOMA STREAM

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TABLE OF CONTENTS

Acknowledgements i

List of Tables iii

List of Figures. v

Abstract viii

I. Introduction 1

II. Description of the Study Area 3

III. Methods and Materials. 6

 A. Physical and chemical methods. 6

 B. Algal biomass estimates. 8

 C. Simuliid collections 9

 D. Statistical methods. 11

IV. Results and Discussion. 17

 A. Limnology. 17

 B. Simulium collected 18

 C. Some quantitative aspects of the life history of
 S. species A and virgatum. 19

 D. Seasonal bionomics 28

 E. Abiotic and biotic environmental coactions 30

 F. Simulium drift.. . . . 40

 G. Predictive models and variable interactions. 52

V. Summary. 56

VI. Literature Cited. 59

VII. Appendix A. Tables. 68

VIII. Appendix B. Figures. 99

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LIST OF TABLES

1.	Descriptions of Stations 1 through 9 including depth and current measurements.	69
2.	The yearly means and standard errors of the means (S.E.) of selected limnological parameters observed at Stations 4 and 8 from 31 June 72 through 15 August 73.	70
3.	Correlation matrices for the limnological parameters measured at Stations 4 and 8 from 31 June 72 through 15 August 73.	71
4.	Checklist of the <u>Simulium</u> collected at Honey Creek, their life forms, associated substrata, and longitudinal location	72
5.	The number of eggs counted, percentage of eggs already laid, the number of immature oocytes remaining (rated 0 - 4), and the presence or absence of a blood meal remenant (+ or -) in ovipositing <u>Simulium</u> species A and <u>virgatum</u> females.	73
6.	<u>Simulium virgatum</u> cohort statistics for Stations 3 and 6, 15 August through 19 September 72.. . . .	75
7.	Life tables for <u>Simulium virgatum</u> larval cohorts collected at Stations 3 and 6 from 15 August through 19 September 1972.	76
8.	Correlation coefficients between <u>Simulium</u> species A and <u>virgatum</u> age groups and <u>S. trivittatum</u> total densities averaged over Stations 1, 3, 4, 5, 6, and 7 compared with selected limnological parameters estimated at Station 4	77
9.	Significant polynomial regression expressions and figure references for <u>Simulium</u> species A and <u>virgatum</u> age group densities for stream means compared with selected limnological parameters measured at Station 4	78
10.	Significant polynomial regression expressions and figure references for <u>Simulium</u> species A and <u>virgatum</u> total densities for stream means compared with selected limnological parameters measured at Station 4	80
11.	Correlation coefficients between <u>Simulium</u> species A and <u>virgatum</u> total immature densities and selected variables for Stations 1, 3, 4, 5, and 6.	81

12.	Significant polynomial regression expressions between <u>Simulium</u> species A and <u>virgatum</u> immature densities and selected variables for Stations 1, 3, 4, 5, and 6.	82
13.	Correlation coefficients between <u>Simulium</u> species A and <u>virgatum</u> total larval densities and selected limnological parameters measured at Stations 8 and 9	83
14.	Significant polynomial regression expressions and figure references between <u>Simulium</u> species A and <u>virgatum</u> densities and selected parameters at Stations 8 and 9	84
15.	Linear correlations between <u>Simulium</u> species A, <u>virgatum</u> , and <u>trivittatum</u> larvae and their associated fauna at Stations 1, 3, 4, 5, 6, 8, and 9.	85
16.	Locations of the drift nets for each of the 24 hour investigations.	86
17.	Linear correlations among selected limnological parameters measured below Station 4 and used in the drift analyses	87
18.	Correlations between <u>Simulium</u> species A and <u>virgatum</u> age class and <u>trivittatum</u> total drift rates and selected parameters.	88
19.	Significant polynomial regression expressions and figure references for <u>Simulium</u> species A and <u>virgatum</u> age classes and <u>trivittatum</u> total drift rates and selected limnological parameters.. . . .	89
20.	Linear correlations between <u>Simulium</u> species A and <u>virgatum</u> drift rates and the benthic densities of the associated fauna and <u>S.</u> species A and <u>virgatum</u>	91
21.	Summary of the 3-way ANOVAs to determine significant <u>Simulium</u> activity patterns.	92
22.	Linear correlations between the mean 2-hr drift rates and the mean 2-hr pH, alkalinity, temperature, dissolved oxygen, and light intensity estimates	93
23.	Multiple regression analyses between <u>Simulium</u> species A, <u>virgatum</u> and <u>trivittatum</u> benthic densities at Stream Means and Station 8 and concomitantly measured variables	94
24.	Multiple regression analyses between <u>Simulium</u> drift rates and selected concomitantly measured abiotic parameters.	95
25.	Multiple regression prediction expressions <u>Simulium</u> total benthic density and adult female drift rate from Stream Means, Station 8 and the drift data matrix.	97
26.	Summary of prediction equation evaluation.	90

LIST OF FIGURES

1. Map of Honey Creek, Murray County, Oklahoma.	100
2. Longitudinal profile of the gradient of Honey Creek, Murray County, Oklahoma	102
3. Algal extract optical density degradation and correction factor curves	104
4. Seasonal fluctuations in selected physical parameters of Honey Creek estimated at Stations 4 and 8 from 31 June 72 through 15 August 73	106
5. Seasonal fluctuations in the selected chemical parameters of Honey Creek at Stations 4 and 8 from 31 June 72 through 14 August 73.	108
6. Algal biomass estimates for Stations 1, 3, 4, 5, 6, 7, 8, and 9 from 5 August 72 through 15 August 73	110
7. Seasonal changes in the depth and current velocity at Stations 1, 3, 4, 5, and 6 from 15 July 72 through 15 August 73.	112
8. Number of larval instars of <u>Simulium</u> species A and <u>virgatum</u> . .	114
9. Weight plotted as a function of head-capsule-width for <u>S.</u> species A and <u>virgatum</u>	116
10. Growth curves for <u>Simulium virgatum</u> at Stations 3 and 6	118
11. Survivorship curves for <u>Simulium virgatum</u> at Stations 3 and 6	120
12. Seasonal fluctuations in the total benthic densities of <u>Simulium</u> species A and <u>virgatum</u> for Stations 1, 3, 4, 5, and 6 from 5 August 72 through 15 August 73	122
13. Seasonal fluctuations in the total benthic densities of <u>Simulium</u> species A and <u>virgatum</u> for Stations 8 and 9 from 31 June 1972 through 15 August 73.	124
14. Seasonal fluctuations in the total benthic densities and percentage age composition of <u>Simulium</u> species A and <u>virgatum</u> for Stations 1, 3, 4, 5, 6, and 7 (stream means) . .	126
15. Seasonal fluctuations in the benthic density of <u>Simulium</u> <u>trivittatum</u> for stream means.	128

16.	Significant polynomial regressions for small larvae, species A medium and <u>virgatum</u> medium, large and ultimate larval benthic densities.	130
17.	Significant polynomial regressions for <u>Simulium</u> species A and <u>virgatum</u> medium, large, and ultimate larvae and pupae benthic densities.. . . .	132
18.	Regression of <u>Simulium</u> species A ultimate larval density on coulter counts	134
19.	Significant polynomial regressions of <u>Simulium</u> species A and <u>virgatum</u> totals	136
20.	Significant linear regressions of <u>Simulium</u> species A and <u>virgatum</u> total densities with depth and current velocity at Stations 1, 3, 4, and 6.	138
21.	Significant regressions of <u>Simulium</u> species A and <u>virgatum</u> at Stations 4, 5, and 8	140
22.	Significant polynomial regressions for <u>Simulium</u> species A and <u>virgatum</u> at Stations 8 and 9.	142
23.	Seasonal changes in the trichopteran larval densities at Stations 1 and 8	144
24.	Seasonal fluctuations in the 24-hr drift rates of <u>Simulium</u> species A and <u>virgatum</u> immatures and adults	146
25.	Seasonal fluctuations in the larval drift rates of <u>Simulium trivittatum</u>	148
26.	Depth and current velocity estimates at drift nets A and B for each 24-hr study.	150
27.	Substrate appression exhibited by <u>Simulium</u> species A and <u>virgatum</u> at Honey Creek	152
28.	Significant polynomial regressions of larval drift rates on benthic density.	154
29.	Significant regression of immature Simuliidae drift rates on algal biomass.	156
30.	Significant polynomial regression of <u>Simulium</u> drift rates on selected limnological parameters	158
31.	Significant polynomial regressions of <u>Simulium</u> drift rates on selected limnological parameters	160
32.	Significant polynomial regressions of <u>Simulium trivittatum</u> larval drift on dissolved oxygen and discharge.	162

33.	Diel drift patterns for <u>Simulium</u> species A larvae and adults.	164
34.	Diel drift patterns for <u>Simulium trivittatum</u> larvae and adults and <u>Simulium</u> small larvae.	166
35.	Diel drift patterns for <u>Simulium trivittatum</u> larvae	168
36.	Diel patterns for the yearly means of the selected abiotic variables measured below Station 4.	170

ABSTRACT

From 31 June 1972 through 15 August 1973 Simulium benthic densities were estimated at weekly intervals at 9 stations along Honey Creek. The species of Simulium collected, in order of decreasing abundance, were: species A (to be described elsewhere), virgatum, trivittatum, vittatum and venustum. Polynomial regression analyses between changes in the simuliid benthic densities and concomitantly estimated limnological parameters are presented and their relative influence of pre-imaginal survival discussed. Increasing algal biomass and water temperatures exhibited a consistent positive regression with species A, whereas the interaction of algal biomass (mostly Phormidium) and travertine deposition exhibited a consistent negative interaction with virgatum. Discharge fluctuations had a negative effect on trivittatum densities. Inter- and intraspecific coactions were evaluated; however, only Trichoptera larvae exhibited a negative effect. None of the simuliid larvae were significantly negatively correlated although the times of peak abundance of virgatum and species A were well separated. Detailed cohort analysis and life tables are presented for virgatum. The number of instars for both virgatum and species A were calculated and growth curves from field data presented for virgatum.

Seventeen 24-hr drift studies were conducted throughout the sampling period, and the effects of selected limnological parameters on the 24-hr total drift rates for virgatum, trivittatum and species A evaluated using regression techniques. In general these interactions paralleled the

responses exhibited by these factors and benthic densities. The influence of some selected factors on the diel periodicity of the simuliid larvae and their possible role as "zeitgebers" are presented.

Using multiple regression techniques both predictive and biologically realistic models of factor interactions were calculated. For species A drift seemed to be the best predictor of benthic density whereas algal biomass seemed best for S. virgatum. Predictive models were unsuccessfully tested and the implications of this failure discussed.

I. Introduction

The ecology of the family Simuliidae has received a fair amount of attention; however, the majority of these studies have dealt with the vector potential and associated biology of the adults (Dalmat, 1955; Crisp, 1956; and many others). Information on the quantitative population ecology of the immature stages is lacking for all but a handful of English (Zahar, 1951; Davies and Smith, 1958; Maitland and Penney, 1967; Obeng, 1967; and Ladle, et al., 1972), Northern European (Carlsson, 1962; Ulfstrand, 1968; Rühm, 1969 and 1970a and b), African (Chutter, 1968), Alaskan (Sommerman, et al. 1955), and Canadian (Davies, 1950; Fredeen, et al. 1951; and Abdelnur, 1968) species. Although some of the larger taxonomic contributions (Nicholson and Mickel, 1950; Stone and Jamnback, 1955; Anderson, 1960; Stone, 1964; and Stone and Snoddy, 1969) and several other investigations (Puri, 1925; Wu, 1930; Peterson, 1956; and Anderson and Dicke, 1960) have presented information on the life history of the United States species, there has not been an in-depth study of the quantitative population ecology of this group. In the Southern United States west of the Mississippi River few reports of simuliids have appeared in the literature with the exception of the following taxonomically oriented papers: Coquillett (1903), Malloch (1903), Hungerford (1913), Knab (1915), Stains and Knowlton (1943), Stone (1948), Wiseman and Eads (1960), and Stone and Boreham (1965). Due to the taxonomic complexities of the immature stages, regional ecological investigations of lotic systems have not separated the immature simuliids beyond the generic level (Hornuff, 1957; Harrell, 1969; and McKinley, et al. 1972) negating any autecological information from this source.

To reduce this paucity of information on the local species of Simuliidae as well as add to the limited knowledge of the general larval ecology, a multifaceted investigation was initiated at Honey Creek, Murray County, Oklahoma in June 1972 with the following objectives: 1) To determine the species of Simuliidae present; 2) To evaluate their life history and general biology; 3) To establish their phenological patterns while concomitantly recording selected environmental conditions; and 4) To evaluate the effects of these environmental conditions on the quantitative autecology of each species and synthesize predictive models. Honey Creek was especially suited for this type of investigation due to the large permanent simuliid population present throughout the year and the travertine substrata which facilitated quantitative sampling.

II. Description of the Study Area

Honey Creek is a medium sized rheocrene originating in the Cool Creek and McKenzie Hill geological formations of the Arbuckle Mountains and flowing northeast emptying into the Washita River (Figure 1). The geological formations change sequentially from cherty limestone and sandstone to "Fernvale" limestone and eventually Washita alluvium (Ham, 1969). The longitudinal gradient is almost continually descending the most rapid of which is in the vicinity of Bridal Veil and Turner Falls (Figure 2). The Arbuckle Mountains themselves descend from a maximum elevation of 420 meters to the Washita River at 235 meters, yielding a total relief of 185 meters (Ham, 1969). Using the Dalmat (1954) stream classification Honey Creek would sequentially change from a "young" stream at its source to a "mature" stream as it meanders through the Washita River flood plain. During the wetter seasons most acrual comes from intermittent streams. These tributaries as well as approximately the upper 10.8 KM of Honey Creek above Spring No. 1 were dry from midsummer through the late fall or early winter depending of precipitation. The most consistent sources of water were Spring 1 and 2 which drained limestone aquifers. On 1 April 1973 Spring 1 discharge was $0.137 \text{ m}^3/\text{sec}$ and Spring 2 was $0.128 \text{ m}^3/\text{sec}$ while the entire stream below Station 7 had a discharge of $0.456 \text{ m}^3/\text{sec}$ suggesting that $0.191 \text{ m}^3/\text{sec}$ was attributable to runoff. Using the criteria suggested by Hynes (1972) the substrata above Spring 2 were classified as rubble and pebble. Below Spring 2 photosynthetic activity, due mainly to elongated runs and pools choked with Myriophyllum as well as the riffle inhabiting Spirogyra, Oedogonium and Phormidium, raised the pH causing the precipitation of calcium and magnesium carbonates which formed thick layers of travertine (Minkley, 1963). Depending on the season of the year, this zone of travertine deposition moved

up and down the stream being further downstream during the winter. The end result was an area of travertine deposition from just below Spring 2 to Cedar Vale Pool (Figure 1). Below Cedar Vale Pool there was a short stretch of rubble riffle before Honey Creek flowed into the Washita alluvium.

Longitudinally, land utilization varied as follows:

1. The intermittent and far upstream portions of Honey Creek drained the tall grass prairie situated on the rounded summit of the Arbuckle Mountains. The water course itself was bounded by shrubs, post and blackjack oaks, and some cedars.

2. The area halfway between Spring 1 and 2 downstream to the boundary of Turner Falls Park was heavily wooded. Areas 1 and 2 were used for cattle pasture. Defecation and urination in the stream at well frequented watering sites probably added to the eutrophication of Honey Creek.

3. Turner Falls Park area was a highly used summer vacation area equipped for picnickers and campers. As shown in Figure 1, the park encompassed the middle third of the stream and most of the area of travertine deposition.

4. The portion of the stream below the park adjacent to U.S. 77 extending to U.S. I-35 was bounded on both sides by private homes and commercialized enterprises.

5. Below I-35 the stream flowed through grassland before emptying into the Washita River.

Although the land was utilized for many different purposes, these uses did not seem to exert a deleterious effect on the simuliid populations. In contrast, the densest larval concentrations were located within Turner Falls Park above Turner Falls. Nine stations were chosen for in-depth study in the area of travertine deposition the locations of which are depicted in

Table 1. Stations 1 through 6 were located within Turner Falls Park while Stations 8 and 9 were located on the property of Mr. W. Geise.

III. Methods and materials.

A. Physical and chemical methods.

At weekly intervals concomitant with the biological observations, physical and chemical parameters were monitored below Station 4 for most of the study (earlier readings were also taken below Stations 2 and 6) and Station 8. Twenty-four hour water samples were taken below Station 4. A list of the parameters considered and their mode of collection and analyses are: 1. Water and air temperatures were measured with a pocket field thermometer. Air temperatures were measured in the shade. 2. Depths were measured concomitantly with bottom samples at Stations 1-7 using a ruler. Stream depth above Station 8 was monitored with a permanent depth stick until it was lost during a spate on 19 November 1972; subsequent readings were with a ruler at the same location. 3. Since depth readings at Stations 1-7 were normally less than 5-cm, current velocities were estimated with a modification of Darcy's Pitot Tube as described in Welch (1948). 4. Stream discharge was estimated just below Station 6 using the formulas and methods described in Welch (1948). Current velocities were estimated using a pigmy Gurley Meter. 5. As suggested by Reisen and Prins (1972), the amount of rainfall between sampling dates can be used as an index of habitat disruptment caused by spates. In this study a rainfall factor was calculated as the average rainfall per day between sampling dates and expressed in centimeters. Rainfall data was collected at Sulphur-Platt National Park by the U.S. Park Service as reported in Haggard (1972 and 1973). 6. Light intensity was measured at 2-hr intervals for each of the 24-hr drift studies using a Weston Illumination Meter Model-756 and recorded in Ft-Candles (abbreviated Ft-c'dle). Unfortunately this meter was not sensitive enough to record moonlight, so a synthetic moonlight factor was calculated; where

available moonlight was equal to the amount of time the moon was out at night (hours) multiplied by a subjective moonphase rating where 1 was a new moon and 3 was a full moon. Moon phase as well as the time of moon rise and set were obtained from the U.S. Weather Service, Will Rodgers Air Port, Oklahoma City, Oklahoma. Day length values were the total number of hours between sunrise and sunset as determined from the Nautical Almanac Office (1965). 7. As an index of suspended solids as well as the amount of suspended food, 5-ml water samples were collected in 100-ml of commercial Isotone solution, taken back to the laboratory, and the total number of particles counted using a Coulter Particle Counter (Williams and Hynes, 1973). Triplicate counts were conducted on each of the duplicate samples collected under the following machine parameters: Aperture size = 100 microns, Aperture current = 0.707, amplification = $\frac{1}{2}$, window limits were set at 10 and infinity. Background counts were conducted for every sample and the final values adjusted accordingly. Relative particle size distributions were calculated automatically by the Automatic Particle Size Plotter. 8. Dissolved oxygen concentrations were determined using the alkali-azide modification of the Winkler method (Taras, et al., 1971). Samples were immediately fixed and titrated in the field within one-half hour of collection. 9. pH was measured using a portable battery operated Beckman pH meter (Model NO. 210). Values presented were the maximum reading attained after probe immersion. 10. Total alkalinity was estimated by titration with dilute HCl to a pH of 3.7 (Taras, et al., 1971). 11. Dissolved phosphate, nitrate -N, sulphate, turbidity, and conductivity were estimated colorimetrically using a portable Hach Water Chemistry Kit (Hach, 1973). Samples were taken below Stations 4 and 8 at monthly intervals from 30 September 1972 through 15 August 1973.

B. Algal Biomass Estimate.

At the conception of this investigation substantial periphytic densities were not observed on the riffles at Stations 1 through 9, and subsequently this parameter did not seem of consequence. Later observations revealed large increases in periphyton necessitating the formulation of some index of algal abundance. Taras, et al. (1971) included a colorimetric method for algal biomass determination using a quantitative extraction of chlorophyll-A; however, samples have to be processed immediately after extraction or frozen for not longer than several days prior to extraction. With certain modifications it was postulated that stored, already extracted samples, could be used as an index of algal biomass fluctuations. Samples were collected from a known area of substrata, immediately immersed in 70% ethanol, and stored in this solution for varying lengths of time before processing. Algal cells were not homogenized. Since chlorophyll-A degrades into a series of unknown compounds whose optical properties are not understood, it seemed that Hach broad spectrum wavelength optical density using a red color filter (Hach filter NO. 2408) would give more meaningful results than specific wavelength Spec-20 determinations. To evaluate the degradation process comparatively, duplicate samples were collected on 14 July 1973, returned to the lab, and processed according to the procedures outlined in Taras, et al. (1971) except that the cells were not ruptured and pigments were extracted using 70% ethanol. Samples were observed concomitantly at varying time intervals and the fraction of the maximal optimal density (y) calculated where: $y = \text{obs. optical density} / \text{max. optical density}$. These results are depicted graphically in Figure 3. The degradation curve for the Hach (H) and the Spec-20 (Wavelength = 665) estimates were variable initially, but after 15 days these values became comparable. To calculate a correction

function, the reciprocal of the Hach determinations ($1/H$) was evaluated as a function of time (Figure 3). This function appeared sigmoid, but because the time intervals of sampling varied, standard sigmoid curve fitting techniques were not applied, and consequently the function was partitioned into exponential and asymptotic portions. A regression function (Figure 3) was calculated and was used to correct samples processed up to 50 days after collection. This function fit the data well ($r=0.9817$). Samples stored for more than 50 days were corrected by multiplying the observed Hach optical density times a correction factor, the upper asymptote, where: correction factor = 3.5. Samples were also standardized for the area of stream bottom sampled and the volume of 70% ethanol used in the extraction. For consistency data was expressed as mg/cm^2 of algal biomass as calculated from the formulae presented in Taras, et al. (1971).

C. Simuliidae collections.

1. Estimation of benthic densities. Benthic densities were estimated at Stations 1 through 9 using a modification of the Surber sampler described in Welch (1948). The stream bottom area sampled was 39 cm^2 ; net opening was 36 cm^2 ; bag length was 25 cm and constructed of nylon monofilament screen cloth (Turtox NO. C) with a mesh aperture size of 0.2 mm. Baffles were not included due to the small size of the sampler. Due to their stringent depth and current requirements (Philipson, 1957; Maitland and Penney, 1967; and others), Simuliidae larvae were characteristically contagious in their benthic micro-distribution precluding completely random sampling. Single samples were always taken at each station in areas supporting dense concentrations of black-flies while duplicate samples were taken when numbers became sparse. Estimates of associated faunal benthic densities, depth, current velocity, and algal biomass were taken concomitantly and subsequently were biased for simuliid dispersions.

No additional sampling criteria were imposed and it was considered that samples were random within the perimeter of blackfly habitation and representative for each station as well as for simuliid age structure and species composition. Blackflies were dislodged with a 2.5-cm wide paint scraper and usually travertine was dislodged to a depth of about 0.5-cm. Subsequent samples were always taken adjacent to the previous weeks samples for consistency. Specimens were preserved in the field in 70% ethanol and returned to the laboratory for examination. Counts were made and expressed as numbers/cm².

2. Drift samples. As reviewed by Waters (1972), Hynes (1972), and Bournaud and Thibault (1973), the downstream movement of aquatic insects, or organic drift, provides an index of density induced emigration as well as diel activity patterns. Reisen and Fox (1970) also suggested that this technique was useful in monitoring adult lotic dipteran emergence. Two identical portable drift samplers similar to those described in Reisen and Prins (1972) were situated at two different stations above Turner Falls. The samplers were 25-cm square with a 1-m long bag of netting material identical to that used in the Surber samples. Samples were taken at 2-hr intervals for a 24-hr period on each of the 17 study dates along with concomitantly measured light intensity, temperature, dissolved oxygen, pH and alkalinity. Benthic densities were estimated immediately upstream from each of the drift nets prior to the positioning of the drift samplers. Samples were processed essentially the same as Reisen and Prins (1972) except that 1st and 2nd larval instars were separated from the detritus by washing the samples through a series of two U.S. Standard Seives; seive 1 = Tyler mesh equivalent 32, 500 micron aperture; seive 2 = Tyler mesh equivalent 48, 297 micron aperture. Counts were made and standardized to the following

units: 1) for diel activity patterns: nos./m³/hr; 2) for 24-hour total drift: nos./m³/day calculated by summing over the standardized drift rates for the 12 2-hr samples. Values reported were means for the two nets standardized to eliminate discrepancies due to differences in discharge through each of the nets.

3. Taxonomic survey. In addition to the routine sampling schedule described earlier, the entire stream was surveyed for blackflies on the following days: 15 December 1972, 1 April 1973, 17 July 1973, and 28 October 1973. Notes were made on habitat preference, substrata associations, faunistic associations, and longitudinal location.

D. Statistical methods.

1. Separation of the number of larval instars was accomplished using the head-capsule-width versus numbers frequency distribution method for soft-bodied insect larvae originally described by Dyar (1890). Specimen manipulation and measurement was similar to Johnson and Pengelly (1970). The pooling of class marks followed the procedures outlined in Sokal and Rohlf (1969).

2. Life tables and survivorship. By monitoring the changes in benthic density at Stations 3 and 6 at 4 day intervals, it was possible to estimate life table statistics. After visiting marked egg masses daily, it was discovered that the period from oviposition to eclosion at 25°C. took about 4 to 5 days. On August 14, 1972 at Stations 3 and 6 the entire riffle was denuded of simuliids by vigorously scrubbing the travertine substrata with a scrub brush. That evening Simulium virgatum oviposited at both stations. From this point additional egg masses were removed at 4 day intervals to preserve cohort integrity. Unfortunately it was not possible to eliminate immigration or emigration by drift. The density of the larval population

and the total area covered by the cohort were observed at 4 day intervals. Rough estimates of the total cohort area were obtained by measuring the maximum length and maximum width. Investigations at both stations were terminated when all the cohort had apparently pupated and emerged. Life table statistics were calculated using the formulae presented in Southwood (1966).

3. Growth rates. By measuring each of the specimens collected in the life table study, a mean cohort head-capsule-width could be estimated. By then determining the weight to head-capsule-width relationship by regression techniques, cohort biomass as well as average cohort growth rates could be calculated.

4. Biotic and abiotic environmental coactions. The relationships between each of the age groups of each of the dominant simuliid species and each of the selected abiotic and biotic variables were evaluated using curvilinear, or polynomial, regression techniques similar to those outlined in Draper and Smith (1966). Due to the difficulty of interpretation, polynomials higher than third order were not considered. As soon as the correlation coefficient (or index of correlation for the curvilinear functions*) became significant, higher order polynomials were not considered. If the third order correlation was non-significant the relationship was considered to fluctuate randomly. For the presentation of this data scatter diagrams were not included due to the number of data points involved and the number of regressions presented.

*The index of correlation was calculated by taking the square root of the coefficient of determination, R^2 ; and thus was actually an absolute value. To aid in interpretation positive or negative signs were added based on the nature of the regression expression and the signs of the dominant coefficients.

5. Model building. a. Philosophy. Basically models can be constructed either by a priori insight into the nature of the coactions to be modelled or a posteriori evaluation of the data. A priori theoretical models such as those suggested by Lotka (1920, 1925), Volterra (1926), and Nicholson and Bailey (1935) who derived mathematical functions to describe biological events by intuitive insight and deductive reasoning. These models have yet to be evaluated in the field due to the effects of extraneous factors not included in the model. A posteriori models have evolved with the advent of experimental statistics and digital computers and are of three main types: 1) life tables, 2) computer simulation, and 3) regression or least squares. Life tables as suggested by Deevey (1947) provide a useful summary of the vital statistics of a population from which r (rate of increase) values can be estimated. Fluctuations in these values under different sets of environmental conditions have been used to generate population models (Harcourt, 1969). The main disadvantage to this technique centers on the assumptions of cohort integrity. Discrepancies induced by unmonitored additions or deletions invalidate the conclusions. At Honey Creek, simuliid populations exhibited a multi-brood phenology with complete generation overlap precluding the application of these techniques. Computer simulation models as reviewed by Clymer (1972) are of real promise in evaluating population dynamics; however, the designation of the intercompartmental flow functions rely heavily on either a priori or regressions methods. Least-square regression techniques are widely accepted as a statistical tool to represent the functional relationship between a designated dependent variable and a set of independent variables. These techniques have been utilized in predictive model formulation by Morris (1957, 1963), Hardwick and Lefkovitch (1971), and others; however, this technique has received some criticism from

Watt (1962), Varley and Gradwell (1970), Luck (1971), and others. The main criticisms center on the assumptions of the least square techniques, the requirement of linearity between the dependent and independent variables, and the possibility of significant colinearity among the independent variables which unjustly increases the overall correlation of the expression without adding to its realism. For this study, regression techniques were chosen for model formulation because: 1) the techniques are well worked out and easy to apply; 2) the model requires the least subjectivity or intuitive insight; e.g. the interrelationships between the variables themselves generate the model rather than the wishes of the researcher; and 3) the end product is an easy to use predictive expression which is simple to test.

b. Protocol and model assumptions. Benthic sampling, at least within the area of the simuliid population, was considered random while drift rates were sampled completely at random. Independent variables were not fixed, but rather were considered to be a Model II regression (Sokal and Rohlf, 1969). The assumptions of homogeneous variances and normal distribution of the variables were considered realistic for the data collected although a lack of replication precluded actual evaluation. Multiple regression techniques assume linearity between the independent and dependent variables (Draper and Smith, 1966); however, many biotic interactions are curvilinear. To fulfill this assumption several previous workers (Pearson and Franklin, 1968; Reisen and Fox, 1970; Reisen and Prins, 1972; and Pearson and Kramer, 1972) have used a Log_{10} transformation of the dependent variable. If all variables functioned in a multiplicative fashion this method would suffice; however, if the interactions were mixed linear and curvilinear, this technique would weight the results for the curvilinear functioning variables. To

preclude this error variables were screened initially using third degree polynomial regressions and appropriate transformations utilized to fulfill the assumptions of linearity. To prevent meaningless variable loading, a step-up multiple regression was used thereby reducing colinearity, e.g. if 2 variables were correlated, only the variable with the highest correlation with the dependent variable would be loaded initially; in the next step of the analysis, the second variable would be loaded into the expression only if its partial correlation based on the already fitted function was significant. If independent variables are highly correlated, both are never added to the predictive expression.

Multiple regressions were employed in two ways in this study: 1) to generate realistic biological models, and 2) to generate predictive expressions. The biological models were calculated to depict the interactions between the designated dependent variable and all possible variables both biotic and abiotic. For this model slope values were not presented; only R , R^2 , and the increase in R^2 as utilized by Pearson and Kramer (1972). The predictive models were limited to a more stringent set of criteria to reduce the size of the model, and only readily measured variables were considered, e.g. the density of other organisms were not included because for the effort expended monitoring another population, the simuliid density might just as well be monitored.

c. Mechanics. Third degree polynomial regressions were performed using computer program LAPEL115 which was stored on disk at the University of Oklahoma computer center. Step-up multiple regressions were calculated using computer program BMD02R described in Dixon (1970). This program allows for the transgeneration of new variables based on a series of user designated transformation options, and the deletion of specified variables. Thus, if an

independent variable was transgenerated because of its curvilinear coaction, the untransformed linear variable was deleted to prevent the possible loading of the same variable twice.

6. Analysis of variance (ANOVA). To compare means in time series data 2-way ANOVA without replication were employed with the main effects being the specified means and time (date of observation) (Sokal and Rohlf, 1969). To test the differences between blocks of hours, activity periods, in the 24-hr drift studies, 3-way ANOVA without replication using orthogonal comparisons were conducted. The ANOVA was a mixed model with time and hours considered fixed effects and net position considered random. Orthogonal comparisons were thus tested with the nets x time interaction term based on the expected mean squares (Sokal and Rohlf, 1969). Unless otherwise specified the level of significance for all analyses was 0.05.

IV. Results and Discussion

A. Limnology. The seasonal fluctuations of the selected physical and chemical variables and algal biomass are presented in Figures 4, 5 and 6, respectively, and the yearly means are presented in Table 2. There was no significant difference between Stations 4 and 8 for dissolved oxygen, alkalinity, coulter counts, conductivity, phosphate, or nitrate -N. Algal biomass curves seemed to closely parallel each other for all stations (Figure 6); however, the carrying capacities varied. pH was significantly higher at Station 4 than at Station 8 which was attributable to the higher standing crops of algae at Station 4 (Table 2). The greatest discrepancies between the two stations seemed to come during the fall and early winter of 1972 (Figure 5), which corresponded to alkalinity increases at Station 8 during the same period. There was a significant correlation between pH and alkalinity at Station 8 ($r = -0.391$) while there was no relationship at Station 4 ($r = 0.180$). This negative interaction has been observed in limestone rock holes by Reisen (1973) who attributed these findings to lower pH's dissolving the limestone substrata and thus allowing more bicarbonate to remain in solution as the buffer system shifted to the left. This same interaction was similar for the main stream, for as pH increased due to photosynthetic activity caused mostly by Myriophyllum sp. (Minckley, 1963), the measureable alkalinity correspondingly decreased as the bicarbonate was used photosynthetically and the travertine (Ca- and $MgCO_3$) was precipitated from solution. During the winter months when Myriophyllum photosynthetic rates were reduced, precipitation rates correspondingly decreased allowing more of the bicarbonates to remain in solution, and thus be detectably higher at Station 8. Water temperatures were also colder allowing more CO_2 to enter the system by

diffusion. Increased stream discharge from November 1972 through 1973 also facilitated this downstream increase in bicarbonates.

The correlations among the selected limnological variables are presented in Table 3. Dissolved oxygen was not correlated with algal biomass, but rather with decreasing water temperatures (Table 3). Water samples were all taken at the base of riffles where physical agitation kept the dissolved oxygen concentrations near 100% saturation. During the summer months dissolved oxygen concentrations within the Myriophyllum beds often became supersaturated; however, the physical agitation of the water flowing over the riffles caused a decrease in the dissolved oxygen concentrations to approximately 100% saturation. The remainder of the significant interactions seemed readily discernable and followed the explanations presented previously by Minkley (1963) and Hynes (1972).

The correlation matrices (Table 3) also provided some insight into possible colinearity among the variables. In later discussions when environmental coactions are considered, the reader should remain cognizant of the possibility of false relationships due to variable interactions; for example: a significant negative regression with temperature may also lead to a significant positive regression with dissolved oxygen, even though dissolved oxygen may not have been the cause effecting the observed fluctuations in the biotic variable.

Changes in current velocity and depth for Stations 1, 3, 4, 5, and 6 are presented in Figure 7. These variables were measured concomitantly with benthic density.

B. Simulium collected. A check list of the simuliid species collected, their life forms, associated substrata, and longitudinal locations in Honey Creek are presented in Table 4. Subgeneric designations follow Wirth and

Stone (1968) and Stone and Snoddy (1969). Simulium species A will be described as a new species at a later date and was tentatively placed in the subgenus Hagenomyia based on its taxonomic affinities with S. (Hagenomyia) pictipes Hagen.

By collecting ovipositing females and larvae after eclosion, eggs and early instar larvae were associated. By comparing the key characteristics especially the apodeme patterns on the cephalic apotome of the immature larvae with those of the ultimate or last instar larvae with developed histoblasts; and by dissecting the respiratory histoblasts and comparing these with the pupal filaments, all of the immature stages were associated. Mature pupae on moist paper toweling allowed to stand in a shell vial at room temperature emerged in a day or so allowing the association of pupae and adults. The greatest taxonomic problems were with the early stages (instars 1 to 3). Throughout most of this investigation unless special methods were employed, the early stadia of species A and virgatum were not separated. They were readily discernable from venustum, vittatum and trivittatum.

Species A was the most abundant species collected followed in order of decreasing abundance by virgatum, trivittatum, vittatum and venustum. Species A and virgatum were most abundant in the open sunlit portions of the stream with travertine substrata. During the winter months their range was extended downstream to below I-35. This winter downstream range extension has been noted for other species (Ladle, et al. 1972) and probably related to increased discharge and reduced water temperatures during this period of the year. Simulium trivittatum, S. vittatum and S. Venustum larvae were most widely distributed during the fall and winter months.

C. Some quantitative aspects of the life history of S. species A and virgatum. Simulium virgatum and species A both laid their eggs in dense masses

on water splashed rocks or travertine bordering riffles and waterfalls. During the spring when species A densities were high, grasses, and travertine encrusted detritus were also used as oviposition sites provided they were splashed with water. Oviposition occurred during the evening crepuscular period and was typically communal in nature with the size of the swarms varying seasonally. On 5 August 1972 a typical oviposition swarm of S. virgatum was closely observed. The swarm was first noticed about 1900 hours hovering over a portion of travertine continually splashed by the stream waters. The swarm consisted of about 100 flies and was conical in shape as described by Smart (1934a). The swarm was not readily disturbed even by the netting of several specimens. Females continuously dropped out of the swarm and entered the water to oviposit. Layer upon layer of yellowish-white eggs were laid. Occasionally a female would become entangled in the glue of the egg mass and was unable to escape and drowned. Such females continued to oviposit until spent. Females usually entered the swarm from downstream (wind velocities were negligible during this period). These females could have been reentering the swarm after being washed downstream after ovipositing; however, this was never observed. The upstream movement of lotic insects prior to oviposition as part of a colonization cycle to replenish populations at the source has been previously presented by Roos (1957), Lehman (1970) and Pearson and Kramer (1972) and specifically for simuliids by Carlsson (1962) and Müller (1966). Oviposition continued until 2100 shortly after sunset. The size of the egg mass produced was estimated to be 10.3 cm long and 3.8 cm wide, and about 1.5 mm thick at the center. The eggs turned orangish-brown by the next morning and were black on the following day as development progressed. Several sweeps with a small hand net yielded 12 gravid females and no males. Subsequent observations for both S. virgatum

and species A were consistent with the previous description and similar to the observations of Smart (1934a), Stone (1964), and Stone and Snoddy (1969) for S. pictipes Hagen. Although oviposition site preferences, and seasonal and diel periodicities overlapped, the species composition of the oviposition swarms remained homogeneous.

The number of eggs laid per female was hard to estimate. Sporadic collections of ovipositing females were made, their abdomens dissected, and the numbers of eggs counted, the percentage of the eggs laid, and the number of unripe eggs rated subjectively 1 to 4 (Tables). The number of eggs ranged from 200 to 400 for both species A and virgatum which was in good agreement with most of the previously presented Simulium estimates included by Davies and Peterson (1956), Peterson (1959) and Abdelnur (1968); but somewhat less than the number of immature oocytes reported for emerging blackflies by Chutter (1970). Practically all of the flies examined had completely digested their blood meals prior to oviposition. Based on the rating of the number of immature oocytes, the age composition of the oviposition swarms was considered heterogeneous.

By marking freshly laid egg masses and visiting them daily, it was possible to estimate the length of time from oviposition to first eclosion. At stream temperatures between 25.0 and 26.7°C. development took approximately 4 days for the average sized egg mass. Those eggs deposited first and covered by subsequently laid eggs were found to take the longest to hatch by Gambrell (1933) as were larger egg masses which were observed to take longer to complete eclosion. Stone (1964), Stone and Snoddy (1969), Wu (1930) and others also found that eclosion commenced about 4 to 5 days after oviposition.

In order to determine initial cohort size, it was necessary to estimate egg mass densities. By carefully removing the travertine on which the eggs

were laid, it was possible to remove the entire egg mass and take it to the laboratory. Here a given area was scraped from the center of the mass, mounted on microscope slides in Hoyer's medium, and counted at 10x. Three egg masses collected on 22 July 1973 had an average egg density of 4656.67 eggs/cm² with a standard error of the mean of 271.33. By calculating the total area of the egg mass, it was possible to extrapolate the total number of eggs laid. For example, an egg mass laid on 15 August 1972 at Station 6 was calculated to contain a total of 90,128 eggs. With a conservative estimate of 300 eggs/laid per female per night, it would have taken the combined efforts of about 300 females to lay an egg mass of this size. In May 1973 species A egg masses as large as 181.5 cm² were observed suggesting that oviposition swarms must attain size greater than 2500 females.

The number of simuliid larval instars has been a moot point. Estimates in the literature include 4 (Puri, 1925; Smart, 1934b), 6 (Yakuba, 1959; Stone, 1964; Stone and Snoddy, 1969; and others) and 7 (Carlsson, 1962; and Johnson and Pengelly, 1970). Studies in which larval measurements were made have been used mostly for growth experiments (Phelps and DeFoliart, 1964; Ladle, et al, 1972) with the exception of Johnson and Pengelly (1970) who estimated 7 larval instars for Simulium rugglesi Nichol and Mickel. Estimates of the number of larval instars for Simulium virgatum and species A using the head-capsule-width-frequency distribution method are presented in Figure 8. Specimens for this study were collected from eclosion to pupation during cohort analysis experiments at Stations 3 and 6. Initial counts were for 0.02 mm classes; however, these were later pooled into 0.04 mm classes and plotted in Figure 8. For Simulium virgatum there were 6 well defined peaks suggesting 6 larval instars; however, there was more overlap for Species A especially among the older instars. Poor peak definition was attributed to

apparent size differences in the male and female pupae. An average of 5 randomly chosen male and female pupae for S. virgatum weighed 0.00534 and 0.00653 grams, respectively. Estimates for species A were: males = 0.00318 grams, females = 0.00467 grams. Due to these discrepancies in size more older individuals had to be measured to delineate the peaks. Due to the high degree of instar overlap, age designations for most of this investigation were subjectively chosen based on the following criteria:

small larvae: head capsule width less than 0.3 mm; not separated into virgatum and species A.

medium larvae: between 0.3 and 0.5 mm.

large larvae: greater than 0.5mm, but without well-developed dark respiratory histoblasts.

ultimate (last) larvae = greater than 0.5 mm and having well defined black respiratory histoblasts.

pupae: males and females were not separated; for species A all filament configurations were pooled.

When total larval densities are presented, the small larval class has been partitioned into virgatum and species A categories based on the percentage species composition of the collection.

By taking the weights of random measured specimens, a weight to head-capsule-width curve was calculated (Figure 9). Weights used were alcohol dry weights similar to those used by Reisen (1972) and Reisen and Prins (1972). After dependent variable transformation, regression expressions were significantly correlated (species A, $r = 0.8691$; virgatum, $r = 0.9820$). Mean cohort growth curves for S. virgatum at Stations 3 and 7 were calculated from the regression expressions in Figure 9b and are presented in Figure 10. These curves agreed with those presented for other simuliid species by Davies and Syme (1958), Phelps and DeFoliart (1964), Obeng (1967), and Ladle, et al. (1972).

Population parameters for three cohorts of Simulium virgatum at Stations 3 and 6 are presented in Table 6. Environmental conditions during this study were presented in Figures 4, 5, and 6. At Station 3 all of the virgatum larvae eventually pupated and emerged leaving only species A larvae. At Station 6 two cohorts, a and b, were established initially, but after 31 August 1972 their population areas had intermingled and were indistinguishable. By 16 September 1972 cohort pollution, indexed by an increase in the standard error of the mean of the head-capsule-width and the density of species A as well as a field-observed progressive lack of uniformity in the dispersion, made accurate determination of the population area impractical and a rough estimate of 13,000 cm² was used for subsequent calculations. Cohort pollution seemed to increase during virgatum pupation.

Several trends seemed to emerge. Density decreased with increasing age and size as indexed by increasing head-capsule-width. Biomass (calculated by multiplying the regression solution of the weight vs head-capsule-width-curve times the benthic density) (Figure 9) initially decreased rapidly, but later remained constant even though the individual larvae increased in size. The total population area increased as the larvae aged and moved progressively into faster and deeper water away from the egg mass, usually downstream. This observation of early instar movement has been observed for other species by Yakuba (1959), Rubstov (1965), Kureck (1969) and Rühm (1969, 1970). At Station 6 when the mean population head-capsule-width reached 0.48 mm (or about 4th instar), the total population area was maximized, and only minor alterations were observed from this point on. At Station 3 pupation and emergence decreased total cohort numbers causing a reduction of the population area.

From the estimates of total population (cohort) numbers in Table 6, life tables were calculated and presented in Table 7. For these statistics cohorts 6a and 6b were pooled. As indicated in Table 7, sampling schedules (column x) were somewhat erratic making the values of e_x less meaningful. Another sampling error (indicated by those rows marked with an *) occurred when the estimated population numbers for $x + 1$ were greater than x . Immigration and emigration rates were not measured consistently; however, drift rates measured below Stations 5 and 6 on 30 September 1972 did indicate that greater quantities of larvae were drifting off Station 6 than were drifting on from Station 5 (Station 5 = 104 total virgatum larvae in 24 hrs; Station 6 = 321 virgatum larvae). This data indicated that the observed discrepancies were most likely caused by an under-estimation of benthic density or total population area. Death rates (d_x) during this period must certainly have been minimal to have remained undetected, so survivorship (l_x) values during these periods were considered constant and d_x values zero.

To aid in interpretation, survivorship curves (l_x values) are presented in Figure 11. The time of greatest mortality, or emigration by drift, was from eclosion to about 4th instar giving the curves, especially for Station 4, a typical invertebrate type III appearance (Deevey, 1947). From field observation as well as from drift data presented later, population losses seemed more gradual from this point to pupation, the next significant population movement (Maitland and Penney, 1967; Ulfstrand, 1967; and others). For virgatum this movement was of minimal distance, and consequently population losses for these age groups were less than those reported by Yakuba (1959). Semushkina (1962), and LeBerre, et al. (1964) who found either equal or older instar dominated emigration rates. In Honey Creek all riffle areas fed fairly deep pools which supported high populations of Phoxinus erythrogaster

(Rafinesque), Campostoma anomalum (Rafinesque), Lepomis megalotus (Rafinesque) and Etheostoma spectabile (Agassiz). These fishes readily consumed dislodged blackflies during periods of normal discharge which was consistent with the findings of Chaston (1968), Reisen (1972), and Elliott (1973), and suggested that few of the larvae survive once they have drifted into pools. Another statistical parameter which supported the eclosion mortality hypothesis was e_x which consistently was maximized after $x = 0$; at Station 3 when $x = 11$ days, at Station 6 when $x = 4$ days.

Initial d_x values were higher for Station 3 than Station 6. Two possible factors may have been important here: 1. The current velocity at Station 3 was lower (Station 3 = 86.546 cm/sec, Station 6 = 207.530 cm/sec on 19 August 1972) perhaps causing larvae to move farther from the site of eclosion to find suitable attachment sites and thus increasing their chances of being accidentally swept away. 2. Initial densities at Station 6 were much higher than those for Station 3 (Table 6). With more individuals emerging more silken strands were being attached to the substrate as the larvae dispersed perhaps making it easier for successive larvae to more readily secure a "foothold" with the proleg and posterior circlet crochets.

The length of larval life from eclosion to pupation ranged from 21 to 35 days for virgatum at 25 to 27°C. which was slightly longer than values reported for the northern species by Wu (1930) and Rühm (1970b). By observing marked individual pupae of both virgatum and species A during this time, pupation was estimated to last from 4 to 5 days.

Male mating swarms for both Simulium virgatum and species A were observed at the base of riffles which agreed with the observations of Wu (1930), Nicholson and Mickel (1950), Davies and Peterson (1956), Peterson (1962), Williams (1970), and others. When emerging females entered the swarm, they

were seized immediately and taken to the ground where copulation occurred. Insemination was accomplished in a matter of seconds after which the pair separated quickly and flew away. No females of virgatum or species A were ever collected by sweeping the grasses along the stream, so it was assumed that they immediately left the stream after emergence and mating (Carlsson, 1962).

As summarized by Fallis (1964), female virgatum have been reported to feed on horses in Mexico. Due to their taxonomic affinities, species A was speculated to have similar feeding habits as S. pictipes which has been reported to feed on man, horses, mules and moose (Fallis, 1964). During the hours of close field observation, the author was never bitten or approached by either species. Horses were pastured between I-35 and the Washita River during 1972 and the 1st 4 months of 1973. The pasture above spring 2 was used to graze herford cattle as was the above mentioned pasture after May, 1973. The propinquity of these suitable blood meals most likely added to the success of both species.

Females after feeding returned to the stream to oviposit, seeking clean sunlit sections of travertine. S. virgatum was less tolerable of periphyton than was species A which also oviposited on trailing grasses, moss, algae and occasionally travertine encrusted detritus. The regional distributions of these species in Oklahoma seemed to be limited to streams with travertine or similar type substrata. Both species were collected at Prices Falls, Murray County and Travertine Falls, Pontotoc County, Oklahoma.

D. Seasonal bionomics. The seasonal changes in the benthic densities of Simulium virgatum and species A for Stations 1, 3, 4, 5, and 6 are presented in Figure 12 and those for Stations 8 and 9 are presented in Figure 13. Benthic densities of species A were generally higher than the densities of virgatum. Species A was most abundant during the spring and early summer of 1973 while virgatum was most prevalent during the late summer, fall and early winter of 1972. These peaks imply increases in numbers and not generations, for larval development continued all year long although the rate of development was reduced during the periods of colder water temperatures. No egg masses were observed for either species from 19 November 1972 through 4 March 1973, although emerging adult flies were collected throughout the year. To analyze changes in age composition, Stations 1, 3, 4, 5, 6, and 7 were averaged over each of the designated age groups (reference = stream means), small, medium, large and ultimate larval and pupal densities, and the percentage age composition calculated. The total densities for species A and virgatum as well as the percentage age composition are presented in Figure 14. In Figure 14 the entire area between each of the lines was used to depict changes in the relative percent composition of that age class. The percentage of small and medium sized larvae were highest when population densities were greatest which further supported the trends depicted in the virgatum life tables (Table 7). It seemed that the older larvae turning to pupae in late winter were the overwintering stages. By the end of February all the pupae were gone and replaced by younger age groups. This apparent synchrony was due to a phenomenon of water chemistry and decreasing temperature rather than any inherent population attribute. Discharge increases during November, 1972 (Figure 4) resulted in stream nutrient enrichment (Figure 5) which was followed by a rise in periphytic

algal biomass (Figure 6). A major floral component during this time was Phormidium which was considered an important element in travertine precipitation by Minckley (1963). Accelerated algal growth during these periods removed nutrients from the water reducing the amount present in water samples as well as increasing the pH causing a precipitation of travertine (Minkley, 1963; Hynes, 1972). Reduced virgatum pupal developmental rates during this time allowed the pupal cases to be overgrown by the Phormidium and eventually "cemented" in the travertine. Bottom samples revealed large quantities of dead virgatum pupae (densities ranged from 0.0/cm² during early December, 1972 to a maximum of 1.695/cm² in 17 February 1973 at Station 6). Species A pupating during this time, although less in numbers, shared a similar fate. This theory of travertine deposition mortality was also supported by the discrepancies in total alkalinities between Stations 4 and 8 during this period as discussed earlier (Figure 6).

Another series of environmental factors undoubtedly contributed to the mortality of emerging adults during the winter period. Those pupae able to escape the Phormidium were able to develop and eventually emerge. The temperature of the stream at this time remained between 10 and 20°C.; however, air temperatures occasionally dropped to below 0°C. especially in the early morning hours. Thus adults emerged from a moderate water temperature into freezing air temperatures. During a snow storm on 17 February 1973, for instance, large numbers of adult flies were observed slowly creeping along the ground or floating on the water surface. They seemed unable to fly even after being agitated by the author. Those individuals unable to leave the water most likely drowned or were consumed by fishes, while the prognosis for those individuals who made it to shore did not seem much better as they were easy victims for predators as well as subject to cold mortality.

The seasonal abundance of Simulium trivittatum calculated by averaging Stations 1, 3, 4, 5, 6, and 7 is presented in Figure 15. The individuals collected in the benthic samples represented the population surplus since this species preferentially utilized trailing grasses as substrata. These individuals represented that portion of the population which was either dislodged accidentally, or forced to emigrate due to crowding or receding stream waters. Population densities were highest during the fall months; however, both larvae and pupae were present throughout the year on trailing grasses. Once during the spring (April, 1973), the author was bitten by a single female. Although no other encounters occurred during this study or have been reported in the literature for the midwest, anthropophilism appears characteristic for this species in California according to the findings of Anderson and Voskuil (1963).

E. Abiotic and biotic environmental coactions. Density estimates for the different age groups were essentially homogeneous in phenology; however, due to variability in the magnitude of these estimates coupled with numerous zero values and missing data for certain times of the year average estimates were used in the regression analyses. Total numbers of larvae and pupae were coded by $y = y + 0.005$ which did not alter the least square estimates such as slopes and correlations, but did change the intercepts and means (Sokal and Rohlf, 1969).

Correlation values for the larval and pupal classes for species A and virgatum stream means with selected limnological parameters collected at Station 4 are presented in Table 8. Significant correlations were presented for the lowest degree polynomial attaining significance ($\alpha = 0.05$). Significant polynomial regressions are presented in Table 8 and depicted graphically in Figures 16, 17, and 18. For linear regressions, the positive maximum, mean,

and minimum values were plotted; for higher order expressions maximum, mean, minimum and two other values were plotted.

Small larvae (Figure 16a) and species A medium, large, and ultimate larvae (Figures 17a, b, and c) showed a significant positive regression with algal biomass, while medium and large virgatum larvae and pupae (Figures 17a, b, and d) exhibited a significant negative linear response. Algal biomass was highest during April and May (Figure 6) which paralleled the time of greatest species A density. Since the majority of small larvae collected at this time belonged to species A, small larvae tended to follow the trends for species A, especially species A medium. The synchrony between species A and algal biomass was due either to increases in temperature and day length which stimulated them both simultaneously, or due to trophic coactions. As reviewed by Burton (1973) simuliid larvae have been reported to graze on periphytic filamentous algae such as Spirogyra and Oedogonium which were both abundant on the travertine during the spring months. Although gut analyses were not included, field observations showed that the algae in the vicinity of blackfly larvae was always trimmed back to the point where the substrata was visible. Also species A seemed to tolerate dense periphyton and the small larvae even utilized it as a substrata which contrasted the observations of Sommerman, et al. (1955) and Carlsson (1962) for northern species. The negative interaction of virgatum with increasing algal biomass was most likely due to the pupal mortality presented earlier, or perhaps to a lack of seasonal synchrony with periods of maximum algal production. This negative interaction hypothesis substantiated the findings of Sommerman, et al. (1955) and Carlsson (1962).

Small larvae exhibited a positive parabolic curve with increasing water temperature (Figure 16b) which was attributed to midwinter and midsummer

decreases in oviposition.* After the initial species A dominated spring increases, small larvae densities were reduced until the late summer and fall when virgatum dominated. During the periods of coldest midwinter temperatures, simuliid densities were greatly reduced and small larvae virtually absent. Species A medium and large larvae showed a positive linear regression with increasing water temperature (Figures 17e and f) while pupal densities showed a significant negative linear regression (Figure 17h). Positive correlations were related to species A increases in the spring; however, the response of the pupae was more difficult to interpret. Perhaps the early spring pupation of the overwintering larvae, and the decrease in population densities during the summer resulted in this negative response. Medium virgatum larvae showed a positive linear regression with increasing water temperature (Figure 17e), while large and ultimate larvae exhibited a negative parabolic response (Figures 17f and g) and pupae showed a negative linear response (Figure 17h). The late summer dominance of the medium stage resulted in the positive linear response. As shown in Figure 5 temperatures seemed to drop more precipitously in the fall than in the spring, so consequently a late summer, fall, and early winter form would be present during the period of temperature extremes and at lower densities during the more intermediate temperatures of the spring which would explain the negative parabolic response of the large and ultimate larvae. Since pupal densities were higher during the late fall and early winter months (Figure 14), a negative response would be expected.

*For significant curvilinear regression of the form presented in Figure 16b, "parabolic type curves" were considered negative when the midrange values were at the minimum and positive when the midrange values were at the maximum.

The explanations for the responses to increasing day length (Figures 16c, 17u, v, w, and x) were essentially the same as those for temperatures since day length and temperature showed a significant positive correlation ($R = 0.747$). It was difficult to discern whether day length or temperature were the factors triggering the observed fluctuations in the simuliid benthic densities.

Although Wu (1930), Grenier (1953) and Ivaschenko (1972) suggested that dissolved oxygen might exert a significant effect on larval simuliids, Carlsson (1962) experimentally determined that larvae were able to tolerate wide fluctuations in dissolved oxygen saturation levels. As shown in Figure 5 dissolved oxygen for either Station 4 or 8 was never observed below 6.5 ppm which was well above the critical minimum for simuliids according to Carlsson (1962). Water samples were taken at the end of riffles, so that the dissolved oxygen concentrations usually approached 100%. The water flowing directly onto riffles from the elongated Myriophyllum choked runs was supersaturated during the day and often depleted of oxygen during the predawn hours. For example, on 17 July 1973 diurnal dissolved oxygen curves taken just below a pool about 50 meters upstream from Station 1 had a 24-hr variation in dissolved oxygen ranging from 11.2 pp. (148% saturated) at 1200 to 6.1 ppm (72% saturated) at 0200; while concomitant readings below Station 4 were 8.2 ppm (106% saturated) and 7.7 ppm (92% saturated), respectively. Hornuff (1957) reported dissolved oxygen concentrations of over 12.0 ppm in similar pools along Honey Creek. These higher values were above the critical maximum suggested by Carlsson (1962) based on the consequences of sudden changes in gas pressure which he observed to cause the precipitation of oxygen bubbles in the tissues of salmonids (Carlsson, 1956). Later Carlsson (1967) reported that supersaturation caused the formation of gas bubbles on the cephalic fans of simuliid larvae which was always fatal. Diel changes in dissolved oxygen tension at Honey Creek were extensive enough to cause the damage reported by Carlsson (1962,

1967); however, these changes were apparently gradual enough to prevent mortality as these symptoms were never observed in Honey Creek simuliids. Thus, the changes in the dissolved oxygen at Honey Creek did not seem critical and the significant regression presented in Figures 17i, j, k, and l were most likely related to the significant negative correlations between dissolved oxygen and temperature ($r = -0.936$) or day length ($r = -0.679$).

S. virgatum larvae showed a significant negative linear regression with discharge (Figure 16d, e, and f). As shown in Figure 4, discharge was minimal during the late summer and fall of 1972 when virgatum densities were highest. Usually increased discharge was followed by increases in nutrients and eventually algal biomass. This interaction may have caused the negative effect of current as depicted in Figure 16 and may also have been responsible for the significant negative linear regression with rainfall (Figure 16i). Alternatively, spates may have scoured the travertine directly reducing population densities.

Alkalinity and pH at Station 4 were not significantly correlated ($r = 0.180$) even when higher order functions were considered. As mentioned earlier a possible cause for this discrepancy was the precipitation of the travertine which precluded detection of some of the carbonates in the water samples. The significant interactions of the simuliid larvae with pH and alkalinity are presented in Figures 17m, n, o, and p and Figures 17q, r, and s respectively. Significant virgatum functions were all negative parabolic curves and probably related to interactions with the carbonate buffer system. The cubic responses of species A with alkalinity were perhaps related to the algae-alkalinity phenomenon although algae and alkalinities were not correlated with one another ($r = -0.202$).

Although coulter counts were theoretically a measure of the amount of available suspended food (Williams and Hynes, 1973), they consistently displayed

a negative response or none at all (Table 8, Figures 16g and h, Figure 18). In addition to abundance of suspended foods this technique was also an indicator of suspended particles and seemed to fluctuate independently of the other parameters (Table 3). Perhaps the negative effect of auxotrophy discussed by Carlsson (1962) may have some relevance although turbidity estimates rarely exceeded 0.5 JTU's except during spates.

In general, the responses to the abiotic variables of the different age groups were consistent at least amongst adjacent age classes. Ultimate and pupal classes seemed to have different responses than medium or large larvae. Small larvae were weighted for species A and more closely paralleled the responses of species A medium larvae. This was also shown in the interactions of the larval totals with the limnological parameters from Station 4 listed in Table 10 and depicted in Figure 19. Significant differences in the responses among the different age classes caused the deletions observed.

Although significant negative coactions among the simuliids due to differences in phenologies and possibly competition, both scramble and interference (Birch, 1957), were expected, the only significant correlation was between virgatum and trivittatum ($r = 0.3115$). As depicted in Figure 19h, this interaction was positive ($y = 1.3398 + 6.8364x$, where $y = \text{virgatum}$ density and $x = \text{trivittatum}$ density) and most likely due to similarities in the two species seasonal occurrence (Figures 14 and 15).

The time series correlations between changes in larval density and depth and current velocity as well as interspecific coactions for Stations 1, 3, 4, 5, and 6 are presented in Table 11 and the significant polynomial regressions are presented in Table 12. Almost all investigators who have evaluated simuliid larval distributions have considered depth and current velocity as two of the more important dispersion regulating factors (Dalmat

1955; Phillipson, 1957; Carlsson, 1962 and 1967; Egglshaw, 1964; Ulfstrand, 1967; Maitland and Penney, 1967; Chutter, 1968; Depner, 1971; Ivashenko, 1972; and others). Field observations showed that simuliid larvae were usually found in similar types of riffle areas through which there was suitable discharge. The blackflies (Table 2) were never collected in water with a current velocity of less than 70 cm/sec or in those areas where current velocities consistently exceeded 300 cm/sec. Although the mode of measurement may have been important here, these current velocity observations were much less than the critical values reported by Philipson (1957). Only after or during spates were larvae ever found in water deeper than 30 cm and species A and virgatum seemed to prefer even shallower depths. Depth and current velocity readings (Figure 7) stayed well within these extremes throughout the course of this investigation. The effects of changes in depth and current velocity on seasonal population changes were hard to interpret. Depth and current velocity readings were always estimated where the bottom samples were taken, and bottom samples were always collected in areas supporting simuliid larval concentrations; so the readings taken represented the conditions under which the population was living rather than the limiting values found in neighboring parts of the stream. Depth, although not always significant, showed a consistent negative response (Figures 20a and b, 21a). The mean simuliid densities were always at depths less than 6 cm suggesting this value was near the optimum. The response to current was more difficult to interpret being both negative and positive for different species at different stations. Density means did consistently fall near 200 cm/sec perhaps suggesting this was near optimum for these species.

Similar polynomial regression analyses were conducted on the total densities of Simulium species A and virgatum at Stations 8 and 9, the results of which are presented in Tables 13 and 14 and in Figures 21 and 22. As

mentioned earlier except for pH and algal biomass, there was no significant difference between the limnological parameters measured at Stations 4 and 8; however, there were noticeable differences in the responses of the simuliids. As shown in Figures 13a and b blackflies were completely absent from Stations 8 and 9 during the summer months which undoubtedly altered the response patterns and caused the discrepancies in the correlations (Tables 8 and 13) and the regressions (Table 10 and 14; Figures 19, 21, 22). At Station 8 for species A temperature had a similar response to that mentioned earlier; however, pH, alkalinity, and day length were noticeably non-significant. At Station 8 for virgatum, no similarities of response were observed; in fact, even different variables were significant. The response of virgatum to increasing water temperature was essentially the same as that for species A mentioned earlier. Being absent during the summer months at Station 8 caused the negative slope at high temperatures; however, the cause for the inflection point at the lower temperatures was not readily discernable. The positive parabolic response to increased rainfall (Figure 22b) was most likely due to the absence of virgatum larvae during the summer when rainfall was low and the negative effect of spates on the population density during the winter.

Most investigators (Fredeen and Schoemanhuk, 1960; Carlsson, 1962; Kureck, 1969; Pearson and Franklin, 1968; and others) have considered both inter- and intraspecific competition, exploitation (Birch, 1957), for food and attachment sites as being a critical regulatory factor in larval blackfly populations. Burton (1971) has reviewed the occurrences of both cannibalism and predation, interference (Birch 1957), observed among blackflies. To test the nature of these interactions at Honey Creek, a series of polynomial regressions were calculated among the different species of simuliid larvae (Tables 11, 12, 13, and 14). The correlations were significant for the responses at Stations 4, 8, and 9; however, none of the slopes were negative.

At Station 9 the positive linear regression suggested that both species were being equally influenced by other factors. Station 4 and 8 showed a positive quadratic response with both low and high densities. The low range depression was most likely due to the effect of winter conditions when both species exhibited lower benthic densities, while the high range depressions could relate to: 1. competition for virgatum densities were low during the spring when species A were highest; 2. differential predation by Trichoptera larvae described later; or 3. phenological segregations due to the interactions with other controlling environmental factors. Since the majority of the benthic densities at Stations (1, 3, 5, and 6) were not correlated, and since those correlations which were significant were positive (4, 8, and 9), it would seem that these two species did not significantly effect one another in a negative fashion. Possible explanations for this apparent coexistence, or amensalism, included: 1. the sampling technique did not actually detect the negative interaction; 2. the time scale of slightly over 1 year was not long enough to detect actual species population replacement trends; 3. the separation of phenological patterns coupled with population declines during the winter months for both species confounded the results and prevented the negative interactions from becoming statistically significant; or 4. there was actually no significant negative interaction among the simuliid species.

Almost all ecological studies on blackflies have included lists of predators and parasites which have ranged from viruses through birds and fish. Throughout this investigation care was taken to search for parasites, especially the Mermithidae (Nematoda) (Welch, 1964) and Microsporidia (Protozoa) (Peterson, 1960; Frost, 1970; Gassouma, 1972; and others); however, none were observed. Adult mermithids were occasionally recovered from drift samples; however, since no simuliids were found infected and several chironomid larvae

were, it was assumed these worms were not simuliid parasites. Davies (1959) found mites of the genus Sperchon parasiting blackfly pupae and adults. Another member of the family Sperchonidae, Spherchonopsis verrucosa (Protz.) (as determined by the characters presented in Pennak, 1953), was collected in the benthic samples during the summer months. This species was never found within or attached to pupal cases, and all of the adult flies examined were free of mites. The linear correlations between Simulium species A and virgatum and the associated fauna is presented in Table 15. Values were only presented for those species consistently appearing in benthic samples. Of the fauna listed in Table 15, the Diptera, Ephemeroptera and Coleoptera were considered herbivores and possible competitors for the periphyton while the Trichoptera probably competed for space and filterable food and were possibly predators. Although Wu (1930) and Bahrova (1971) described a parasitic or predatory association of chironomid larvae and simuliid pupae, none of the chironomids found at Honey Creek were observed in intimate association with the simuliids. For the most part they were herbivores burrowing through the algae or travertine and rarely were found on the travertine surface where the blackflies attached and pupated. Reports of immature trichopteran predation, especially the families Hydropsychidae and Philopotomidae, have been recently reviewed by Burton and McRae (1972). These insects usually share blackfly habitats and have similar feeding habits (Slack, 1936; Hynes, 1972; Williams and Hynes, 1973; and others). During this investigation hydropsychid populations became established at Stations 1 and 8. The specific determination of the trichopteran species from Honey Creek was difficult, since few associated larvae and adults are known from Oklahoma. Using the characters presented in Ross (1944) the simuliid associated larval specimens were determined as Hydropsyche near betteni Ross, Cheumatopsyche sp. (no keys available), and Chimarra obscura (Walker). The larvae of Hydropsyche bifida

Banks, H. simulans Ross, Smicridea sp., and Chimarra feria Ross were also collected from Honey Creek while the adults of Hydropsyche species A (near solex Ross), H. orris Ross and Cheumatopsyche analis Banks were taken by light trap. As shown in Figure 23, Trichoptera larvae were virtually absent throughout the winter and probably overwintered as either pupae or eggs. As shown in Table 15 there was not any significant correlation between the blackflies and caddisfly larvae. By comparing Figures 13a and 15, it seemed that there was some form of negative interaction occurring, especially at Station 8 where caddisflies remained prevalent during the summer months while the blackflies were eliminated. The absence of species A, the early summer dominant, from Station 8 was difficult to explain using only the measured limnological factors, since there was no significant differences between Stations 4 and 8 with the exceptions of pH and algal biomass. The midsummer densities of species A and virgatum at Station 1 were less than the densities at the other stations above Turner Falls during the same time period which may also have been attributable to larval caddisfly interactions. Whether this interaction was predation or competition for space was not resolved.

Significant positive correlations of blackfly larvae with ephemeropteran naiads were related to phenological similarities.

F. Simulium drift. Organic drift in streams has recently received considerable attention by ecologists. The growing volume of literature on this subject as well as the emerging concepts have been reviewed by Hynes (1972), Waters, (1972) and Bournaud and Thibault (1973). Although most results for the majority of organisms appeared fairly consistent, studies dealing with simuliids have yielded a variety of conflicting results. The emigration stimulus seems to be related to the interaction of age with photoperiod. Rubstov (1964) and Rühm (1970) suggested that the younger larvae would be better able to migrate because their smaller size would

facilitate passive transport by the current. Yakuba (1961) investigated the different age classes drifting and found mostly larger, or older, larvae migrating downstream. Tarshis and Neil (1970) and Carlsson (1962) found all age classes participating equally in emigrations. In addition to photoperiod which appears to be the "zeitgeber" stimulating nocturnal movements, the magnitude of the drift seems to be influenced by a variety of factors including sudden changes in abiotic factors such as current velocity, depth, temperature or dissolved oxygen tensions, increased simuliid larvae density, and the activity or density of the associated fauna (Carlsson, 1962, 1967; Pearson and Franklin, 1968; Disney, 1972; and Reisen and Prins, 1972).

Seasonal changes in the total 24-hr drift rates of Simulium species A and virgatum for all age classes are presented in Figure 24 while the total larval drift rates for S. trivittatum are presented in Figure 25. The drift rates presented are means between nets A and B which have been standardized for the volume of water passing through them. Comparisons between nets A and B for each age group using ANOVA techniques showed there were no significant differences thereby justifying the averaging of the nets. The locations of nets A and B for each study is presented in Table 16 and the depths and current velocities for each of the nets for each study are presented in Figure 26. The drift nets were moved to different stations because of increases in stream discharge or the amount of vacationer-induced-disturbance.

With a few minor exceptions the seasonal drift patterns fairly well followed the seasonal abundance patterns depicted in Figure 14. All age groups, in light of cohort survival (Tables 6 and 7), appeared to drift proportionately. Small larvae contributed by far the greatest numbers to the drift, supporting the previously presented hypothesis given for the high d_x values for $x = 0$. Movements from the egg mass to suitable attachment sites after eclosion enhanced their chances of being swept away by the current and probably was the cause of observed small larval drift (Rühm, 1970a).

Mass movement on silken threads or "life lines" as reported by Rubstov (1964) and Tarshis and Neil (1970) was never observed for either species A or virgatum. In fact efforts to induce this behavior by shadowing, changing the direction and velocity of flow, or crushing larvae upstream was unsuccessful; although when actively dislodged such as during collecting, the larvae would produce these silken threads. The morphology of the silk glands of both species appeared comparable to the descriptions presented by Hungerford (1913) and Puri (1924). Both species A and virgatum were observed to exhibit a previously undescribed behavioral pattern. In response to above mentioned stimuli, the larvae of both species would curl, usually to the left, and press themselves tightly to the travertine substrata (Figure 14c and d). Even removal of the substrata from the stream would not immediately cause an alteration of this posture; however, if continually shaded they would return to their normal feeding position (Figure 27a and b), or if the current flow was altered for a long time period, they would begin emigrating by geometrid type movement to more suitable attachment sites. Disturbed S. trivittatum also exhibited this behavior although to a less extent. They seemed to show a greater tendency to move by silken threads when disturbed. The ecological, or adaptive, significance would seem to be related to the type of substrata normally utilized. If virgatum and species A were to use silken threads of the dimensions reported by Rubstov (1964), they would stand a good chance of being swept into the pools below the riffles and consumed by fishes. Since their substrata was more or less continuous, movement by the geometrid, or "inch-worm" method, would allow them to sufficiently alter their position to find suitable depth and current conditions or pupation sites. Species such as trivittatum which live on trailing vegetation or even those living on cobble lack a contiguous substrata and movement to another

blade of grass was perhaps best accomplished by the life line method; the shortest distance between the two points.

Techniques similar to those used to evaluate relationships between changes in limnological parameters and benthic densities were also employed to evaluate possible causes for changes in the drift rates. Linear correlations among the limnological parameters used in these analyses are presented in Table 17. Variables 8, 9 and 10 were measured only for studies 6 through 17, and consequently had 5 less degrees of freedom. The values for these parameters (Table 2) did not appear to be limiting and correlations with simuliid larvae would be difficult to interpret, so consequently these variables were not included in the following analyses. A summary of the correlation coefficients for the polynomial regressions for both immature and adult 24-hr drift totals are presented in Table 18 and the significant expressions presented in Table 19. Again the lowest significant degree of the polynomial was used and its correlation presented. These regressions are presented in Figures 28 to 31.

As reviewed by Waters (1972) there are three types of autochthonous drift; 1. catastrophic 2. accidental, and 3. behavioral. Catastrophic drift was not directly measured in this study and would be caused by such factors as pollutants, floods, etc. The rainfall factor was a possible index of past catastrophic spates indirectly monitoring these perturbations. Accidental drift, the passive removal of organisms accidentally caught in the current, would be constant all day, and represent a baseline for the behavioral drift. Behavioral drift was that portion of the drift attributable to the activity and movements of the larvae. One of the frequently presented explanations for behavioral drift was that it comprised the portion of the population in excess of the carrying capacity of the stream (Waters, 1961). As discussed by Reisen and Prins (1972), if this theory were true, drift would

respond in a positively curvilinear manner to increasing benthic density and approach the form of the curve presented by Dimond (1967). As depicted in Figure 28 the significant regression expressions were all positively linear with the exception of species A large which was positively parabolic. Higher level polynomials did not significantly improve the fit. These findings were similar to those presented by Reisen and Prins (1972) and supported the theories of Müller (1966) and Elliott (1967) who suggested that drift may be a function of life history phenomena and thus increase linearly with increasing density. In other words, organisms have a series of typical population movements throughout their life history some of which increase their vulnerability to drift, and it is these movements which are synchronized by light intensity or day length. For virgatum and especially species A these movements seemed to relate to eclosion and the subsequent larval movements to suitable feeding sites in deeper and faster water and did not appear density dependent relating to such factors as intraspecific competition for attachment sites.

As shown in Figure 29 drift rates for species A also showed a consistent positive linear regression with increasing algal biomass which could be interpreted in 2 ways: 1. Population increases during the spring when algal biomass was high correspondingly increased the accidental drift rate, since density and drift were also positively correlated; 2. The utilization of filamentous algae as a substrata increased their chances of being dislodged and swept away by the current. The responses of virgatum (Figure 29a, c and e) were difficult to interpret in light of the previously presented hypothesis on the negative relationship between algal biomass and benthic density. The negative portion of the curve was consistent with this hypothesis, while the positive slope at the higher algal biomass estimates possibly related to competition with the algae for clean substrata resulting in increased virgatum

movements and subsequent drift. The positive linear relationship between virgatum ultimate drift and algal biomass (Figure 29e) probably also related to this substrate incompatibility and the searching of the ultimate larval instar for suitable pupation sites.

S. virgatum larvae exhibited decreasing drift rates with increasing pH (Figure 30a, b, and c) which was most likely related to the interaction of pH and photosynthesis during periods of increased algal biomass. pH itself was not thought to actually depress drift especially over the range of values observed during this study (Table 2, Figure 5).

Species A large larvae and pupae and last instar virgatum larvae exhibited a significant cubic response to increasing rainfall (Figures 30d, e, and f). The higher drift rates at lower rainfall values probably related to increased larval movements to find suitable attachment sites during periods of drying with higher rainfall probably related to increased habitat disruption for these spates were often observed to denude and scour the riffles faunistically.

Pearson and Franklin (1968) included turbidity in their subset of limnological parameters; however, a related measurement, coulter counts, only exhibited a single significant polynomial regression with medium virgatum larvae (Figure 30g). The response surface was similar to that observed for virgatum ultimate larvae for both rainfall and discharge (Figures 30e and d) and may have been related to the increased number of particles present during higher stream flow. A similar explanation was proposed for the significant drift rate of female virgatum and increasing coulter counts (Figure 31d).

Pupal (Figure 30j) and female (31a) species A drift rates were higher during periods of higher discharge. Drifting pupae usually consisted of two types: 1. those recently pupated; and 2. those ready to emerge. Both these groups as well as emerging females were susceptible to increased discharge. Increased female virgatum drift rates during periods of low discharge (Figure 11b)

probably related to the phenological pattern and its correspondence with periods of discharge increase.

Although Pearson and Franklin (1968) and Reisen and Prins (1972) found simuliid larval drift significantly correlated with increases in water temperature, drift in Honey Creek was independent of water temperature even though species A benthic densities showed significant positive correlation (Table 10). As presented in Table 17, dissolved oxygen and water temperature exhibited a high negative correlation ($r = -0.959$) and presumably the negative response of virgatum pupae to dissolved oxygen (Figure 31c) was related to the increased pupation and emergence during the cooler water temperatures of autumn.

The negative response of virgatum males (Figure 31e) and females (Figure 31f) to increasing alkalinity was attributed to the travertine deposition mortality presented earlier. Emergence and oviposition seemed to occur during the periods of reduced alkalinity as indexed by male and female drift rates.

Simulium virgatum ultimate larval drift showed a significant negative regression with increasing moonlight (Figure 30k). The negative interaction between available moonlight and drift has been presented previously by Anderson (1966) who based his theories on the frequently observed midnight depression of drift rates. Moonlight, however, was only occasionally maximized during the midnight hours; in fact, moonrise may be timed, so that the maximum moonlight occurs at any time during the night (Bowden, 1973a). Schumacher (1970), Nemeč (1971), and Bowden (1973b) have suggested that activity patterns of some insects are synchronized with the lunar cycle; however, since the total drift of both species A and virgatum was independent of the moon phase factor, this relationship seemed irrelevant for the simuliids of Honey Creek. These findings supported those of Reisen and Prins (1972) who also found no evidence of lunar cycles regulating the drift of stream organisms.

Simulium trivittatum larvae showed a negative curvilinear and linear response to increasing dissolved oxygen and discharge, respectively (Figure 32). This would suggest that during the period of intermediate dissolved oxygen concentrations, drift rates were lower; or perhaps, that populations were higher and drift was greater during period of intermediate temperatures. The increased drift rates during periods of reduced discharge could be interpreted as increased population movements during periods of drying. As mentioned previously, trivittatum preferentially utilized trailing grasses as attachment sites. As the discharge became less, the stream receded from its banks, necessitating the emigration of the larvae to find grasses still trailing in the current.

Pearson and Franklin (1968) and Disney (1972) suggested that interspecific coactions among the benthos may induce simuliid drift. Correlations between the densities of simuliid larvae and associated fauna and larval drift rates are presented in Table 20. Significant positive correlations substantiated this hypothesis of interspecific coaction induced drift. Small larvae and Lutrochus luteus LeConte larvae showed a highly significant positive correlation ($r = 0.914$). L. luteus larvae fed on algae and were most prevalent during the periods of maximal algal biomass in the spring of 1973 (Figure 14). L. luteus larvae were often observed feeding adjacent to, and occasionally within, simuliid egg masses and possibly their movements during the critical eclosion periods could have caused the higher drift rates observed. A similar hypothesis is presented for the species A medium larvae which was also significantly correlated with L. luteus larvae ($r = 0.885$). The relationship between species A medium and Centroptilium naiads was difficult to conceptualize although Centroptilium did exhibit a marked diel periodicity of activity. Simuliid intraspecific coactions have been evaluated previously and were not considered of importance here. S. trivittatum was not included

in this evaluation for none of the travertine inhabiting benthos were routinely found in association with the trivittatum larvae on the trailing grasses. Chironomidae larvae were occasionally associated; however, these species have not as yet been determined, but were presumably different than those found associated with species A and virgatum on the travertine.

As reported in the literature, the response of simuliid diel drift periodicity to exogenous "zeitgebers," usually light, seems inconsistent. Waters (1962) and Reisen and Prins (1972) concluded that there was no periodicity in the drift of Simulium sp. larvae.* Müller (1966, 1970a and b), Kureck (1969), Chaston (1968), Bishop and Hynes (1969), Brusven (1970) and Disney (1972) showed quite conclusively in the species they studied that a definite nocturnal periodism exists; and experimental light manipulation by Kureck (1969) and Chaston (1968) suggested that this rhythm was probably exogenous. In contrast Clifford (1972) reported a definite diurnal activity pattern. A basic short coming in all these studies was the absence of a sound statistical evaluation of the results and the relying on the "best example" method to describe activity patterns. This method suffices if:

1. the behavioral pattern is invariably consistent;
2. the organisms are prevalent for only a short time; or
3. only a minimal amount of data is collected.

Due to the incongruencies presented in the literature and the variability observed in the data collected during this study, a need for some sort of a priori statistical test was realized. From the review articles (Waters, 1972; Bournaud and Thibault, 1973), there appear to be the following possible types of periodicity: 1. diurnal, 2. diurnal - morning dominant, 3. diurnal - afternoon dominant, 4. crepuscular, 5. crepuscular - evening

*Subsequent determination of the Simulium larvae in Reisen and Prins (1972) suggested they were near the Simulium tuberosum - complex.

dominant, 6. crepuscular - morning dominant, 7. nocturnal, 8. nocturnal - bigeminus, 9. nocturnal - alternans, and 10. no rhythm. By ANOVA methodology using single degree of freedom comparisons, it was possible to compare the predetermined blocks of time presented in Table 21. Although 17 24-hr studies were conducted, only those studies having sufficient numbers of individuals were included in the analysis. The diel drift patterns for small larvae is presented in Figure 34a. Small larvae showed a significant nocturnal bigeminus peak. This pattern was similar to that for Simulium species A medium larvae (Figure 33b), except that species A medium larvae showed more afternoon activity than did the small larvae. Periodicity seemed to degenerate as the larvae matured (Figures 33c and d) and these older age groups did not exhibit any significant differences among the designated periods (Table 21). With the exception of perhaps being slightly more active during the afternoon, S. virgatum larvae did not display any significant periodicity (Figures 34b, c, and d). The larvae of S. trivittatum exhibited extremely low drift rates; however, these did show a significant slightly bigeminus nocturnal periodicity (Figure 35, Table 21). In contrast to species A and virgatum which exhibited a higher drift rate during the afternoon hours (1400-1800), trivittatum larvae were more active during the morning hours (0800-1200).

The diel patterns of adult emergence as indexed by drift for species A and virgatum are presented in Figures 33 and 34, respectively. In the ANOVA 1800 to 2000 and 0400 to 0600 were chosen for the crepuscular period. As shown in Table 2, day length was variable with a range from 9.7 to 14.5 hours, or a shift of about 2.4 hours for the crepuscular period throughout the year. Since adults were not collected during the winter months and were most abundant during the period of elongated day length (Figure 24), it was assumed that these periods were realistic, especially since sampling intervals were of two hours duration. Both species A and virgatum emerged during the

daylight hours with most emergence occurring in the later afternoon and morning. The evening peak for the females of both species consisted of both emerging individuals as well as those having recently oviposited as determined by abdominal dissection. The spent ovipositing females were not readily discernable from the emerging females, so both categories were pooled. Most male virgatum, and to a lesser extent species A, emerged during the evening (Figure 34e); however, mating swarms were never observed during this time. Perhaps the males fly to the underbrush to rest prior to the morning nuptials; or alternatively these evening peaks represented spent males who had emerged the previous morning and had hovered at the base of the riffles until they died (Stone and Snoddy, 1969).

It has been demonstrated experimentally that light is the principal zeitgeber in the entrainment of the exogenous rhythms of aquatic insects (Holt and Waters, 1967; Chaston, 1968; and Kureck, 1969); however, the relationship to other chemical and physical stimuli has been generally neglected. The yearly means for each of the 2-hr periods for light intensity, temperature, dissolved oxygen, pH, and alkalinity are presented in Figure 36 and the correlations among them presented in Table 22. With the exception of alkalinity which may have been more sensitive to community respiration or changes in pH (Minckley, 1963), all of the abiotic variables were significantly correlated with light. The dissolved oxygen curve seemed more sensitive to photosynthetic activity than temperature although the continuous rise during the hours of darkness (2200 to 0600) was attributed to decreasing water temperatures.

Linear correlation between the diel drift rates and the concomitantly measured abiotic variables are presented in Table 22. None of the simuliids showed a significant correlation with light intensity. The curves for dissolved oxygen and pH seemed more closely correlated to changes in the

drift of small larvae and species A with the greatest activity coming during period of lowest pH and dissolved oxygen. This was hard to interpret biologically unless larval activity was in some way entrained by the 24-hr photosynthetic cycle of the Myriophyllum and/or periphyton. Periphyton reproductive activity patterns and resulting algal drift has been investigated by Müller-Haeckel (1966, 1970) and Müller-Haeckel and Müller (1970) who described a diurnal activity pattern for diatoms and a nocturnal activity pattern for green algae. Müller-Haeckel (1970) presented a series of diel water chemistry curves most of which approximated those presented in Figure 36. Perhaps increased algal drift during the evening periods increased the feeding activity of the larval simuliids resulting in correspondingly more movement and activity and thus higher drift rates during this period. There was, however, no significant difference observed among the 24-hr coulter counts. Observations on the rhythmicity of larval growth and feeding by Kureck (1969) and Ladle, et al. (1972) also did not support this hypothesis. Another explanation for the drift of the small larvae was based on the duration of development. Oviposition was specific for the crepuscular hours and if the larval developmental rate was constant, it would seem that the larvae would emerge synchronously several days later which would be expressed as an increase in the small larval drift rate. This could also explain the degeneration of the rhythmicity with age, for as soon as the larvae matured and became established in suitable feeding sites, larvae movements and thus drift would subside. Due to their percentage species composition, a large portion of the small larval component was incorporated into the species A total larvae, thus weighting their activity patterns. The similarity between the diel periodicity of small larvae and species A medium larvae suggested that this weighting did not impart any erroneous periodicity.

S. virgatum larvae displayed a significant positive correlation with increasing water temperature (Table 21) which was similar to the findings of Reisen and Prins (1972). For certain species entrainment by temperature can replace light as the zeitgeber yielding a "day-active" drifter such as S. virgatum (Waters, 1968; Kureck, 1969).

Although not significantly correlated in these studies light has been quite conclusively shown to be the zeitgeber by Chaston (1968) and Kureck (1969). More sensitive light meters would have permitted the evaluation of changing illumination patterns at night; however, since moonlight would have sporadically increased the readings somewhat, it was theorized that this would not have allowed the necessary improvement of fit. Also, if the transition in light intensity from light to dark were indeed the zeitgeber, activity patterns would change radically with the change in light intensity or shortly afterward as exhibited by the emerging and ovipositing adults shown in Figures 33 and 34.

G. Predictive models and variable interactions. As utilized by Pearson and Kramer (1972), step-up multiple regression analyses were used to present the relative importance of the variables considered previously. To include possible interactions among temperature, pH and alkalinity, two synthetic variables were calculated: 1. TXA = temperature multiplied by alkalinity, 2: PXA = pH multiplied by alkalinity. For these regressions variables found to exhibit significant curvilinear responses in the preliminary polynomial screening were transformed; where $Y = \ln Y$, or if zero values were present, $Y = \ln(y + 0.005)$. Two analyses were conducted on the benthic sample data matrix, one for the stream means and the other for Station 8, and are presented in Table 23. Both biotic and abiotic environmental variables were weighted equally and to prevent the listing of randomly added variables, those parameters increasing the value of R^2 by less than

0.05 were deleted. Algal biomass, except for S. trivittatum, was consistently added early in the analyses and contributed much to explain the observed fluctuations in simuliid densities. For stream means, discharge was initially added to the subset of variables for virgatum; the slope of which was negative suggesting increased discharge and the associated scouring of the travertine substrata during spates significantly reducing benthic densities. Algae was added secondly and also exhibited a negative slope. Of the remaining 7 factors, 3 were associated with the travertine deposition mortality mentioned earlier. For species A coulter counts was the second variable added after algal biomass. Its importance may be interpreted as food related as suggested by the findings of Müller-Haeckel and Müller (1970). The third variable added was chironomid larval benthic density which had a negative slope perhaps stemming from interspecific exploitative competition for the green algae. S. trivittatum was most highly correlated with L. luteus larvae densities which has been discussed previously; PXA was added secondly which was not readily discernable biologically.

At Station 8 algae was again a prominent variable being added first to species A and secondly to virgatum. H. betteni was added secondly to species A and did show a negative slope supporting the predator-prey or competitive coactions postulated earlier. The log of species A density was added first for virgatum and was positively correlated.

Similar analyses were also conducted for the 24-hr drift totals and are presented in Table 24. Algal biomass was again the most highly correlated of the variables considered for species A and virgatum larval drift. The slopes differed, however, with species A being positive and virgatum being negative. Discharge was the most highly correlated variable with S. trivittatum drift and showed a negative slope similar to that presented in Table 19. Of the immature forms only trivittatum showed an improvement of fit (increase in R^2) greater

than 0.015 for moonlight further supporting the discussion presented earlier.

Multiple regressions for the drift rates of species A adults were similar to those for the larval drift rates with algae and rainfall predominating. Adult virgatum showed differences in variable loading between males and females as well as being different from the larval drift rates. It was hard to imagine that a different subset of variables would be responsible for the emergence and drift activity of males and females which were both prevalent at the same time of the year.

Multiple regression predictive equations were calculated for stream means and Station 8 benthic densities, and for benthic density and drifting adult females using the drift data matrix. More stringent criteria were established to terminate the analyses and for benthic densities only the abiotic parameters were considered. Benthic density prediction from drift was utilized to test if drift alone could adequately predict benthic density and thereby negate the collection of bottom samples. Drift was considered an easier to use, more objective method which was less vulnerable to non-random dispersion errors. The results of these analyses suggested that larval drift was the best predictor for species A benthic density being almost twice as positively correlated as the next most important variable, algal biomass. Larval drift was loaded into the equations consistently ahead of algal biomass suggesting that it was a better predictor. Drift rates of the larvae were also better predictors of adult female emergence than were larval benthic density. Correlations for all the predictive models were high and suggesting that the expressions well approximated the variations in the data. At Station 8, however, lack of fit was suggested by subequal increase in R^2 for the first three variables loaded into the expression. The models for virgatum seemed to fit the data slightly better as indexed by the higher R values.

To test the validity of these models over time and space the following sets of data were used: 1. the models calculated from stream means was tested against Station 2; 2. the models calculated for Station 8 were tested against Station 9; 3. the models from the drift data matrix were calculated from studies 6 through 17 and tested against studies 1 through 5. The results of these comparisons are presented in Table 26. None of the series of expected benthic densities were correlated with the observed benthic densities or drift rates. These relationships did not seem suitable to predict Simulium densities at the different areas within the same time frame or data extrapolated over time, even though the fit for the interpolative data was high.

Some possible explanations for the failure of these models to accurately predict over time and space included the following: 1. Intercept and slope values were specific for the data within the analyses, and thus the magnitudes of prediction from extrapolative data may have been aberrant and produced uncorrelated results. The correlations for the interpolative data were high suggesting a realistic fit, however, if this technique is to be applied, a specific sampling site must be used and calibrated. 2. The test data in this study consisted of more or less miscellaneous estimates that did not readily fit into the original analyses conducted. Station 2, used to test both stream means benthic densities and some of the drift data (Table 16) consisted of a heterogeneous series of benthic samples which had to be constantly moved from week to week because of vacationer disturbance. Station 9 differed from Station 8 for it lacked the high Trichoptera populations deemed important in the population trends at Station 8.

V. Summary

In order of decreasing abundance the Simulium species collected at Honey Creek were: Species A, virgatum, trivittatum, vittatum and venustum.

Simulium species A predominated the benthic density estimates during the spring months. Its seasonal bionomics were consistently positively correlated with changes in algal biomass. During the summer months species A was noticeably absent from Station 8 which was attributed to lower algal biomass estimates and/or trichopteran predation or competition. Oviposition occurred during the early evening hours, and emergence during the early morning hours. Mating commenced shortly after emergence after which the females left the stream to search for blood meals. Gravid females returned to the stream to oviposit generally entering mating swarms from downstream which supported the colonization cycle theory of Roos (1954). Drift of the early instars exhibited a slightly bigeminus nocturnal rhythmicity. Older instars exhibited a progressive degeneration of this periodicity suggesting this rhythm may be initiated by eclosion synchronization. Adult emergence was crepuscular with the morning period predominating. Benthic density and drift showed a positive linear relationship suggesting that drift was a density independent phenomenon indiscriminately removing that portion of the population which showed the greatest amount of movement. Larval drift rates were the best predictors of changes in benthic density and adult emergence. Tests of these models were not successful possibly due to the nature of the test data or the need to calibrate each study area.

Simulium virgatum populations were highest during the late summer and fall. Changes in numbers seemed to be negatively correlated with algal biomass due to a buffering of the pH by algal biomass increases (mostly Phormidium)

during the winter causing the pupae to be cemented in the travertine when their development was arrested by cooler water temperatures. Life tables were constructed and the quantitative population dynamics of two cohorts evaluated. Larval mortality was highest during, and just after, eclosion and just prior to pupation which coincided with the population movements at this time as indicated by the higher drift rates. Male and female emergence was highest during the late summer and fall. Mating and oviposition was similar to species A. No diel drift periodicity was noted for this species although emergence times of the adults were similar to species A. Larval drift and benthic density for this species were not well correlated and algae seemed to be a better predictor of benthic density. No single set of factors could explain the changes in both female and male emergence and attempts to test the female and larval predictive models were unsuccessful.

Simulium trivittatum preferentially utilized trailing grasses as a substrata, and consequently benthic density estimates represented population surpluses. Seasonal variations in these surpluses suggested that trivittatum densities were highest during the fall. Benthic density and drift were most highly correlated with changes in discharge. The relationship between benthic density and drift was not evaluated.

The theories involving downstream movements of simuliid larvae were reviewed and evaluated for the species collected at Honey Creek. Light intensity changes were not correlated with diel changes in simuliid drift rates. Moonlight, as indexed by a synthetic factor, was not correlated with drift suggesting that blackfly activity patterns and population changes were independent of lunar cycles. For species A the 24-hr photosynthetic cycle or synchronized eclosion may be the stimulus initiating drift, whereas virgatum drift was most highly correlated with higher afternoon temperatures.

Since adult oviposition activity and emergence was crepuscular transitions in light intensity were considered to be the zeitgeber although other factors stimulating larval pupation activity may also have been involved.

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APPENDIX A

TABLES

Table 1. Descriptions of Stations 1 through 9 including depth and current measurements.

Station Number	Dates Sampled	Depth (cm)		Current (cm ³ /sec)		Remarks
		mean	S.D.	mean	S.D.	
1.	15 Jul - 5 Aug 72 28 Oct - 15 Aug 73	5.541	3.023	162.224	37.696	45° slope; 40-m above Bridal Veil Falls; small run bounded on both sides by grasses; dry from 5 Aug 72 to 28 Oct 72; flooded from October through mid-November 1972.
2.	8 Jul - 5 Aug 72	5.000**	---	136.048	53.272	consisted of 4 different sites just below Bridal Veil Falls; park visitor disturbance necessitated abandonment.
3.	17 Aug - 19 Sep 72* 9 Sep 72 - 15 Aug 73	5.428	4.005	169.633	33.169	15° slope; 30-m below Bridal Veil Falls; flow was reduced during periods of decreased stream discharge
4.	11 Nov 72 - 15 Aug 73	4.084	2.868	204.359	47.829	35° slope; seperated from Station 3 by a 60-m long slow run; established for drift studies due to discharge increase which made Station 5 unsuitable; most of the above Turner Falls water samples were taken below this station.
5.	23 Sep 72 - 15 Aug 73	7.673	5.525	193.057	41.266	60° slope; adjacent to Station 4
6.	15 Aug - 22 Oct 72* 28 Oct 72 - 15 Aug 73	3.661	2.691	220.086	36.502	40° slope; 15-m below Station 5 and about 50-m above Turner Falls; discharge estimates were taken just below this station.
7.	5 Aug - 11 Nov 72	2.781	3.452	113.81	31.942	65° slope; about 10-m adjacent to Station 6; denuded by spate in November 72 and abandoned.
8.	31 Jun 72 - 15 Aug 73	6.000**	---	---	---	lip of a 50-cm waterfall on the downstream edge of an abandoned low-water crossing; 2 1/2-km downstream from Turner Falls
9.	23 Sep 72 - 23 May 73	---	---	---	---	20° slope; 6-m downstream from Station 8; innundated by a downstream dam on 23 May 73; water samples taken just above this station

* Life table studies conducted here; ** based on a single measurement.

Table 2. The yearly means and standard errors of the means (S.E.) of selected limnological parameters observed at Stations 4 and 8 from 31 Jun 72 through 15 Aug 73.

Parameter	Station Number	N	Mean	S.E.
Algal biomass (mg/cm ²)*	4**	43	6.2015	0.7511
	8	49	2.2994	0.3072
Discharge (m ³ /sec)	4	36	1.0596	0.0378
Depth (cm)	8	49	44.3081	1.0138
Water temperature(C)	4	54	19.1852	0.0810
	8	55	18.2182	0.8913
Dissolved oxygen (ppm)	4	54	9.2371	0.1683
	8	54	9.1796	0.2122
pH *	4	52	8.0933	0.0334
	8	53	7.8811	0.0407
Alkalinity (ppm)	4	52	266.2931	6.0301
	8	52	267.4502	11.2209
Phosphate (ppm)	4	13	0.8945	0.4015
	8	13	0.4293	0.1938
Nitrate-N (ppm)	4	10	0.1187	0.0151
	8	10	0.1200	0.0176
Sulphate (ppm)	4	2	30.0000	20.0000
	8	2	19.5000	0.5000
Conductivity (mohms/cm)	4	13	2.154x10 ³	0.0956x10 ³
	8	13	2.258x10 ³	0.1011x10 ³
Coulter counts (cts/ml)	4	52	17,032.40	3,265.29
	8	52	20,944.80	2,847.35
Rainfall (cm)		49	0.3755	0.0578
Day length (hrs)		49	12.5267	0.2251

* significant difference in means between Stations 4 and 8 ($\alpha = 0.05$)

** mean of Stations 1,3,4,5,6 and 7

Table 3. Correlation matrices for the limnological parameters measured at Stations 4 and 8 from 31 Jun 72 through 15 Aug 73. * significant $\alpha = 0.05$

Parameters	1	2	3	4	5	6	7	8	9
Station 4, N = 43									
1. algal biomass**	1.000	.094	.244	-.138	-.194	-.202	-.171	.647*	.051
2. discharge		1.000	-.448*	.420*	.338*	.302*	.271	-.100	.172
3. temperature			1.000	-.936*	-.623*	-.547*	-.079	.747*	-.090
4. dissolved oxygen				1.000	.596*	.403*	.106	-.679*	.107
5. pH					1.000	.180	.108	-.557*	.177
6. alkalinity						1.000	.207	-.396*	-.040
7. rainfall							1.000	-.007	.207
8. day length								1.000	.052
9. coulter counts									1.000
Station 8, N = 49									
1. algal biomass	1.000	.253	.074	.131	-.023	.066	-.173	-.155	.325*
2. depth		1.000	-.521*	.373*	.524*	.252	.199	.501*	-.279
3. temperature			1.000	-.142	-.925*	.013	-.691*	-.166	.839*
4. rainfall				1.000	.180	.043	.226	.207	-.064
5. dissolved oxygen					1.000	.052	.598*	.109	-.742*
6. pH						1.000	-.391*	.300	.175
7. alkalinity							1.000	.005	-.725*
8. coulter counts								1.000	-.216
9. day length									1.000
** mean of Stations 1,2,3,4,5,6, and 7									

Table 4. Checklist of the Simulium collected at Honey Creek, their life forms, associated substrata, and longitudinal location. E = egg, L = larvae, P = pupae, A = adults.

Species collected	Life forms	Micro-habitat preference	Location in stream
Genus <u>Simulium</u> Latreille (<u>Simulium</u>) <u>venustum</u> Say	L	cobble, travertine	Station 8 to I-35
(<u>Eusimulium</u>) <u>vittatum</u> Zetterstedt	L,P	cobble	between Spring 1 & 2
(<u>Neosimulium</u>) <u>trivittatum</u> Malloch	L,P,A*	trailing grass, occasionally travertine	from Source to mouth
(<u>Dyarella</u>) <u>virgatum</u> Coquillet	E,L,P,A*	travertine, occasionally grass and rubble	Spring 2 to below I-35
(<u>Hagenomyia</u>) species A	E,L,P,A*	travertine, occasionally algae, cobble	½ way between Spring 1 & 2 to below I-35

* determinations verified by rearing pupae to adults

Table 5. The number of eggs counted, percentage of eggs already laid, the number of immature oocytes remaining (rated 0 - 4), and the presence or absence of a blood meal remenant (+ or -) in ovipositing Simulium species A and virgatum females.

Date Collected	Specimen Number	Number of Eggs	Percent Empty	Immature Oocyte	Blood Meal
<u>Simulium</u> species A					
19 Aug 72	1	188	15	3	-
	2	178	10	2	-
	3	232	20	1	-
	4	74	60	4	-
	5	160	25	3	-
9 Sep 72	1	72	80	1	-
	2	56	50	3	-
	3	0	100	2	-
	4	168	10	2	-
23 May 73	1	144	30	1	-
	2	262	5	1	-
	3	360	10	1	-
	4	252	15	1	+
	5	18	60	4	-
	6	264	5	1	+
	7	178	30	1	-
	8	304	0	3	-
	9	264	30	0	-
	10	88	40	3	-
	11	24	50	3	+
	12	360	5	2	-
18 Jul 73	1	334	5	1	-
	2	196	10	2	-
	3	246	10	3	-
	4	10	85	4	-
	5	160	20	3	-
	6	448	0	2	-
	7	284	5	4	+
	8	112	60	2	-
	9	26	50	4+	-
	10	34	50	4+	-
	11	152	30	3	-
	12	226	30	2	-
	13	360	30	1	-
<u>Simulium</u> <u>virgatum</u>					
5 Aug 72	1	210	10	2	-
	2	198	10	3	-
	3	142	0	0	+
	4	104	50	3	-

Table 5. (continued)

Date Collected	Specimen Number	Number of Eggs	Percent Empty	Immature Oocytes	Blood Meal
	5	184	20	1	-
	6	142	10	2	-
	7	0	100	3	-
	8	128	20	2	-
	9	204	0	2	-
	10	10	85	2	-
	11	242	10	3	-
	12	130	20	1	+
19 Aug 72	1	314	5	2	-
	2	170	20	3	-
	3	208	25	2	-
9 Sep 72	1	56	70	3	-
	2	0	100	3	-
	3	126	50	4	-
	4	198	30	3	-
	5	8	90	3	-
18 July 73	1	248	30	1	-
	2	6	85	3	-
	3	132	40	3	-
	4	242	15	2	-
	5	0	100	2	-

Table 6. *Simulium virgatum* cohort statistics for Stations 3 and 6, 15 Aug through 19 Sep 72. Values for Station 6a are in parentheses.

Date	Density (nos/cm ²)	Population Area (cm ²)	Total Numbers in this Area	Head Capsule Width		Biomass (g/cm ²)	Density(nos/cm ²) pupae species A	
				mean(mm)	S.E.			
Station 3								
17 Aug	4656.67*	4.8	22532.21	---	---	---	---	---
19 Aug	21.08	309.7	6527.98	0.1124	0.0028	0.00294	---	---
23 Aug	4.34	929.0	4031.99	0.2230	0.0147	0.00114	---	---
26 Aug	1.86	1290.3	2399.99	0.3259	0.0116	0.00087	---	0.46
31 Aug	1.32	1858.0	2448.92	0.4830	0.0321	0.00151	---	1.47
5 Sep	1.14	1316.1	1496.44	0.6752	0.0081	0.00389	---	0.36
9 Sep	0.93	858.1	797.99	0.7021	0.0129	0.00371	---	0.26
12 Sep	0.67	754.8	507.00	0.6950	0.0245	0.00257	---	1.65
16 Sep	0.21	799.5	167.92	0.5360	0.0395	0.00032	0.29	0.53
19 Sep	0.00	---	---	---	---	---	0.14	0.66
Station 6 a and b								
15 Aug	4656.67*	19.4(8.1)	90128.86(37553.65)	---	---	---	---	---
19 Aug	208.81(68.70)	232.3(451.6)	48497.80(31009.98)	0.1007	0.0009	0.02725	---	0.16
23 Aug	94.45(41.08)	464.5(645.2)	43871.60(26500.04)	0.1677	0.0050	0.01804	---	---
26 Aug	22.01(6.41)	1632.3(3141.9)	35925.93(20129.33)	0.2587	0.0047	0.00705	---	0.36
31 Aug***	4.28	13909.7	59648.75	0.4775	0.0058	0.00477	---	1.46
5 Sep	2.93	9993.5	29258.85	0.6095	0.0069	0.00689	0.07	1.15
9 Sep	2.82	11483.9	32436.13	0.6809	0.0071	0.00999	0.04	0.98
12 Sep	1.95	11206.4	21808.80	0.7258	0.0064	0.00888	0.04	0.86
16 Sep	0.81	13000.0**	10522.20	0.7281	0.0195	0.00374	0.70	0.53
19 Sep	0.79	13000.0**	10298.60	0.6615	0.0245	0.00251	0.78	0.84
23 Sep	1.10	13000.0**	14328.60	0.6390	0.0133	0.00307	0.09	0.54

* Egg mass density calculated earlier.

** Population area became too diffuse to estimate accurately; dispersions were not homogenous.

*** At this point populations a and b were no longer seperable and the values for both were pooled.

Table 7. Life tables for *Simulium virgatum* larval cohorts collected at Stations 3 and 6 from 15 Aug through 19 Sep 1972. Column designations follow Southwood (1966).

Days(x)	l_x	d_x	L_x	T_x	e_x	q_x (x1000)	Actual Population
Station 3							
0	1000	710	645.0	1314.0	1.314	710	22,532.21
4	290	111	234.5	669.0	2.306	382	6,527.98
8	179	68	143.0	434.5	2.427	379	4,031.99
11	107	0	107.0	291.5	2.724	0	2,399.99
16*	107	41	86.5	184.5	1.724	383	2,448.92
21	66	31	50.5	98.0	1.485	469	1,496.44
25	35	12	29.0	47.5	1.357	343	797.99
28	23	16	15.0	18.5	0.804	695	507.00
32	7	7	3.5	3.5	0.500	1000	167.92
Station 6							
0	1000	378	811.0	3323.0	3.323	378	127,682.51
4	622	71	586.0	2512.0	4.039	114	79,507.78
8	551	112	495.0	1926.0	3.495	203	70,371.65
11	439	0	439.0	1431.0	3.260	0	56,055.26
16*	439	210	334.0	992.0	2.260	478	59,648.75
21	229	0	229.0	658.0	2.873	0	29,258.85
25*	229	58	200.0	429.0	1.873	253	32,436.13
28	171	99	121.0	229.0	1.339	579	21,808.80
32* **	72	0	72.0	108.0	1.500	0	9,179.46
35**	72	72	36.0	36.0	0.000	1000	10,298.60

* Since total population estimates increased, l_x values were considered to be the same as l_{x-1} .

** Total numbers were estimated from pupal densities only due to cohort pollution.

Table 8. Correlation coefficients between Simulium species A and virgatum age groups and S. trivittatum total densities averaged over Stations 1,3,4, 5,6 and 7 compared with selected limnological parameters estimated at Station 4. Values presented are correlations for the lowest significant level of the polynomial.

	algal biomass **	discharge	temperature	dissolved oxygen	pH	alkalinity	rainfall	day length	coulter counts
benthic density									
small larvae	.373*	.201	.376*	.349	.263	.363	.080	.307*	.217
<u>Simulium</u> species A									
medium	.615*-.333		.305*-.449*	-.408*-.475*	.154		.589*-.369		
large	.613*-.133		.307*-.474*	-.379*-.431*	.192		.525*-.320*		
ultimate	.436*	.213	-.221	.273	.183	.213	-.304	-.452*-.448*	
pupae	.253	.225	-.395*	.457*	.324	.296	-.262	-.296	.220
total	.663*-.251		.399*	.394	.378*-.435*	-.126	.511*	.318	
<u>Simulium virgatum</u>									
medium	-.305*-.435*	.296*-.316	.167	-.410*-.262	-.207	.207			
large	-.314*-.527*	.469* .491*	.294	-.535*-.347*	-.380*-.419*				
ultimate	.283	-.388	-.366	.451*	.469*	.493*-.281	-.490	-.312	
pupae	-.305*-.212	-.296	.320*	.468*	.417	-.200	-.498*-.271		
total	-.467*-.579*	.338	.314	.338	-.547*	.315	-.338	-.523	
<u>Simulium trivittatum</u>									
total	-.356	-.292	-.135	-.025	.353	.309	-.128	-.312	.055

* significant at $\alpha = 0.05$, $N = 43$

** mean of Stations 1,3,4,5,6, and 7

Table 9. Significant polynomial regression expressions and figure references for *Simulium* species A and *virgatum* age group densities for stream means compared with selected limnological parameters measured at Station 4. Data coded: $Y = Y + 0.005$

Variable Labels		Intercept	Degree of the Polynomial			Figure Reference
Y	X		B1	B2	B3	
small larvae	algal biomass	0.4255	0.2053			16A
	water temperature	-7.8049	1.0295	-0.0255		16B
	day length	-4.6061	0.5129			16C
<i>Simulium</i> species A						
medium	algal biomass	-0.0342	0.1868			17A
	water temperature	-0.3709	0.0839			17E
	dissolved oxygen	-217.1122	66.6442	-6.6694	0.2187	17I
	pH	-585.9741	147.4242	-9.2461		17M
	alkalinity	-388.1445	4.0725	-0.0140	0.151x10 ⁻⁴	17Q
	day length	-5.5508	0.5431			17U
large	algal biomass	0.2381	0.0710			17B
	water temperature	0.1056	0.0322			17F
	dissolved oxygen	-93.0746	28.8811	-2.9182	0.0967	17J
	pH	8.4431	-0.9618			17N
	alkalinity	-130.0883	1.3752	-0.0048	0.542x10 ⁻⁵	17R
	day length	-1.5856	0.1842			17V
ultimate	coulter counts	0.9779	-0.259x10 ⁻⁴			16G
	algal biomass	0.0152	0.0742	-0.0096	0.0003	17C
	day length	32.7452	-8.0004	0.6491	-0.0174	17W
pupae	coulter counts	-0.0064	0.0001	-0.552x10 ⁻⁸	0.133x10 ⁻¹²	18
	water temperature	0.4161	-0.0138			17H
	dissolved oxygen	-0.6024	0.0808			17L
	day length	0.5958	-0.0347			17X

Table 9. (continued)

Variable Labels		Intercept	Degree of the Polynomial			Figure Reference
Y	X		B1	B2	B3	
<u>Simulium virgatum</u>						
medium	algal biomass	0.7941	-0.0479			17A
	discharge	0.9262	-0.3423			16D
	water temperature	-0.2541	0.0422			17E
large	alkalinity	24.5601	-0.1677	0.0003		17Q
	algal biomass	0.7244	-0.0407			17B
	discharge	0.9011	-0.3420			16E
	water temperature	3.1228	-0.3279	0.0092		17F
	dissolved oxygen	19.7561	-4.0573	0.2108		17J
	alkalinity	26.1353	-0.1780	0.0003		17R
	rainfall	0.6780	-0.5329			16I
	day length	2.3094	-0.1495			17V
	coulter counts	1.9343	-0.0004	0.271x10 ⁻⁷	-0.563x10 ⁻¹²	16H
	ultimate	discharge	0.1637	-0.0550		
water temperature		0.5880	-0.0558	0.0014		17G
dissolved oxygen		3.7898	-0.7875	0.0414		17K
pH		74.2301	-18.4740	1.1500		17O
alkalinity		5.1434	-0.0362	0.0001		17S
day length		0.6115	-0.0420			17W
pupae	algal biomass	0.1836	-0.0111			17D
	water temperature	0.2891	-0.0098			17H
	dissolved oxygen	2.4356	-0.5233	0.0290		17L
	pH	73.8838	-18.5803	1.1688		17P
	day length	0.7924	-0.0551			17X

Table 10. Significant polynomial regression expressions and figure references for Simulium species A and virgatum total densities for stream means compared with selected limnological parameters measured at Station 4.

Y	Variable Labels		Intercept	Degree of the Polynomial			Figure Reference
	X			B1	B2	B3	
<u>S. species A</u>		algal biomass	0.0700	0.5371			19A
		water temperature	-11.3885	1.5989	-0.0396		19C
		pH	-1415.1122	356.4568	-22.3720		19D
		alkalinity	-895.7165	9.3828	-0.0322	0.361×10^{-4}	19E
		day length	-12.0113	1.2538			19F
<u>S. virgatum</u>		algal biomass	2.6365	-0.1677			19A
		discharge	2.9009	-1.0400			19B
		alkalinity	72.3644	-0.4882	0.0008		19E
		coulter counts	6.6744	-0.0014	0.961×10^{-7}	-0.192×10^{-11}	19G

Table 11. Correlation coefficients between Simulium species A and virgatum total immature densities and selected variables for Stations 1, 3, 4, 5 and 6.

Parameter	species A	<u>virgatum</u>	depth	current
Station 1, N = 34				
<u>S. species A</u>	1.0000	-0.3433	-0.3285	-0.2968
<u>S. virgatum</u>	-0.3520	1.0000	-0.3611*	-0.3373
Station 3, N = 40				
<u>S. species A</u>	1.0000	-0.2911	-0.3997*	-0.2851
<u>S. virgatum</u>	-0.3361	1.0000	-0.3447	-0.1585
Station 4, N = 34				
<u>S. species A</u>	1.0000	0.1464	-0.4002	-0.3535
<u>S. virgatum</u>	0.4142*	1.0000	0.2046	0.4080*
Station 5, N = 34				
<u>S. species A</u>	1.0000	-0.2718	-0.3651*	0.2998
<u>S. virgatum</u>	0.2899	1.0000	-0.2553	0.2867
Station 6, N = 40				
<u>S. species A</u>	1.0000	-0.3632	-0.3083	-0.4581*
<u>S. virgatum</u>	-0.4292	1.0000	-0.2796	-0.2754

* significant $\alpha = 0.05$

Table 12. Significant polynomial regression expressions between Simulium species A and virgatum immature densities and selected variables for Stations 1,3,4,5 and 6.

Variable Labels		Intercept	Degree of the Polynomial			Figure Reference
Y	X		B1	B2	B3	
Station 1 <u>S. virgatum</u>	depth	1.2580	-0.1350			20B
Station 3 <u>S. species A</u>	depth	8.2489	-0.6218			20A
Station 4 <u>S. virgatum</u>	current velocity	-0.4930	0.0050			20D
	<u>S. species A</u>	0.1946	0.1268	-0.0065		21C
Station 5 <u>S. species A</u>	depth	10.2599	-1.1583			21A
Station 6 <u>S. species A</u>	current velocity	18.5738	-0.0666			20C

Table 13. Correlation coefficients between Simulium species A and virgatum total larval densities and selected limnological parameters measured at Stations 8 and 9. * significant at $\alpha = 0.05$.

Limnological parameter	<u>S. species A</u>	<u>S. virgatum</u>
Station 8, N = 49		
algal biomass	0.288*	0.301
depth	0.219	0.335
water temperature	-0.390*	-0.457*
rainfall	0.140	0.411*
dissolved oxygen	0.290	0.389
pH	0.235	-0.199
alkalinity	-0.270	0.296
coulter counts	-0.195	-0.245
day length	0.266	-0.165
<u>Simulium virgatum</u>	0.247	1.000
<u>Simulium species A</u>	1.000	0.673*
Station 9, N = 27		
algal biomass	0.516*	0.286
<u>Simulium virgatum</u>	0.396*	1.000
<u>Simulium species A</u>	1.000	0.396*

Table 14. Significant polynomial regression expressions and figure references between Simulium species A and virgatum densities and selected parameters at Stations 8 and 9.

Variable Labels		Intercept	Degree of the Polynomial			Figure Reference
Y	X		B1	B2	B3	
Station 8						
<u>S. species A</u>	algal biomass	0.0466	0.1836			21B
	water temperature	0.3230	-0.4218	0.0400	-0.0010	22A
<u>S. virgatum</u>	water temperature	0.3948	-0.0868	0.0070	-0.0002	22A
	rainfall	0.0973	-0.4604	1.0152	-0.4191	22B
	<u>S. species A</u>	0.0334	0.2458	-0.0387		21D
Station 9						
<u>S. species A</u>	algal biomass	1.8011	-0.7481	0.1199		22D
	<u>S. virgatum</u>	0.8044	2.0238			22C

Table 16. Locations of the drift nets for each of the 24 hour investigations. Net location numbers correspond to station numbers presented in Table 1.

Study Number	Date	Net Locations	
		Net A	Net B
1	8 Jul 72	2	2
2	22 Jul 72	1	2
3	5 Aug 72	2	7
4	19 Aug 72	7	7
5	9 Sep 72	6	7
6	30 Sep 72	6	5
7	15 Oct 72	6	5
8 - 17	11 Nov 72 - 15 Aug 73	4	3

Table 17. Linear correlations among selected limnological parameters measured below Station 4 and used in the drift analyses. N = 17; except ** where N = 12.

Parameters	1	2	3	4	5	6	7	8	9	10	11	12	13
1. water temperature	1.000	-.958*	-.218	-.848*	.001	.732*	.117	-.136	.347	-.703*	-.179	-.328	-.489*
2. dissolved oxygen		1.000	.166	.758*	.043	-.671*	-.151	-.023	-.425	.897*	.233	.326	.487*
3. pH			1.000	.517*	.082	.063	.527*	-.088	.029	.260	-.141	.200	.469*
4. alkalinity				1.000	.054	-.576*	.074	-.176	-.105	.628*	.160	.460	.605*
5. rainfall					1.000	.281	-.088	-.186	.017	-.348	.516*	-.029	.337
6. day length						1.000	.339	-.275	.455	-.456	.348	-.332	-.035
7. coulter counts							1.000	-.195	-.253	-.087	-.197	.177	.010
8. phosphate **								1.000	.077	-.188	-.364	-.523	-.035
9. nitrate **									1.000	-.202	.500	-.428	.424
10. conductivity										1.000	.125	.091	.441
11. algal biomass											1.000	-.125	.600*
12. moonlight												1.000	-.111
13. discharge													1.000

* significant at $\alpha = 0.05$

Table 18. Correlations between Simulium species A and virgatum age class and trivittatum total drift rates and selected parameters; N = 17.

	Benthic ** Density	Water Temperature	Dissolved Oxygen	pH	Alkalinity	Rainfall	Day Length	Coulter Counts	Algal Biomass	Moonlight	Discharge
Simuliidae drift											
small larvae	.925*	.433	.391	-.187	-.321	.328	.476	-.402	.615*	-.353	.409
<u>Simulium</u> species A											
total larvae	.849*	.430	.287	-.302	-.332	.366	.449	-.496	.742*	-.364	.483
medium	.866*	.429	.283	-.368	-.385	.493	.497	-.514	.821*	-.352	.528
large	.573*	.251	-.338	-.259	-.329	.692*	.317	-.401	.656*	-.385	.808*
ultimate	.511	-.313	.313	-.224	.384	.555	.326	-.456	.769*	-.325	.571*
pupae	.559*	.266	-.441	-.215	.352	.633*	.422	-.286	.598*	-.461	.552*
males	.313	-.324	.257	-.328	.290	.075	.355	-.465	.683*	-.240	.593
females	.253	-.389	.412	.313	.324	.149	.232	-.457	.717*	-.235	.473
<u>Simulium</u> virgatum											
total larvae	.434	.421	-.407	.886*	-.353	.216	.382	.493	-.572*	-.520	.309
medium	.232	.454	-.380	-.768*	-.401	.275	.393	.726*	-.647*	-.531	-.318
large	.502*	.497	-.396	-.777*	-.490	-.301	.169	-.109	-.453	-.484	-.503
ultimate	-.221	.216	-.268	-.213	-.343	.642*	.296	-.281	.494*	-.471*	.870*
pupae	.483	.533	-.579	-.372	-.401	-.396	.402	.261	-.277	-.466	-.586
males	.138	.540	-.321	-.477	-.688*	.240	.452	-.411	-.273	-.388	-.478
females	.001	.406	-.303	-.450	-.651*	.171	.486	-.512*	.457	-.437	-.636*
<u>Simulium</u> trivittatum											
total larvae	***	.607	-.612*	-.288	-.366	-.329	.387	.292	-.427	-.331	-.506*

* significant $\alpha = 0.05$

** for the adults; benthic density = pupal densities

*** insufficient data for evaluation

Table 19. Significant polynomial regression expressions and figure references for Simulium species A and virgatum age classes and trivittatum total drift rates and selected limnological parameters.

Variable Labels		Intercept	Degree of the Polynomial			Figure References
Y	X		B1	B2	B3	
small larvae	benthic density	5.0531	17.4078			27B
	algal biomass	-2.3454	5.1169			28B
<u>Simulium</u> species A						
total	benthic density	-6.5527	8.7909			27A
	algal biomass	-9.8099	8.5292			28A
medium	benthic density	1.5001	4.1121			27C
	algal biomass	-2.9038	2.2752			28C
large	benthic density	-1.4603	5.8455	-0.8326		27D
	rainfall	4.2362	-65.2513	224.4377	-164.8412	29D
	algal biomass	-0.0464	0.5874			28D
ultimate	discharge	3.6601	-6.0252	2.8436		29H
	algal biomass	-0.1471	0.1322			28E
	discharge	-0.0609	0.5357			29I
pupae	benthic density	0.0912	1.0197			27F
	rainfall	0.6448	-12.4517	46.4340	-36.5102	29F
	algal biomass	-0.0833	0.1075			28F
	discharge	-0.1110	0.5409			29J
<u>Simulium</u> <u>virgatum</u>						
total	pH	3795.7365	-935.3556	57.6208		29A
	algal biomass	11.2709	-3.2219	0.1901		28A
medium	pH	715.1873	-176.5351	10.8971		29B
	coulter counts	6.1399	-0.0016	0.119x10 ⁻⁶	-0.245x10 ⁻¹¹	29G
	algal biomass	2.8222	-0.8002	0.0461		28C
large	benthic density	0.2750	0.4408			27E
	pH	371.3416	-90.3051	5.4922		29C
ultimate	rainfall	0.1306	-1.9516	7.3771	-5.7474	29E
	algal biomass	0.0355	0.0148			28E

Table 19. (continued)

Variable Labels		Intercept	Degree of the Polynomial			Figure References
Y	X		B1	B2	B3	
ultimate	moonlight	0.1917	0.0060			29K
	discharge	0.1033				29I
pupae	water temperature					29L
	dissolved oxygen					30C
<u>Simulium trivittatum</u>						
total	dissolved oxygen		0.0331			31A
	discharge					31B
Adults						
<u>S. species A</u>						
males	algal biomass					28G
females	algal biomass					28H
<u>S. virgatum</u>						
males	alkalinity	137.1683	-1.5011	0.0054	-0.641x10 ⁻⁵	30E
females	alkalinity	93.1370	-1.0036	0.0036	-0.429x10 ⁻⁵	30F
	coulter counts	0.2434	-0.101x10 ⁻⁴			30D
	discharge	0.2191	-0.2537	0.0848		30B

Table 20. Linear correlations between Simulium species A and drift rates and the benthic densities of the associated taxa S. species A and virgatum. N = 17.

Drift Rates	Benthic densities				
	Chironomidae	Centroptilium	Baetodes	Lutrocladia - larvae	S. species A
small larvae	0.293	0.334	-0.107	0.914*	0.872
<u>Simulium</u> species A					
total larvae	-0.284	-0.095	0.096	-0.138	-0.184
medium	0.356	0.476*	-0.129	0.875*	0.803
large	0.012	0.218	-0.110	0.221	0.129
ultimate	0.039	0.060	-0.131	0.430	0.339
pupae	-0.076	-0.052	-0.123	0.152	0.015
<u>Simulium</u> virgatum					
total larvae	-0.284	-0.095	0.096	-0.138	-0.184
medium	-0.331	-0.093	0.346	-0.175	-0.218
large	-0.344	-0.138	-0.160	0.148	-0.178
ultimate	-0.151	0.085	-0.012	0.052	-0.034
pupae	-0.239	0.054	-0.122	-0.059	-0.042

* significant at $\alpha = 0.05$

Table 19. (continued)

Variable Labels		Intercept	Degree of the Polynomial			Figure References
Y	X		B1	B2	B3	
ultimate	moonlight	0.1917	-0.0060			29K
	discharge	0.1435	-0.2213	0.1033		29I
pupae	water temperature	-0.0988	0.0083			29L
	dissolved oxygen	0.4682	-0.0446			30C
<u>Simulium trivittatum</u>						
total	dissolved oxygen	3.4778	-0.6660	0.0331		31A
	discharge	0.3332	-0.1048			31B
Adults						
<u>S. species A</u>						
males	algal biomass	-0.1060	0.1985			28G
females	algal biomass	-0.1084	0.1960			28H
<u>S. virgatum</u>						
males	alkalinity	137.1683	-1.5011	0.0054	-0.641×10^{-5}	30E
females	alkalinity	93.1370	-1.0036	0.0036	-0.429×10^{-5}	30F
	coulter counts	0.2434	-0.101×10^{-4}			30D
	discharge	0.2191	-0.2537	0.0848		30B

Table 20. Linear correlations between Simulium species A and virgatum drift rates and the benthic densities of the associated fauna and S. species A and virgatum. N = 17.

Drift Rates	Benthic densities					
	<u>Chironomidae</u>	<u>Centroptilium</u>	<u>Baetodes</u>	<u>Lutrochus luteus</u> <u>larvae</u>	<u>S. species A</u>	<u>S. virgatum</u>
small larvae	0.293	0.334	-0.107	0.914*	0.852*	-0.377
<u>Simulium species A</u>						
total larvae	-0.284	-0.095	0.096	-0.138	-0.144	0.374
medium	0.356	0.476*	-0.129	0.885*	0.813*	-0.451
large	0.012	0.218	-0.110	0.221	0.149	-0.271
ultimate	0.039	0.060	-0.131	0.430	0.339	-0.391
pupae	-0.076	-0.052	-0.123	0.152	0.075	-0.236
<u>Simulium virgatum</u>						
total larvae	-0.284	-0.095	0.096	-0.138	-0.144	0.374
medium	-0.331	-0.093	0.346	-0.175	-0.268	0.550*
large	-0.344	-0.138	-0.160	0.148	-0.148	0.235
ultimate	-0.151	0.085	-0.012	0.052	-0.034	-0.103
pupae	-0.239	0.054	-0.122	-0.059	-0.092	0.374

* significant at $\alpha = 0.05$

Table 21. Summary of the 3-way ANOVAs to determine significant Simulium activity patterns. Values presented are F-ratios; N = number of 24-hr studies included in the analyses.

	N	Orthogonal Comparisons					Main Effects		
		Day vs. Night	Day Morning vs. Afternoon	Night Evening vs. Morning	Crepuscular vs. Night	Crepuscular Evening vs. Morning	Hour Collected	Month Collected	Net A vs. Net B
<u>Simuliidae Drift</u>									
small larvae	17	9.7896*	4.2754	7.9324*	8.2606	1.5537	2.5523*	142.1334*	4.3424*
<u>Simulium species A</u>									
total larvae	17	23.7035*	9.0474*	11.2835*	13.3453*	3.3891	4.9536*	100.2443*	8.1332*
medium	13	5.1264*	1.3909	0.4558	1.7694	0.0876	0.7614	46.7829*	11.6910*
large	12	0.0042	2.2421	0.3730	0.2254	0.3340	0.3037	9.5096*	0.2223
ultimate	5	0.0070	0.0978	0.3391	0.0672	0.4521	0.0773	50.8272*	14.4905*
males	13	60.0010*	17.2305*	0.0099	0.1035	0.0299	7.9769*	15.3712*	0.3715
females	9	4.1760*	0.5669	2.1132	1.2317	2.9424	1.1375	6.5758*	0.8961
<u>Simulium virgatum</u>									
total larvae	17	0.6150	9.3528*	1.2650	0.1539	0.3153	1.1976	73.3316*	1.1530
medium	10	0.4793	1.7472	0.0051	0.2073	0.0123	0.2668	52.1266*	1.2562
large	9	0.6068	2.6411	0.0144	0.0792	0.0072	0.5040	3.4653*	0.0726
males	2	0.1005	0.0297	1.2183	2.2136	3.4301	0.5453	0.5323	0.8955
females	2	0.6451	2.1607	1.2902	2.1451	3.4286	1.0039	0.1824	4.1923
<u>Simulium trivittatum</u>									
total larvae	7	10.3401	0.4979	1.0389	4.9180	0.0184	1.6989	3.5989*	1.8241

* significant $\alpha = 0.05$

Table 22. Linear correlations between the mean 2-hr drift rates and the mean 2-hr pH, alkalinity, temperature, dissolved oxygen, and light intensity estimates. N = 12.

Parameter	pH	Alkalinity	Water Temp.	Dissolved Oxygen	Light Intensity
pH	1.000	0.429	0.468	0.689*	0.951*
Alkalinity		1.000	-0.347	0.709*	0.437
Water Temperature			1.000	-0.192	0.554*
Dissolved Oxygen				1.000	0.620*
Light Intensity					1.000
small larvae	-0.593	-0.554	0.034	-0.709*	-0.452
<u>Simulium species A</u>					
total larvae	-0.627*	-0.601*	0.057	-0.759*	-0.494
males	0.535	0.535	-0.171	0.842*	0.449
females	0.439	0.020	0.112	0.556	0.422
<u>Simulium virgatum</u>					
total larvae	0.307	-0.251	0.828*	-0.207	0.432
males	-0.192	-0.481	0.250	-0.323	-0.219
females	0.157	-0.347	0.377	-0.107	0.022

* significant at $\alpha = 0.05$

Table 23. Multiple regression analyses between Simulium species A, virgatum and trivittatum benthic densities at Stream Means and Station 8 and concomitantly measured variables. Analyses terminated when increase in R^2 was less than 0.015.

Step Number	Independent variable (X) Added or Deleted	R	R^2	Increase in R^2
Stream Means, N = 43				
Y= species A benthic density				
1.	algal biomass	0.6631	0.4397	0.4397
2.	coulter counts	0.6967	0.4854	0.0457
3.	Chironomidae	0.7238	0.5239	0.0385
4.	<u>Baetodes</u> sp.	0.7406	0.5485	0.0246
5.	day length	0.7559	0.5714	0.0229
6.	discharge	0.7679	0.5897	0.0183
Y= <u>virgatum</u> benthic density				
1.	discharge	0.5786	0.3348	0.3348
2.	algal biomass	0.7116	0.5064	0.1715
3.	<u>Lutrochus luteus</u> larva	0.7427	0.5516	0.0452
4.	pH	0.7661	0.5869	0.0354
5.	ln alkalinity	0.7773	0.6043	0.0173
6.	<u>Centroptilium</u> sp.	0.7891	0.6227	0.0184
Y= <u>trivittatum</u> benthic density				
1.	<u>Lutrochus luteus</u> larva	0.3628	0.1316	0.1316
2.	pH x alkalinity	0.4746	0.2253	0.0937
3.	discharge	0.5261	0.2768	0.0515
4.	pH	0.5611	0.3148	0.0380
5.	coulter counts	0.5772	0.3332	0.0184
Station 8, N = 49				
Y= species A benthic density				
1.	algal biomass	0.2783	0.0774	0.0774
2.	<u>Hydropsyche</u> (nr <u>betteni</u>)	0.3612	0.1305	0.0530
3.	day length	0.4256	0.1812	0.0507
4.	<u>Cheumatopsyche</u> sp.	0.4802	0.2306	0.0494
5.	temperature	0.5153	0.2656	0.0350
6.	depth	0.5611	0.3148	0.0492
7.	<u>Baetodes</u> sp.	0.5896	0.3477	0.0329
8.	temperature x alkalinity	0.6074	0.3689	0.0212
Y= <u>virgatum</u> benthic density				
1.	ln S. species A	0.6298	0.3966	0.3966
2.	algal biomass	0.6876	0.4728	0.0761
3.	Chironomidae	0.7157	0.5122	0.0394
4.	<u>Lutrochus luteus</u> larva	0.7332	0.5376	0.0254
5.	<u>Baetodes</u> sp.	0.7537	0.5681	0.305

Table 24. Multiple regression analyses between Simulium drift rates and selected concomitantly measured abiotic parameters. Analyses were terminated when the increase in R^2 was less than 0.015.

Step Number	Variable Labels X - added or deleted	R	R^2	Increase in R^2
<u>Simulium</u> species A total larvae				
1.	algal biomass	0.7415	0.5498	0.5498
2.	discharge	0.7849	0.6161	0.0664
3.	pH	0.8174	0.6682	0.0521
4.	coulter counts	0.8503	0.7231	0.0549
5.	rainfall	0.8758	0.7670	0.0439
6.	alkalinity	0.8923	0.7962	0.0272
7.	day length	0.9238	0.8534	0.0572
<u>Simulium</u> species A males				
1.	algal biomass	0.6831	0.4667	0.4667
2.	rainfall	0.7788	0.6065	0.1399
3.	pH	0.7902	0.6245	0.0179
4.	discharge	0.8165	0.6667	0.0422
5.	coulter counts	0.8593	0.7384	0.0718
6.	moonlight	0.8750	0.7656	0.0272
<u>Simulium</u> species A females				
1.	algal biomass	0.7165	0.5134	0.5134
2.	rainfall	0.7962	0.6339	0.1205
3.	pH	0.8177	0.6686	0.0347
4.	coulter counts	0.8461	0.7159	0.0473
5.	discharge	0.8629	0.7447	0.0288
<u>Simulium</u> <u>virgatum</u> total larvae				
1.	algal biomass	0.6148	0.3780	0.3780
2.	alkalinity	0.6639	0.4407	0.0627
3.	pH	0.6941	0.4817	0.0410
4.	discharge	0.7436	0.5530	0.0713
5.	day length	0.8375	0.7013	0.1484
6.	rainfall	0.8788	0.7732	0.0709
<u>Simulium</u> <u>virgatum</u> males				
1.	pH	0.3808	0.1450	0.1450
2.	moonlight	0.4616	0.2131	0.0681
3.	water temperature	0.4975	0.2475	0.0344
4.	coulter counts	0.5513	0.3039	0.0564
5.	alkalinity	0.5792	0.3355	0.0316
6.	dissolved oxygen	0.6129	0.3757	0.0401
7.	algal biomass	0.6695	0.4482	0.0725
<u>Simulium</u> <u>virgatum</u> females				
1.	coulter counts	0.5118	0.2620	0.2620
2.	water temperature	0.6739	0.4542	0.1922

Table 24. (continued)

Variable Labels		R	R ²	Increase in R ²
Step Number	X - added or deleted			
<u>Simulium virgatum</u> females				
3.	discharge	0.6939	0.4815	0.0274
4.	dissolved oxygen	0.7102	0.5044	0.0229
<u>Simulium trivittatum</u> total larvae				
1.	discharge	0.5057	0.2557	0.2557
2.	moonlight	0.5566	0.3098	0.0540
3.	pH	0.6207	0.3853	0.0755
4.	rainfall	0.6452	0.4163	0.0310
5.	alkalinity	0.6722	0.4519	0.0356

* significant $\alpha = 0.05$

Table 25. Multiple regression prediction expressions Simulium total benthic density and adult female drift rate from Stream Means, Station 8 and the drift data matrix. Analyses were terminated when the F-ratio to enter was non-significant ($\alpha = 0.05$), the increase in R^2 was less than 0.015, or the R was greater than 0.90.

Dependent Variable	Intercept	Independent Variables				
		X1	X2	X3	X4	X5
Stream means, N = 43						
<u>S. species A</u>		algae				
slope	0.07001	0.53709				
R		0.6631				
<u>S. virgatum</u>		dischrg. algae				
slope	3.73994	-0.14948	-0.96981			
R		0.5786	0.7116			
Station 8, N = 49						
<u>S. species A</u>		algae	day l'th temp.	depth	tempxalk.	
slope	-3.63384	0.05543	0.60216	-0.15668	-0.03152	0.00012
R		0.2783	0.3165	0.4578	0.4882	0.4984
<u>S. virgatum</u>		algae	alkalinity			
slope	-0.13303	0.03430	0.00052			
R		0.4982	0.5805			
Drift models, N = 12						
Benthic density						
<u>S. species A</u>		drift				
slope	1.10952	0.08542				
R		0.9441				
<u>S. virgatum</u>		algae	moonl't	rainfall	D.O.	temp.
slope	-18.34210	-0.29454	-0.06203	2.86846	1.71288	0.29400
R		0.5416	0.6785	0.7819	0.8358	0.9509
drift rate ♀						
<u>S. species A</u>		imm.drft	dischrg			
slope	-0.24368	0.01859	0.53396			
R		0.8454	0.9022			
<u>S. virgatum</u>		algae	imm.drft	pH		
slope	-1.27570	0.01337	0.02126	0.15169		
R		0.6301	0.8730	0.9196		

Table 26. Summary of prediction equation evaluation.

Source of Test Data	Dependent Variable and Model Source	r **
Station 2, N = 5	Average of Stations 1,3,4,5,6 and 7	
	<u>S.</u> species A total benthic density	-0.09874
	<u>S.</u> <u>virgatum</u> total benthic density	-0.19401
Station 9, N = 27	Station 8	
	<u>S.</u> species A total benthic density	0.27891
	<u>S.</u> <u>virgatum</u> total benthic density	0.00017
Drift studies 1 to 5	Drift studies 6 to 17	
	<u>S.</u> species A total benthic density	0.09199
	<u>S.</u> <u>virgatum</u> total benthic density	-0.40251
	<u>S.</u> species A female drift	-0.55585*
	<u>S.</u> <u>virgatum</u> female drift	-0.40541

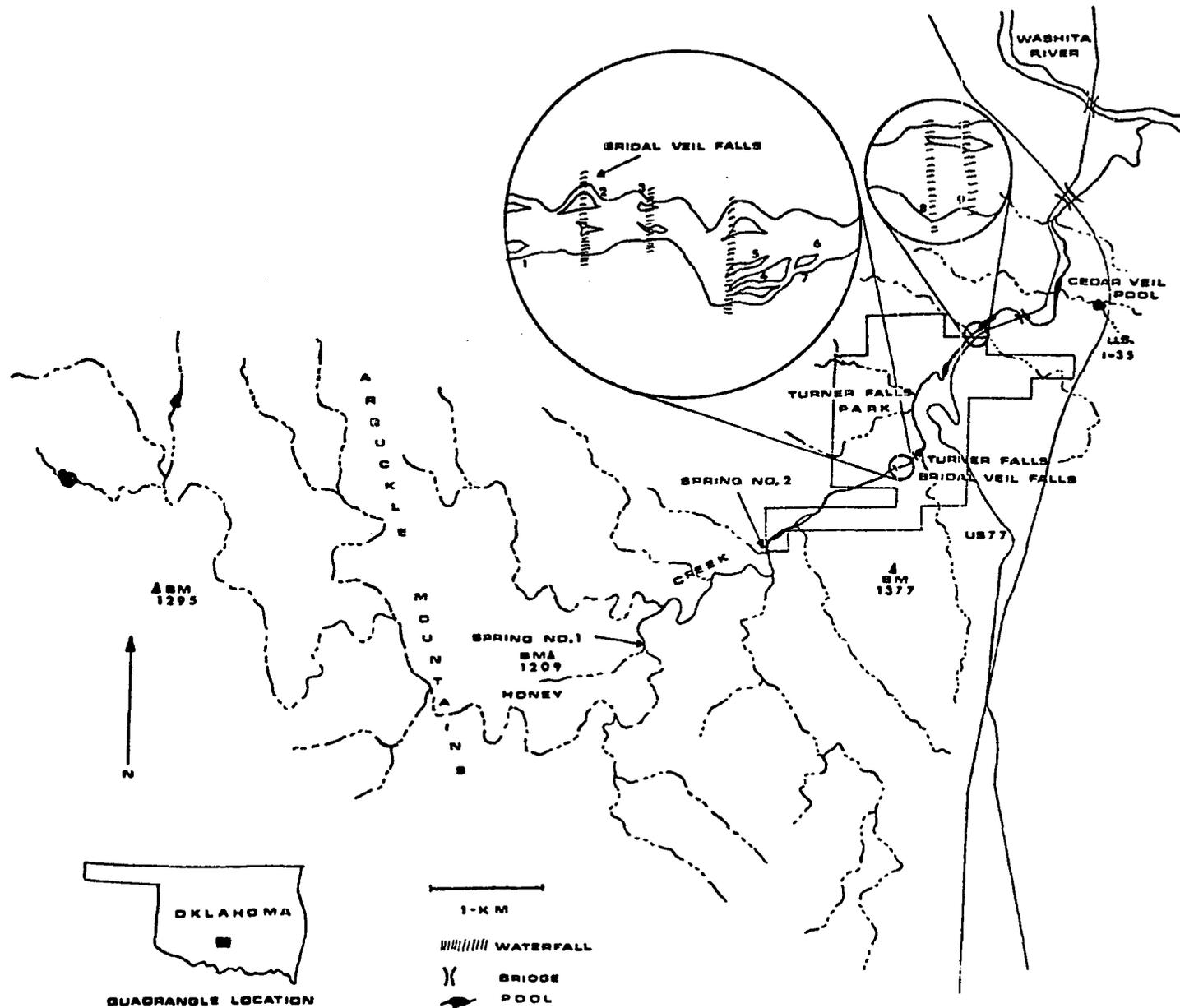
* significant $\alpha = 0.05$

** r = linear correlation coefficient

APPENDIX B

FIGURES

Figure 1. Map of Honey Creek, Murray County, Oklahoma (redrawn from a 1964, U.S. Department of Interior Geological Survey map entitled Turner Falls Quadrangle). Station numbers and locations are included in the enlarged circles.



**Figure 2. Longitudinal profile of the gradient of Honey Creek,
Murray County, Oklahoma.**

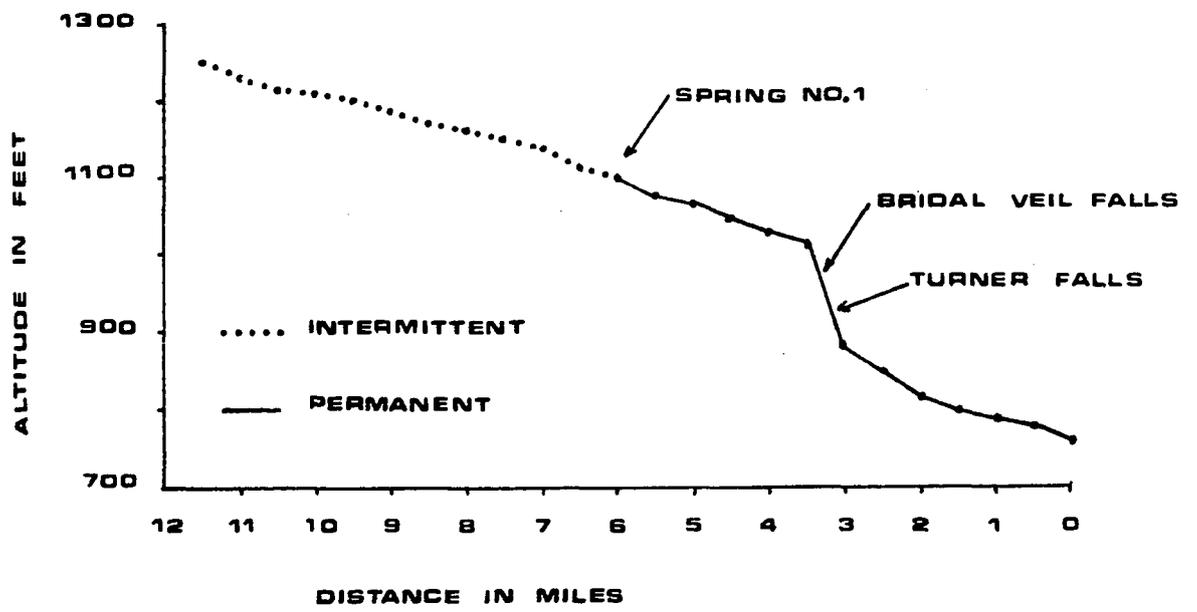


Figure 3. Algal extract optical density degradation and correction factor curves.

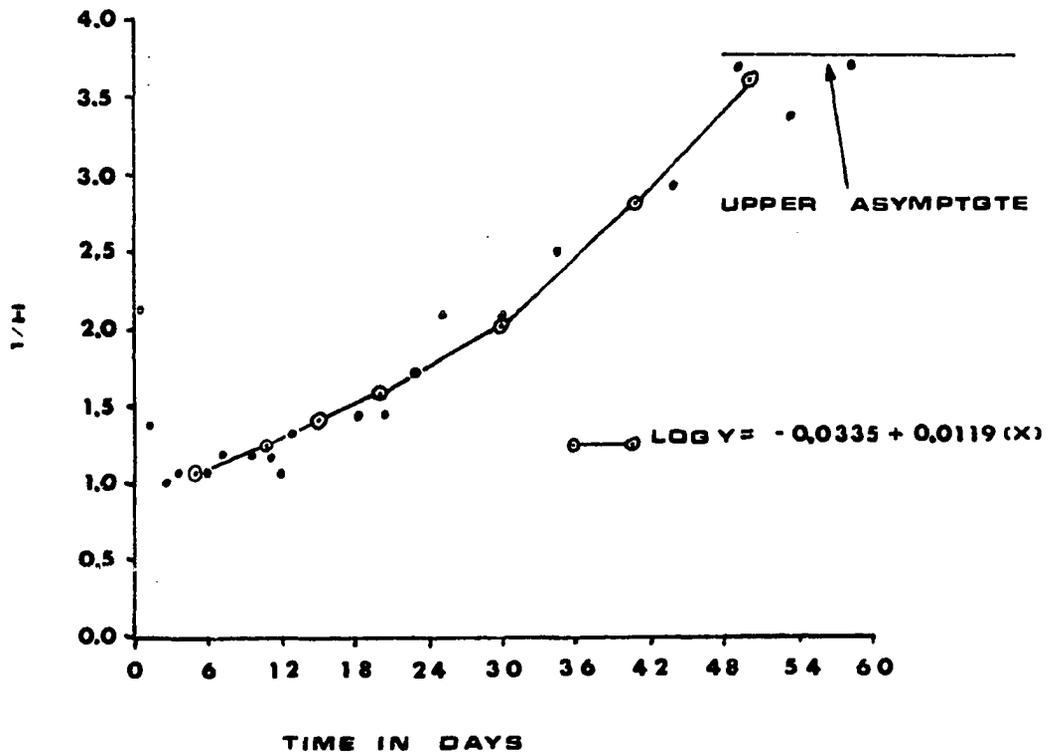
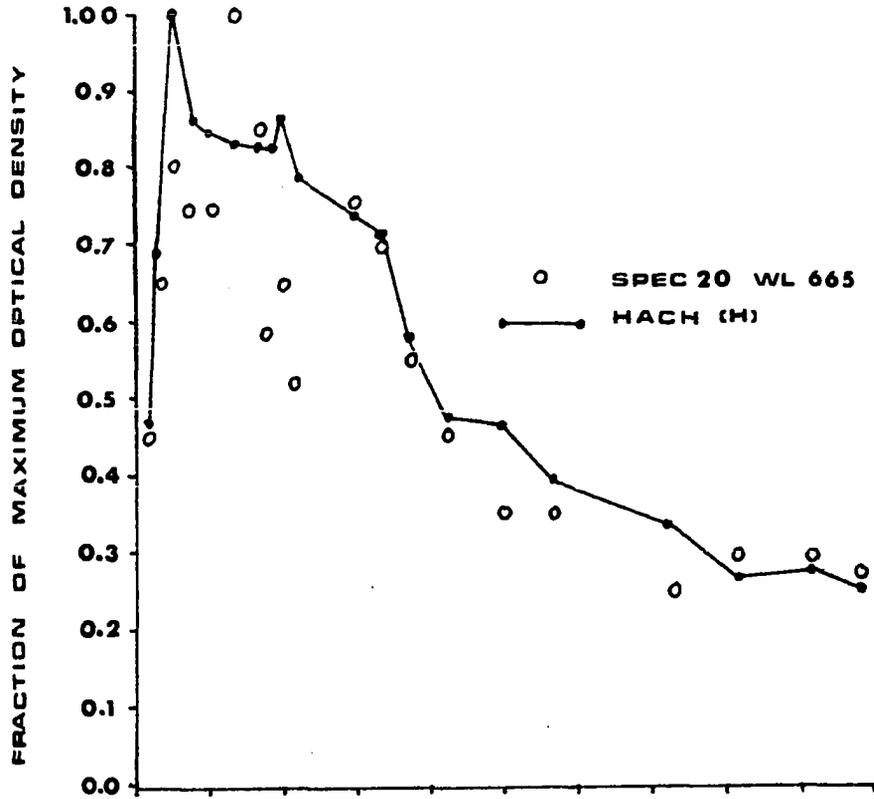


Figure 4. Seasonal fluctuations in selected physical parameters of Honey Creek estimated at Stations 4 and 8 from 31 June 72 through 15 August 73.

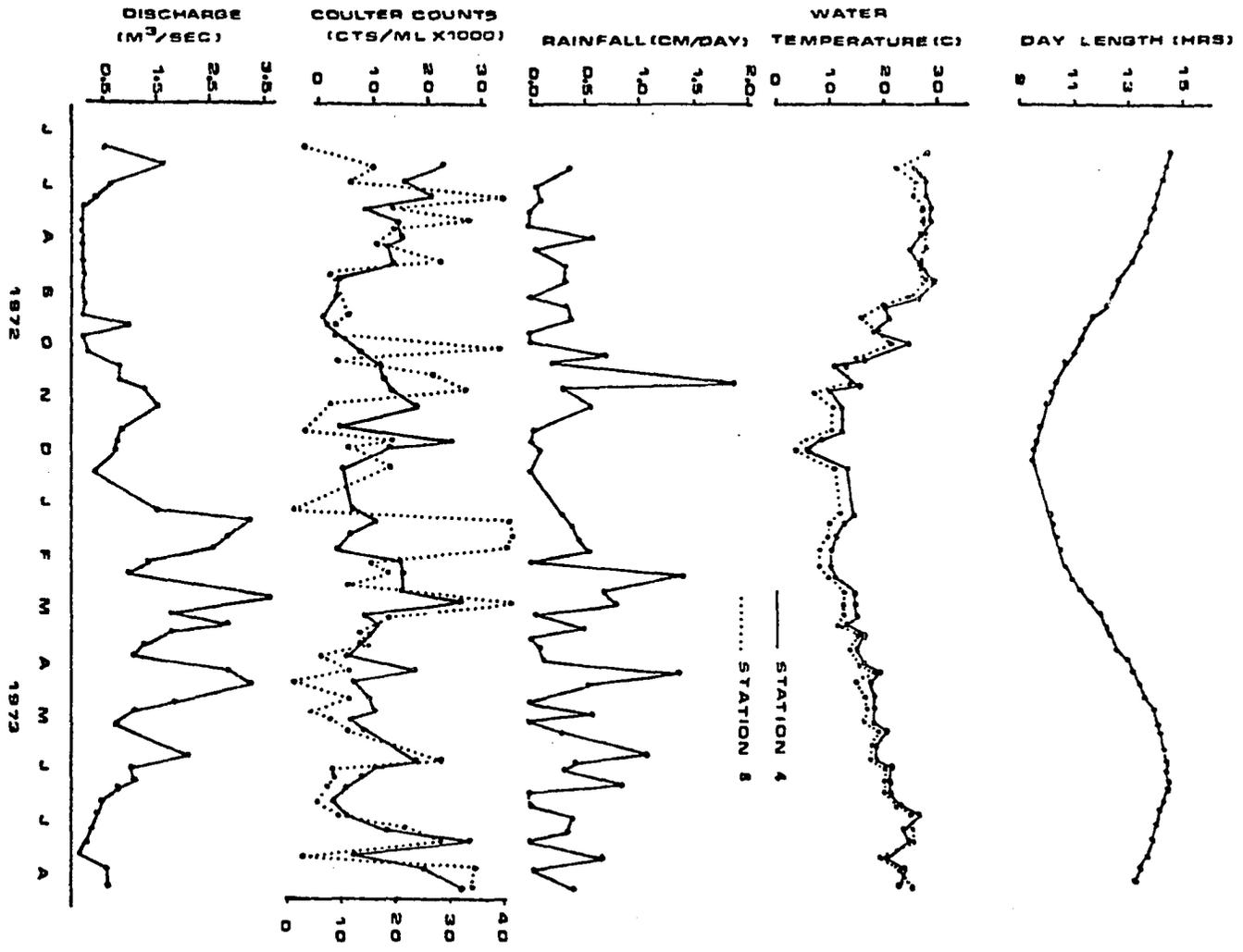


Figure 5. Seasonal fluctuations in the selected chemical parameters of Honey Creek at Stations 4 and 8 from 31 June 72 through 14 August 73.

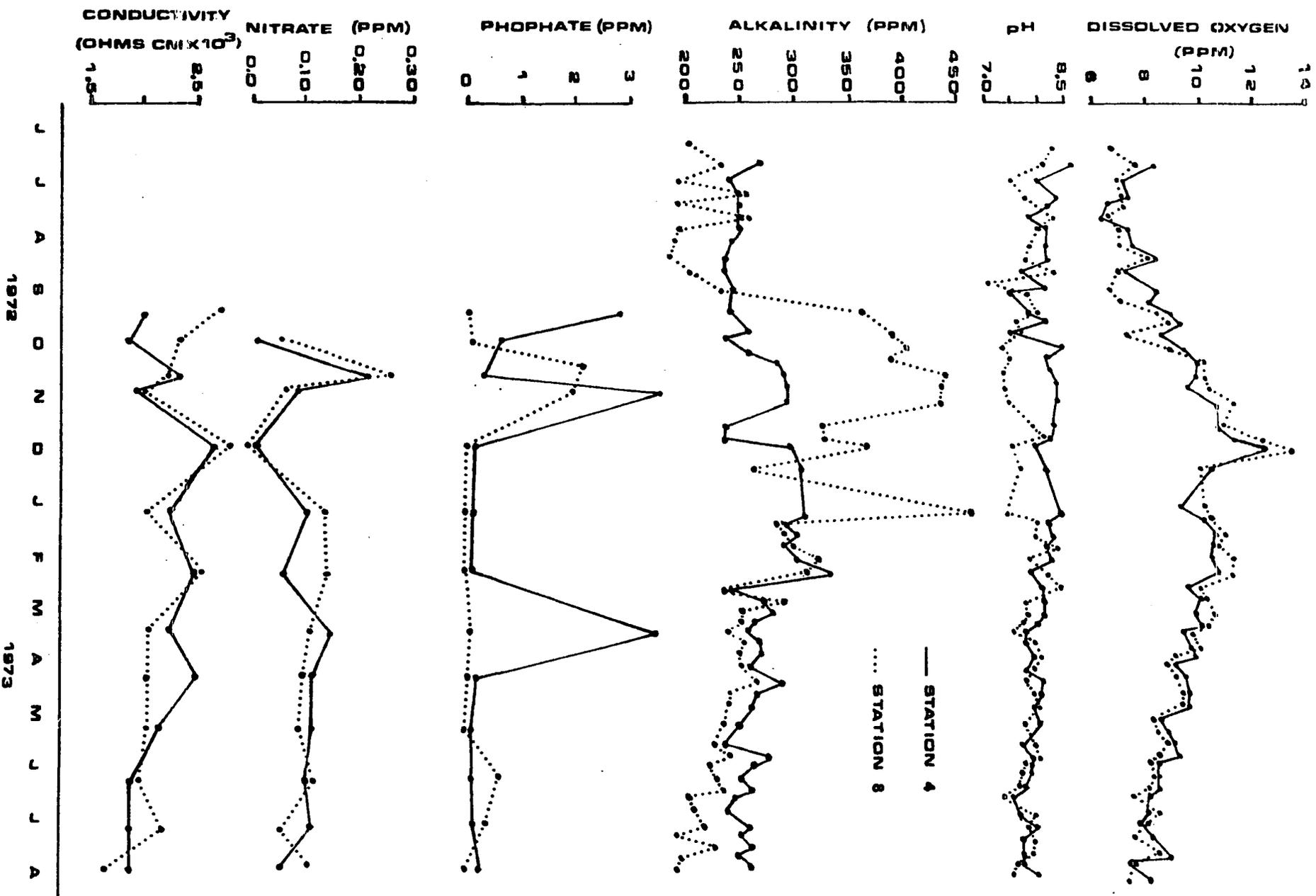


Figure 6. Algal biomass estimates for Stations 1, 3, 4, 5, 6, 7, 8, and 9 from 5 August 72 through 15 August 73.

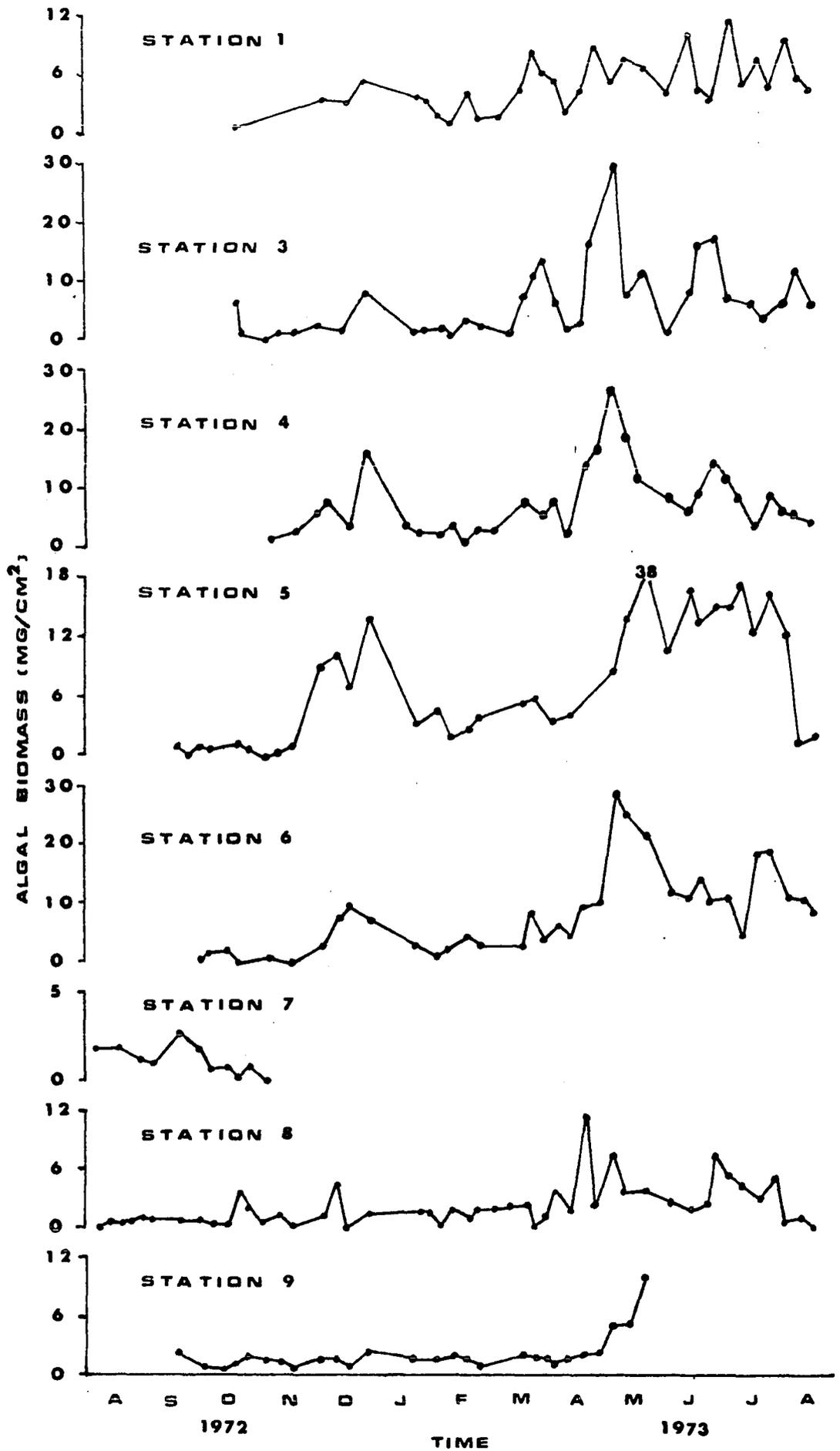


Figure 7. Seasonal changes in the depth and current velocity at Stations 1, 3, 4, 5, and 6 from 15 July 72 through 15 August 73.

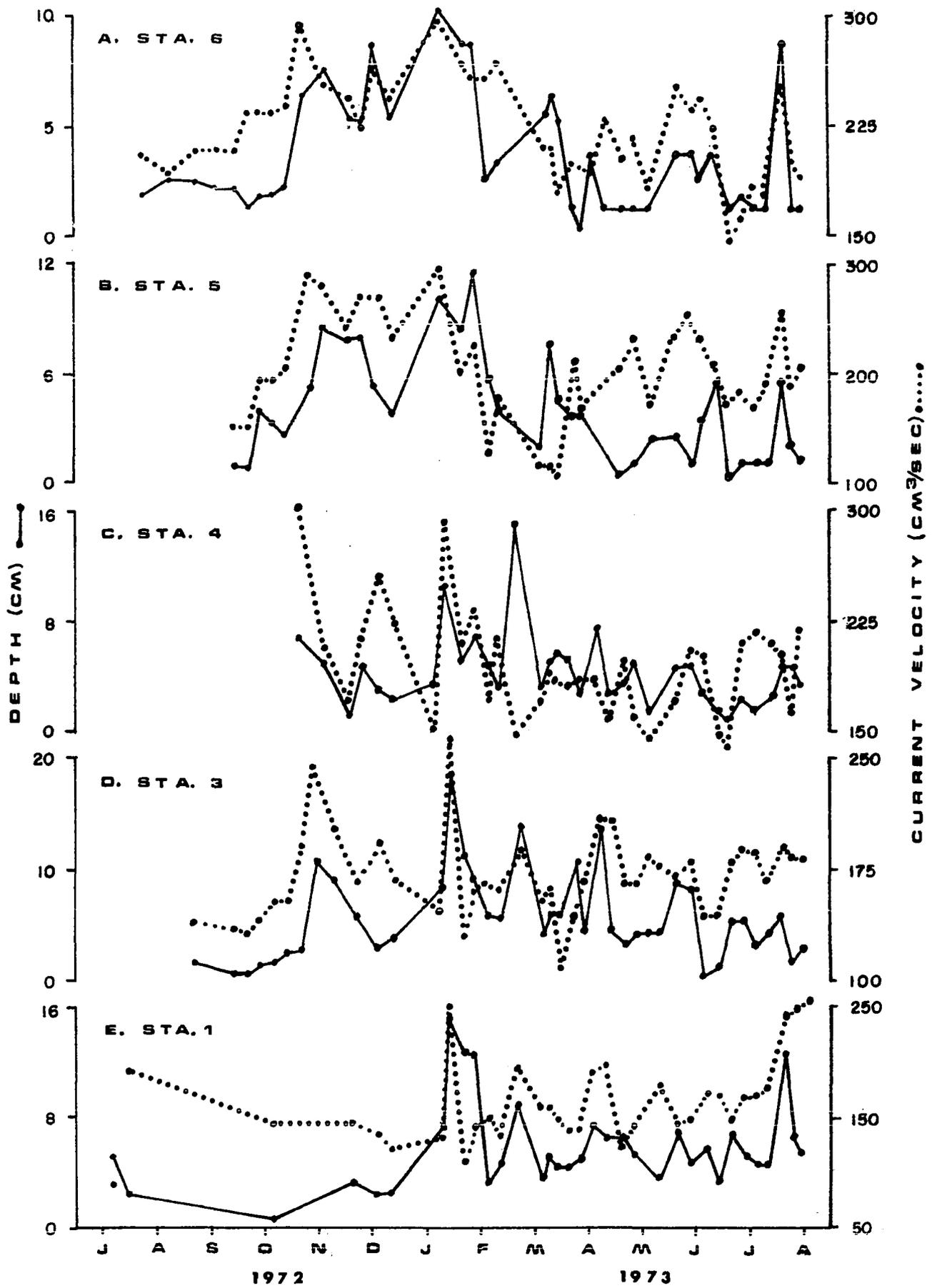


Figure 8. Number of larval instars of Simulium species A and virgatum

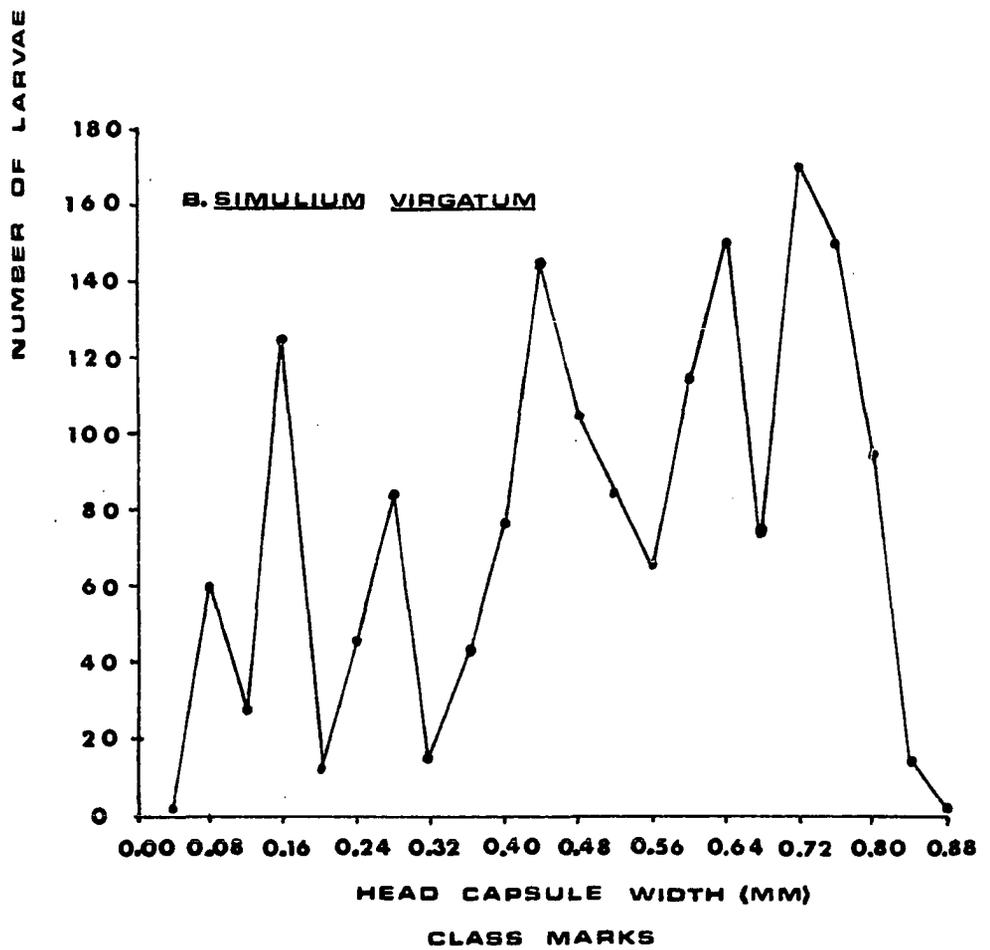
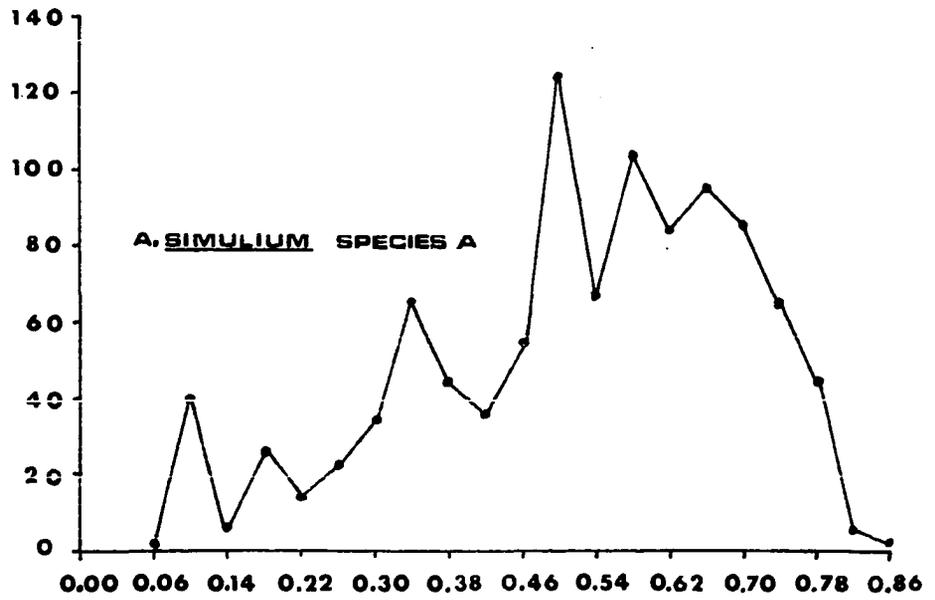


Figure 9. Weight plotted as a function of head-capsule-width for S. species A and virgatum.

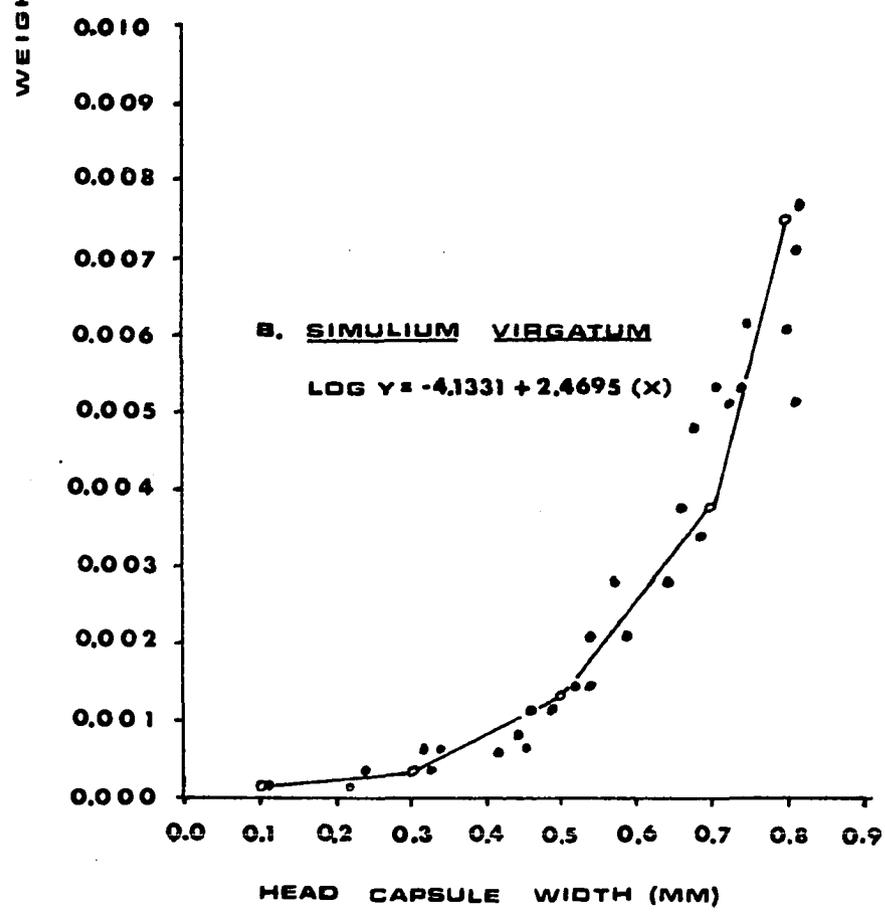
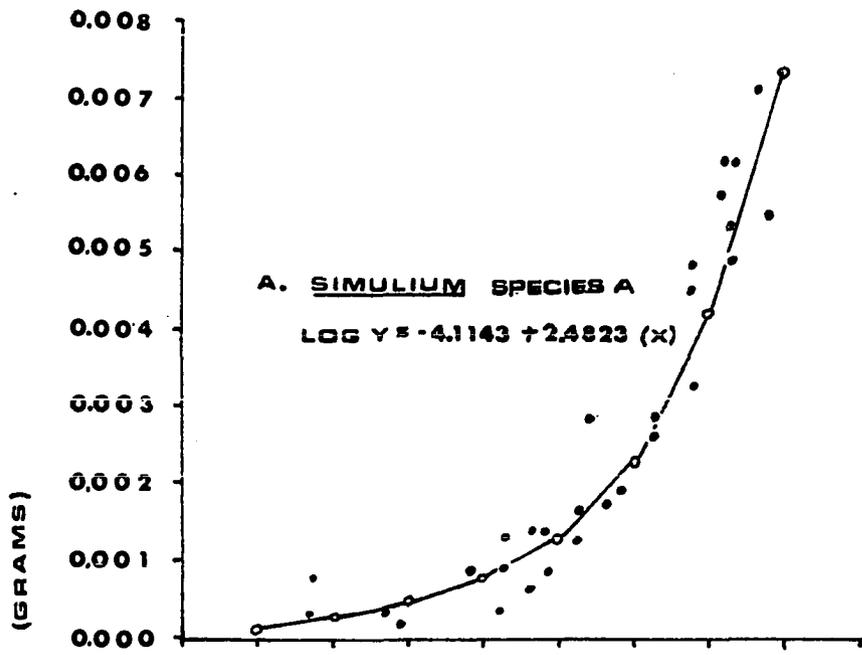


Figure 10. Growth curves for Simulium virgatum at Stations 3 (. . . .)
and 6 (_____).

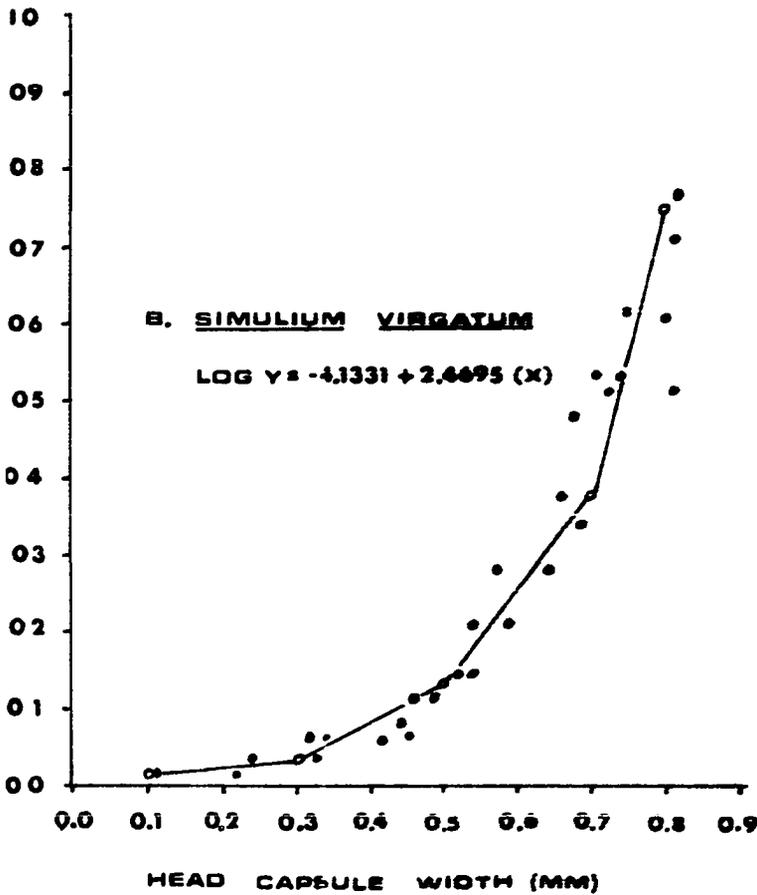
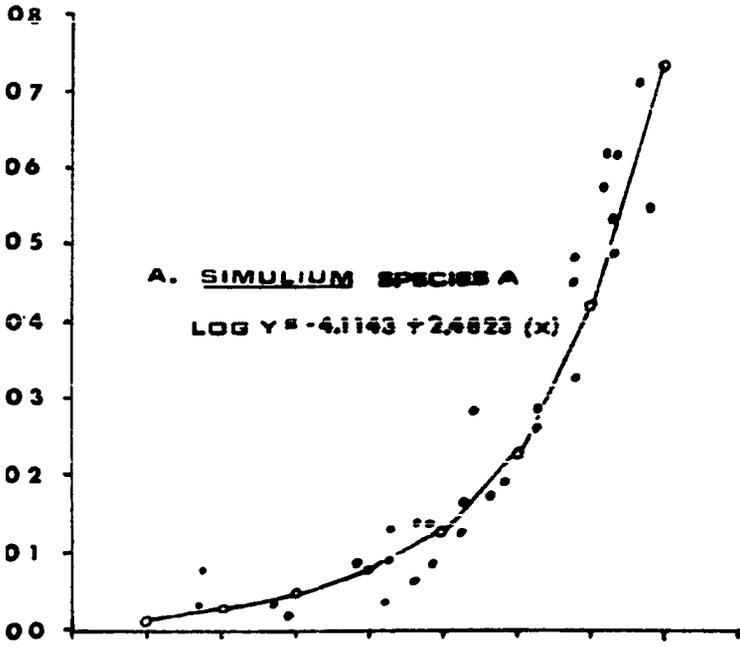
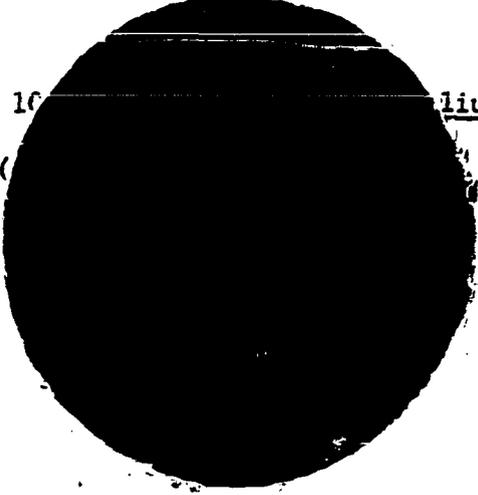


Figure 10  lium virgatum at Stations 3 (. . . .)
and 6 (

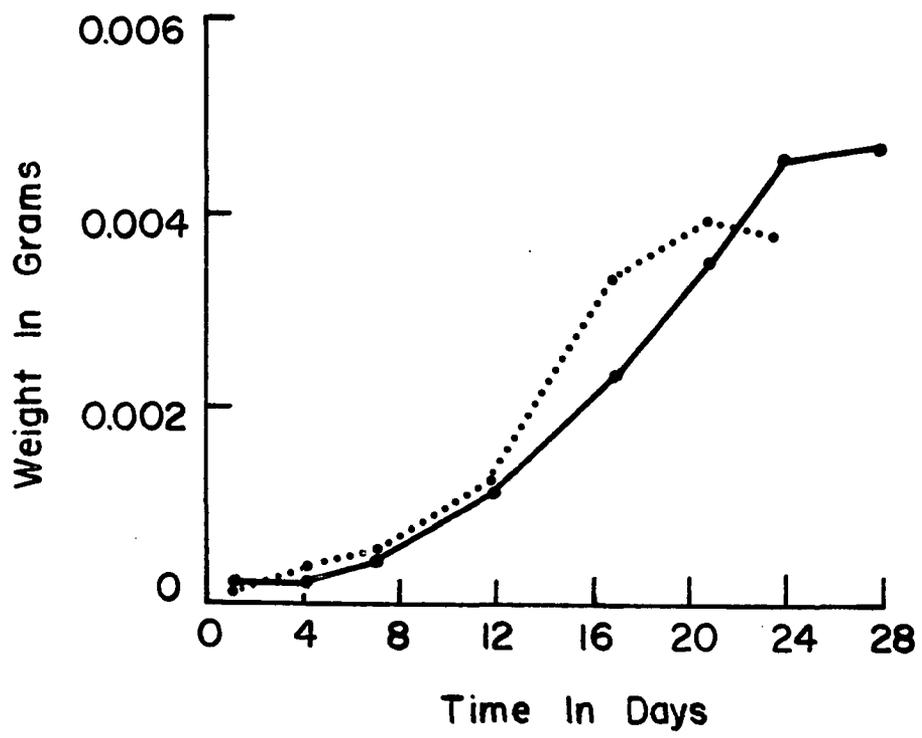


Figure 11. Survivorship curves for Simulium virgatum at Stations 3 and 6.

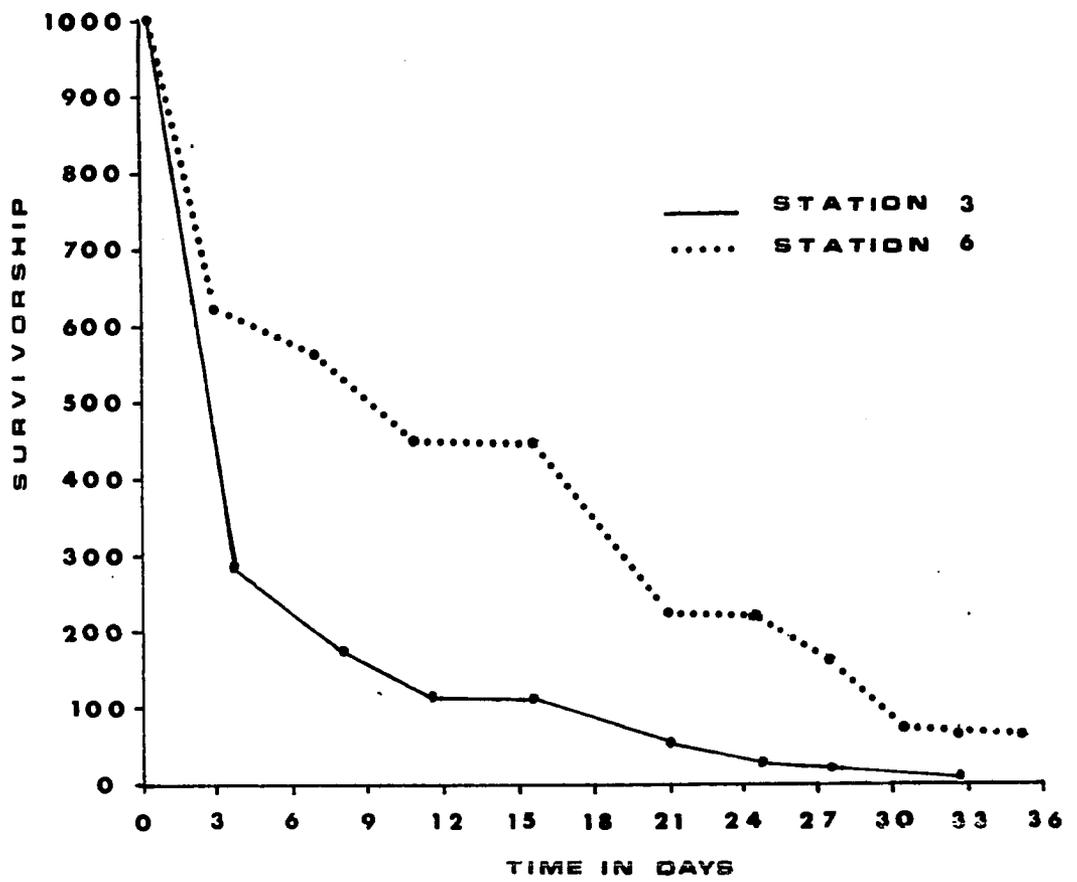


Figure 12. Seasonal fluctuations in the total benthic densities of Simulium species A and virgatum for Stations 1, 3, 4, 5, and 6 from 5 August 72 through 15 August 73

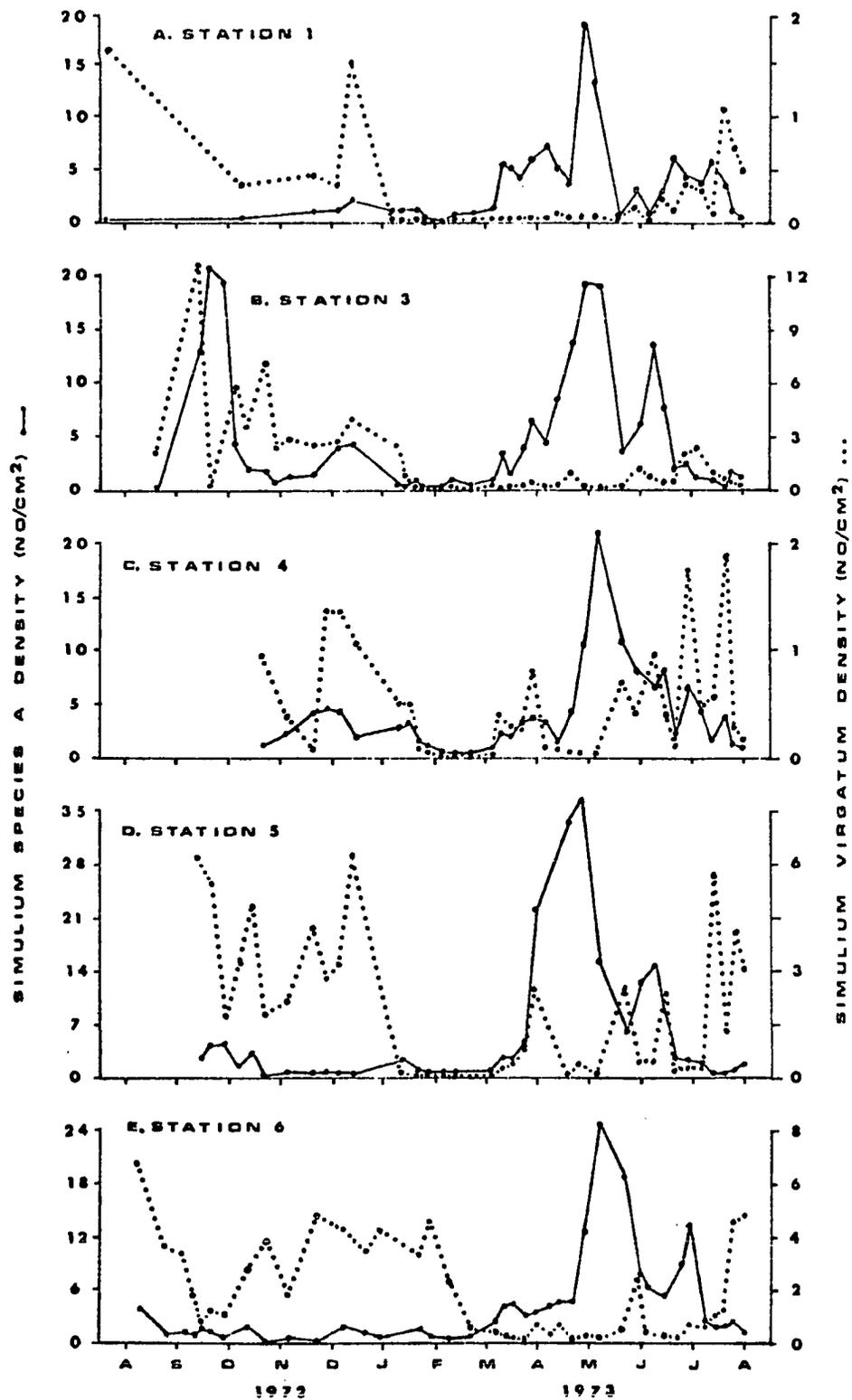


Figure 13. Seasonal fluctuations in the total benthic densities of Simulium species A and virgatum for Stations 8 and 9 from 31 June 72 through 15 August 73.

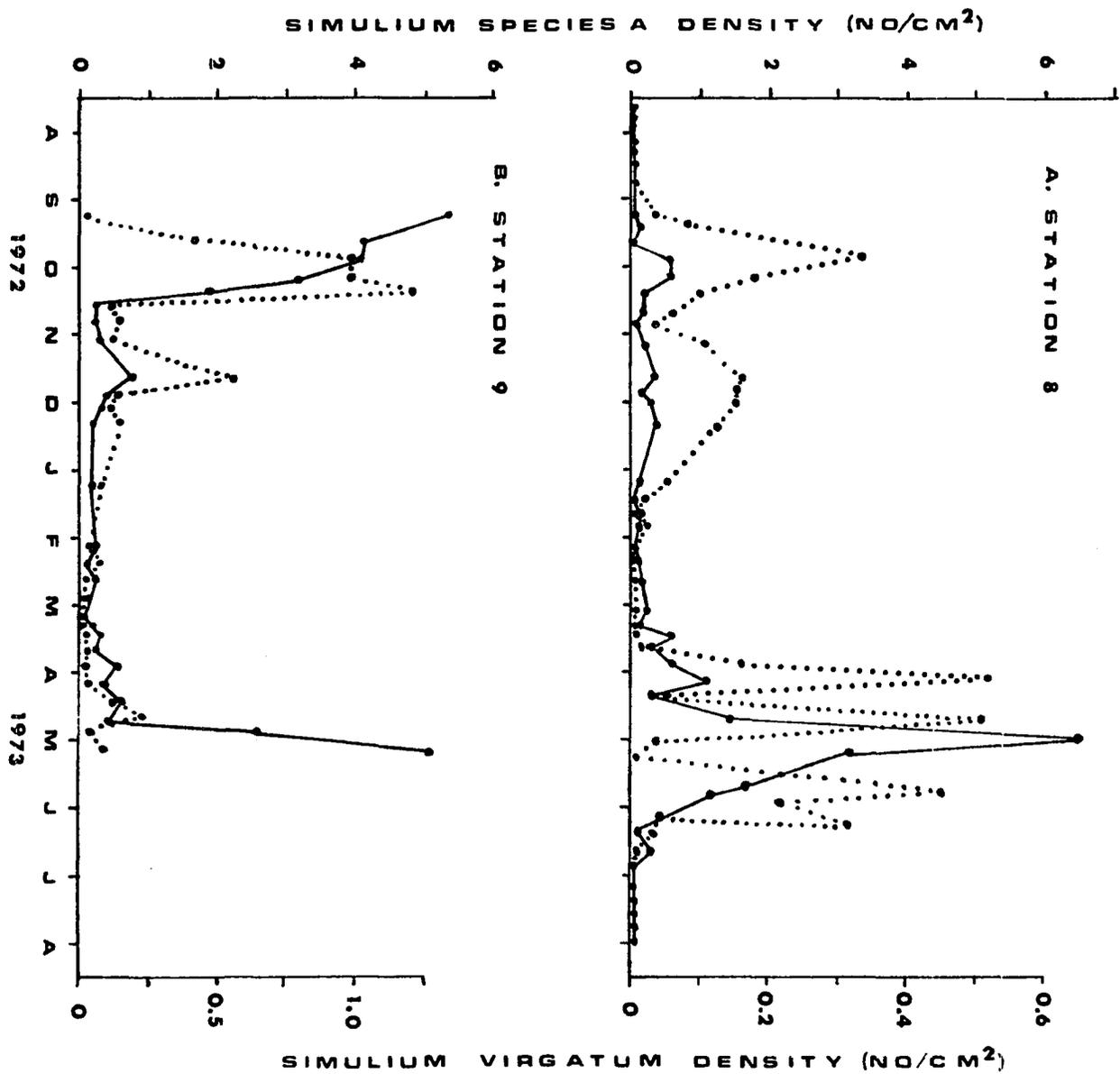


Figure 14. Seasonal fluctuations in the total benthic densities and percentage age composition of Simulium species A and virgatum for Stations 1, 3, 4, 5, 6, and 7 (stream means).

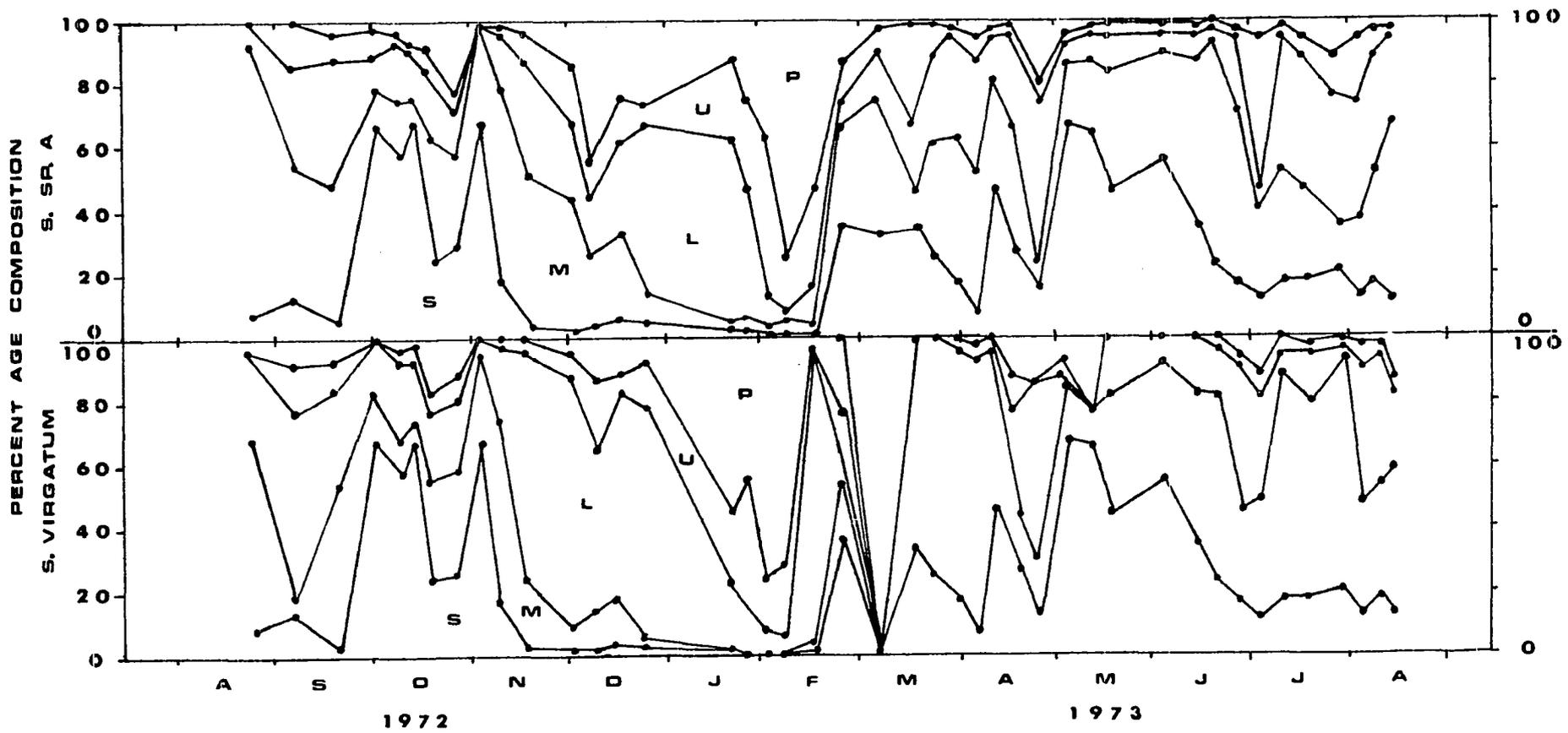
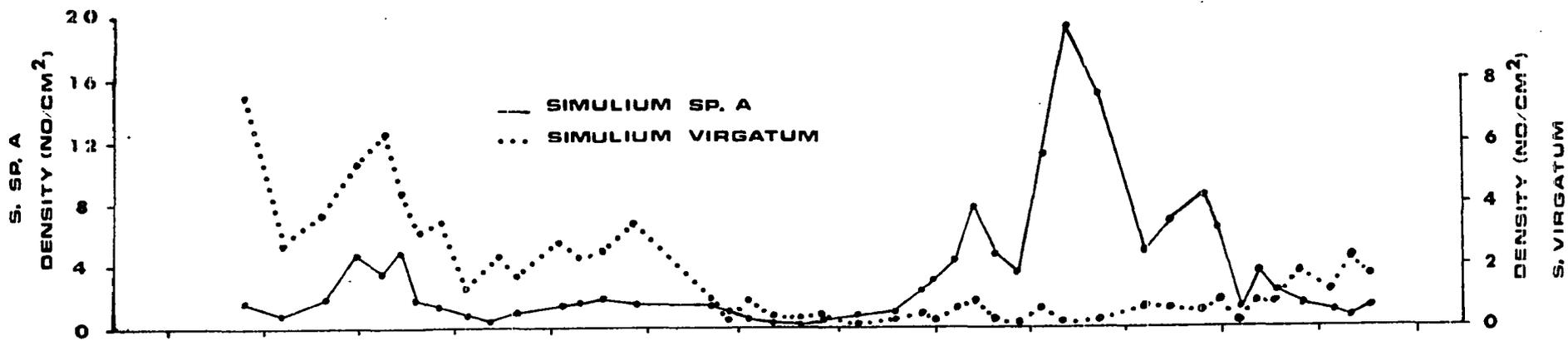


Figure 15. Seasonal fluctuations in the benthic density of Simulium
trivittatum for stream means.

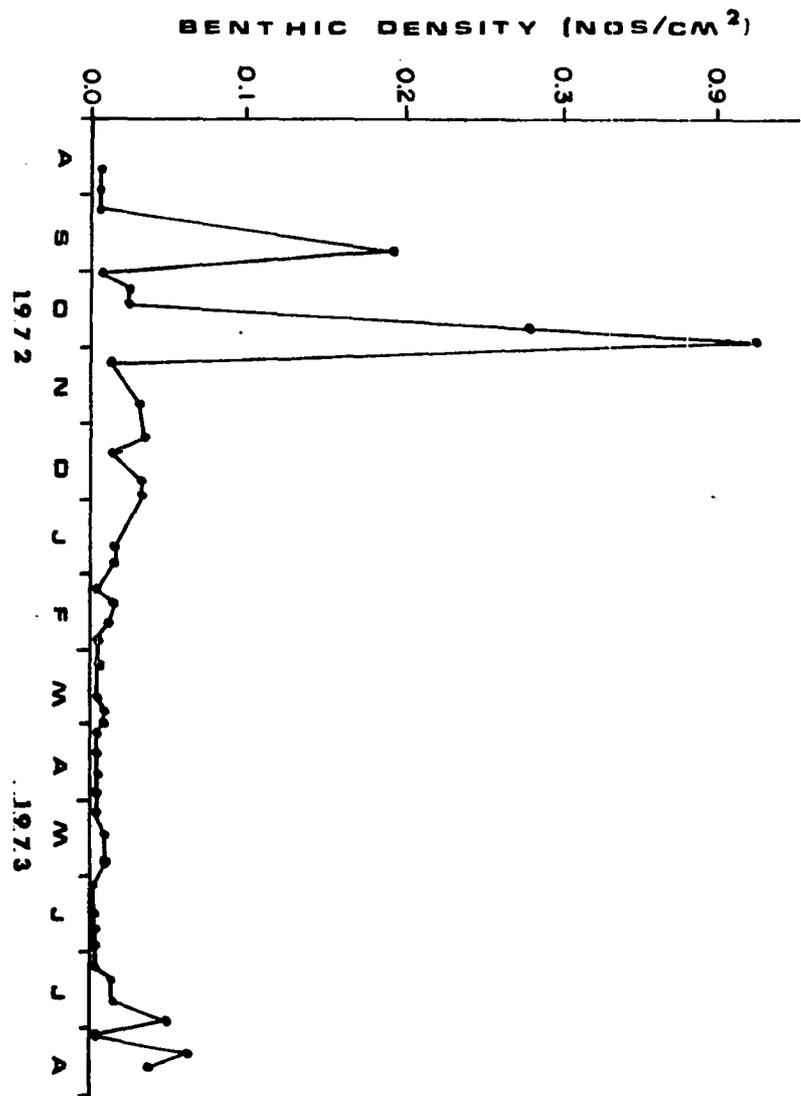
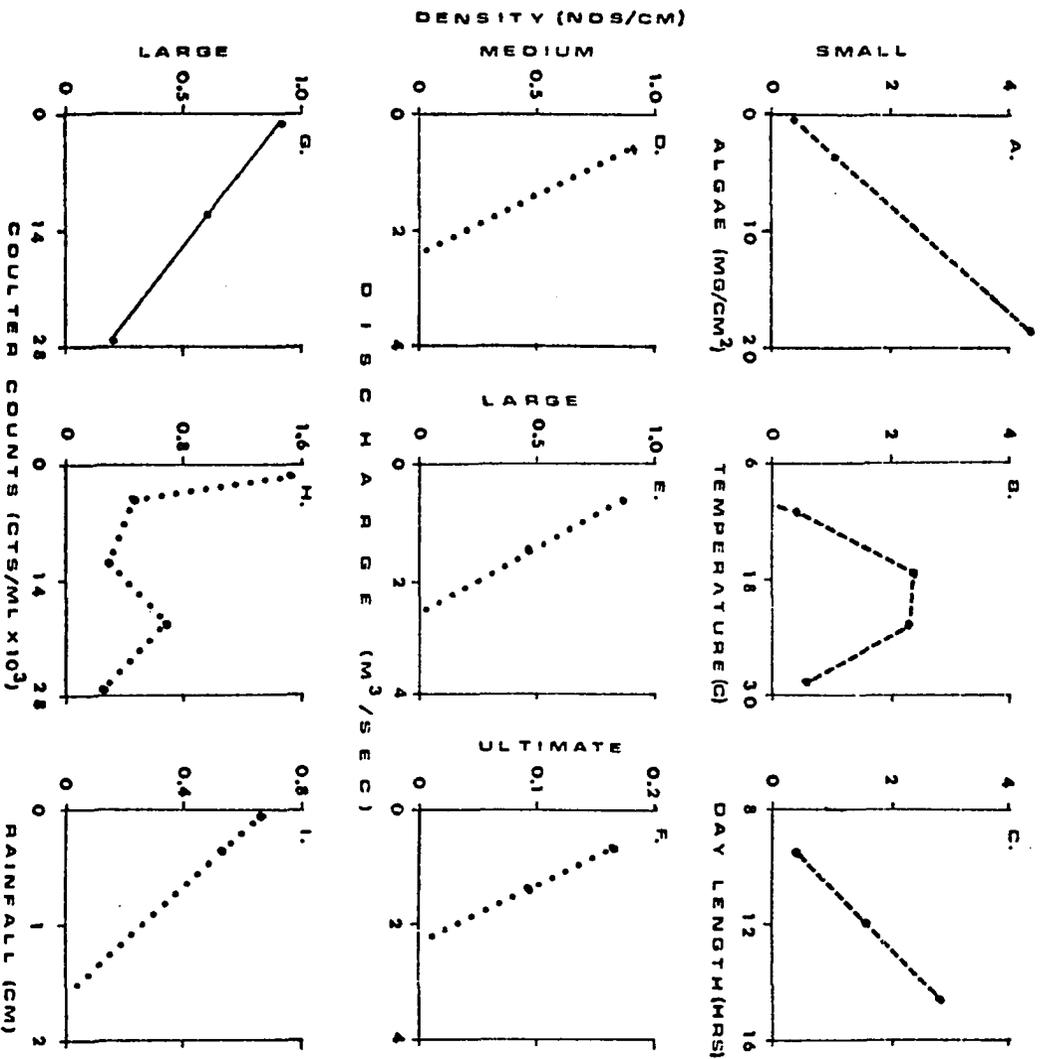


Figure 16. Significant polynomial regressions for small larvae, species A medium and virgatum medium, large and ultimate larval benthic densities.



---SMALL LARVAE ---S. SPECIES A ...S. VIRGATUM

Figure 17. Significant polynomial regressions for Simulium species A and virgatum medium, large, and ultimate larvae and pupae benthic densities. There were no significant pupal-alkalinity interactions and 17T was subsequently left blank.

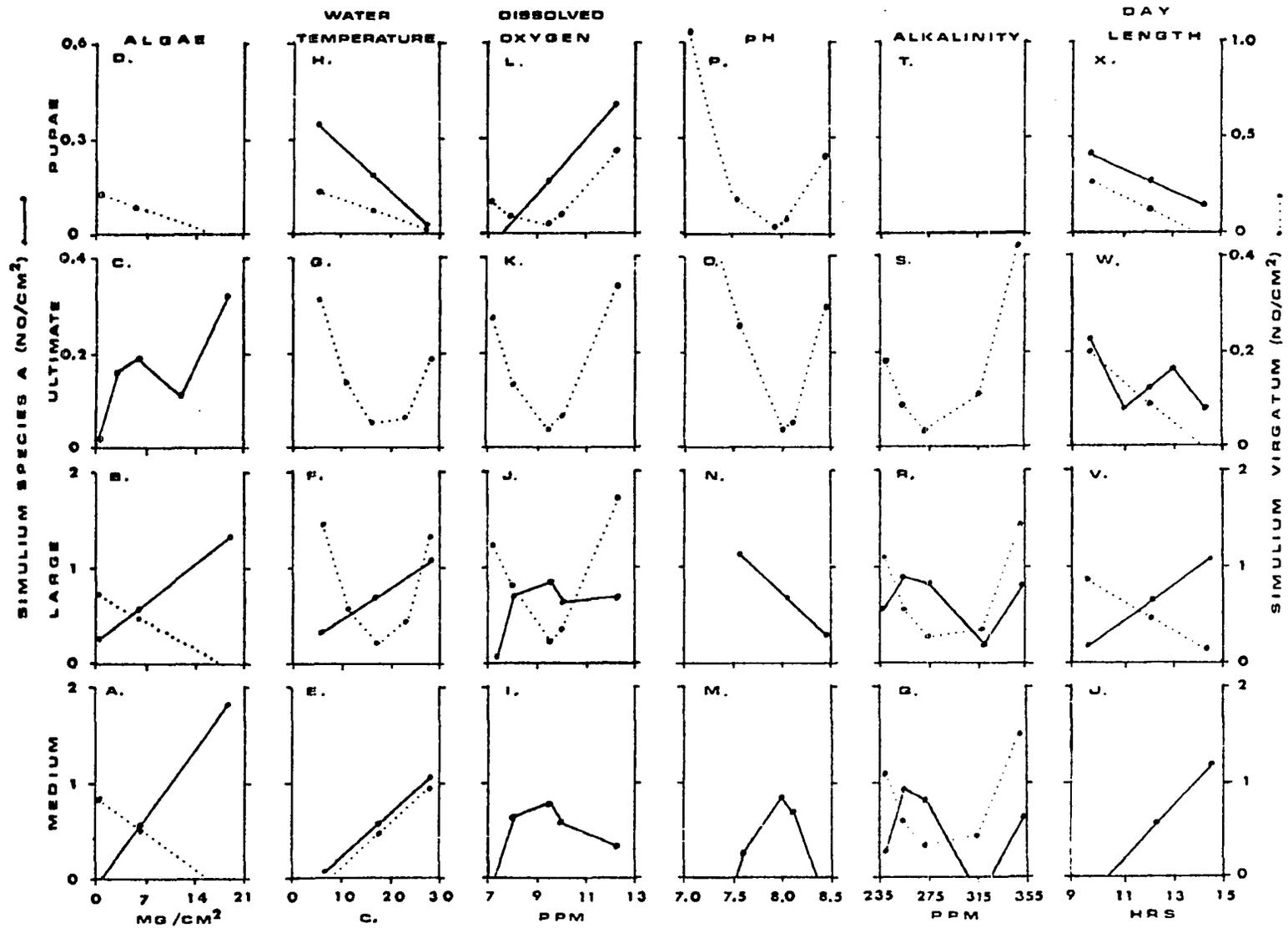


Figure 18. Regression of Simulium species A ultimate larval density on coulter counts.

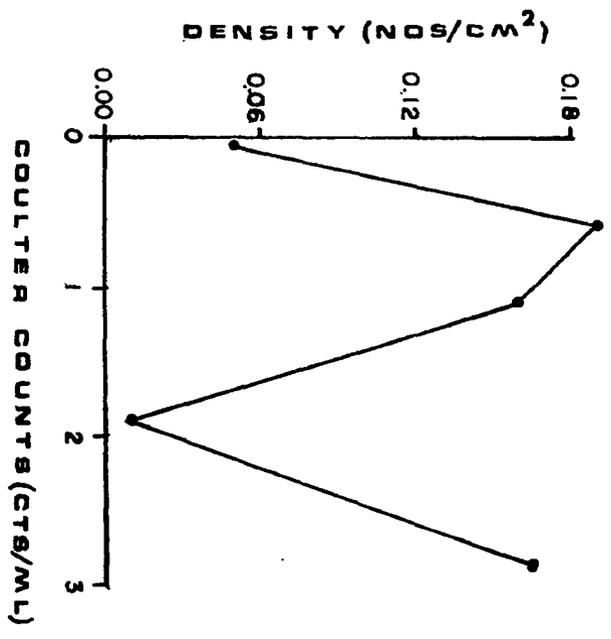


Figure 19. Significant polynomial regressions of Simulium species
A and virgatum totals.

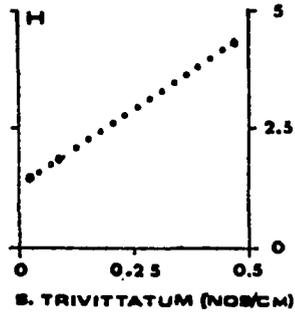
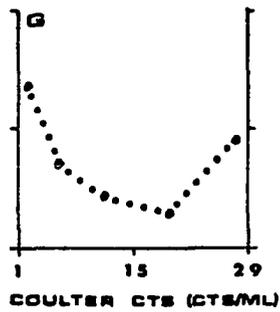
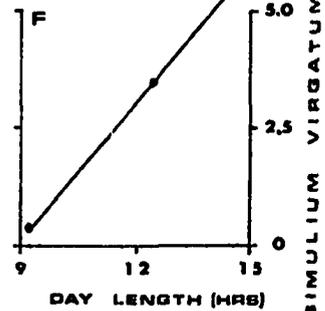
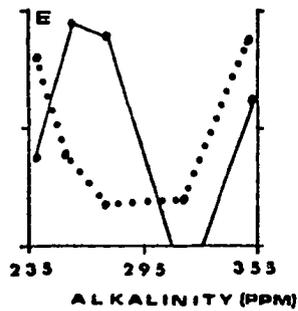
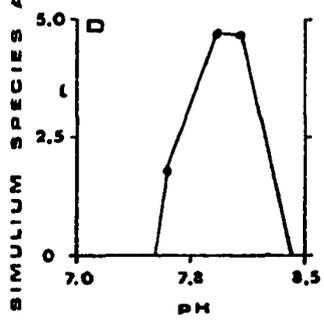
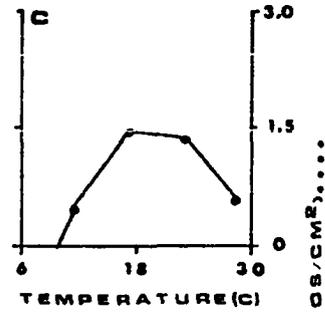
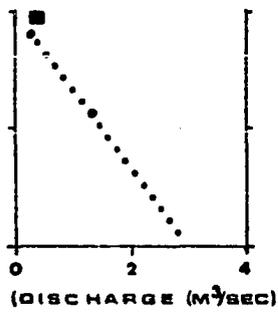
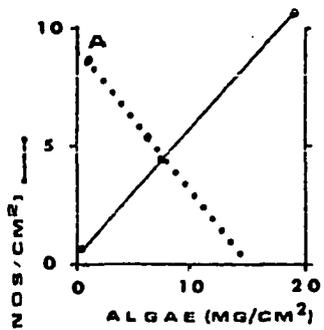


Figure 20. Significant linear regressions of Simulium species A and virgatum total densities with depth and current velocity at Stations 1, 3, 4, and 6.

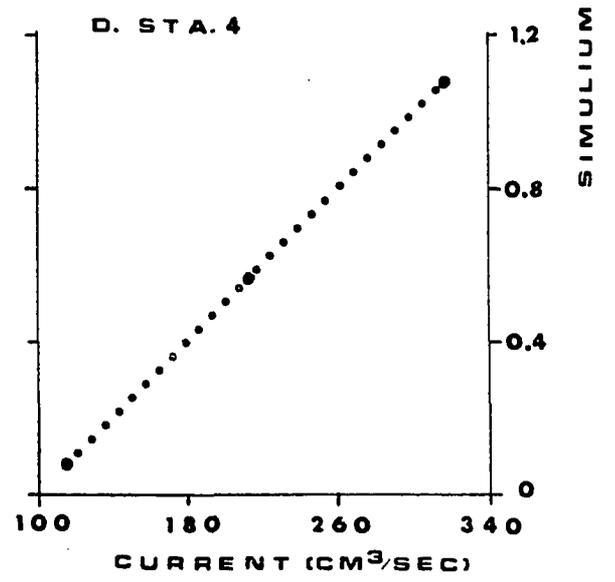
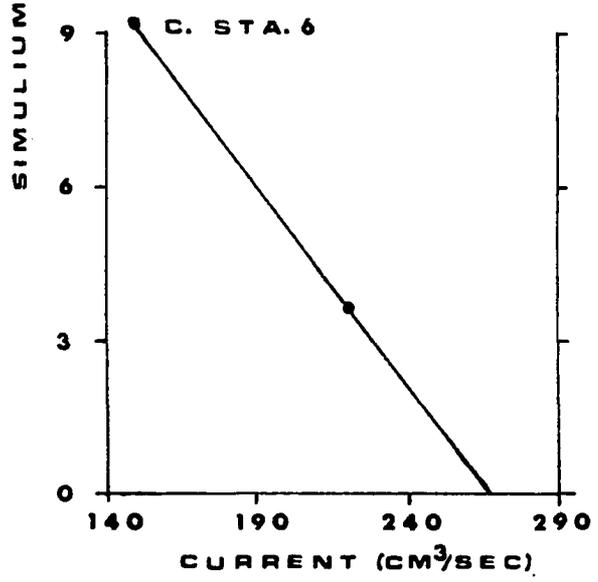
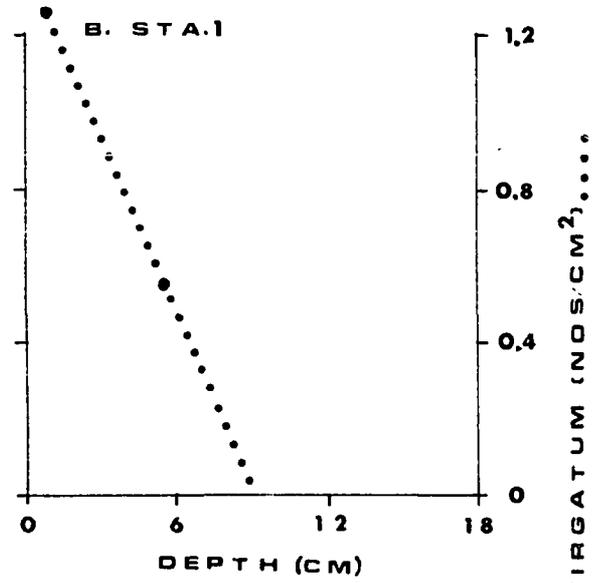
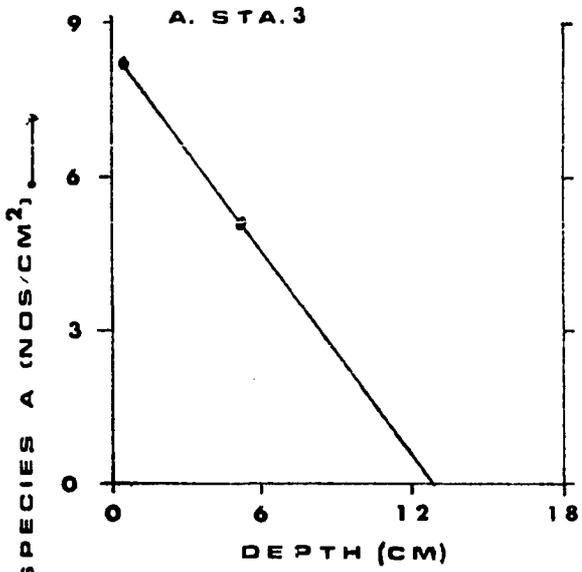


Figure 21. Significant regressions of Simulium species A and virgatum at Stations 4, 5, and 8.

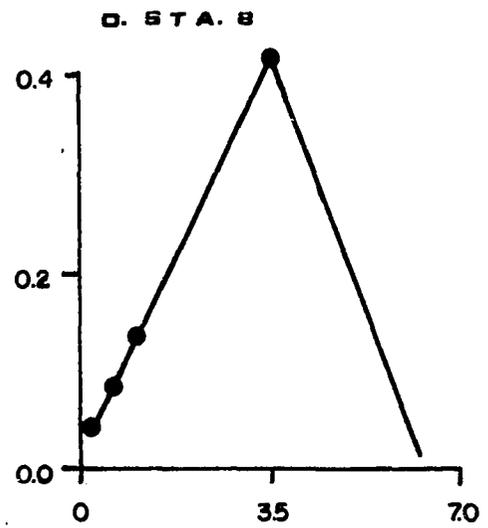
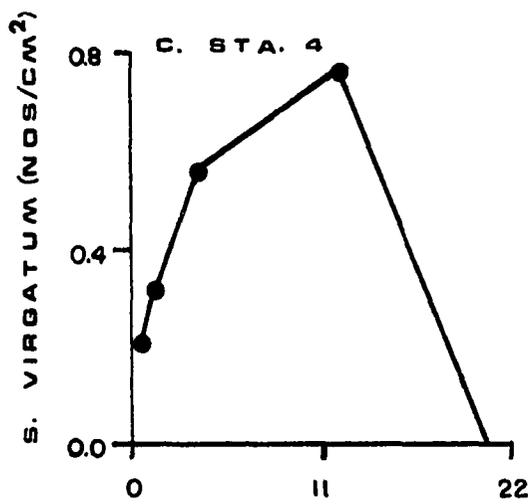
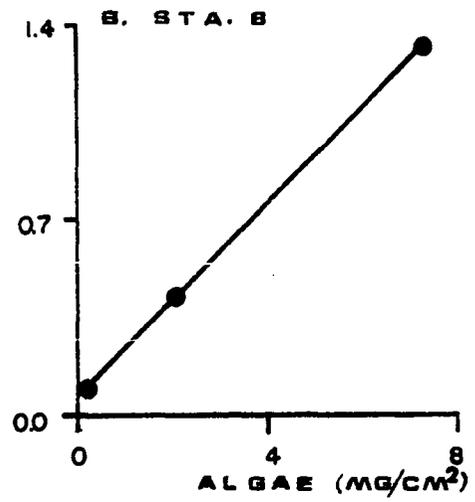
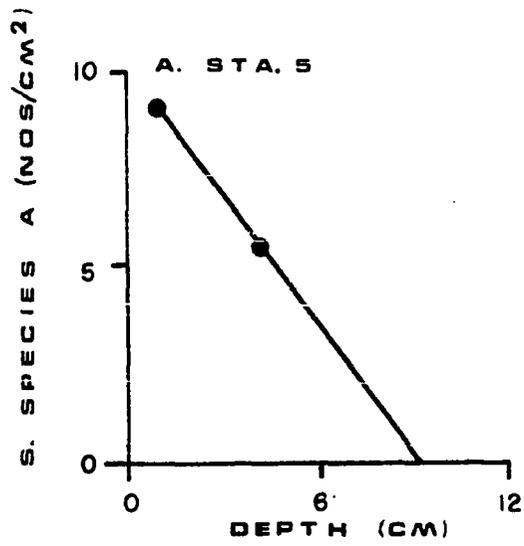


Figure 22. Significant polynomial regressions for Simulium species
A and virgatum at Stations 8 and 9.

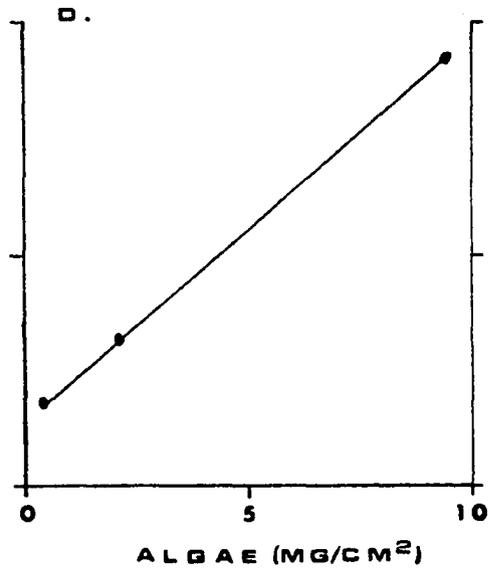
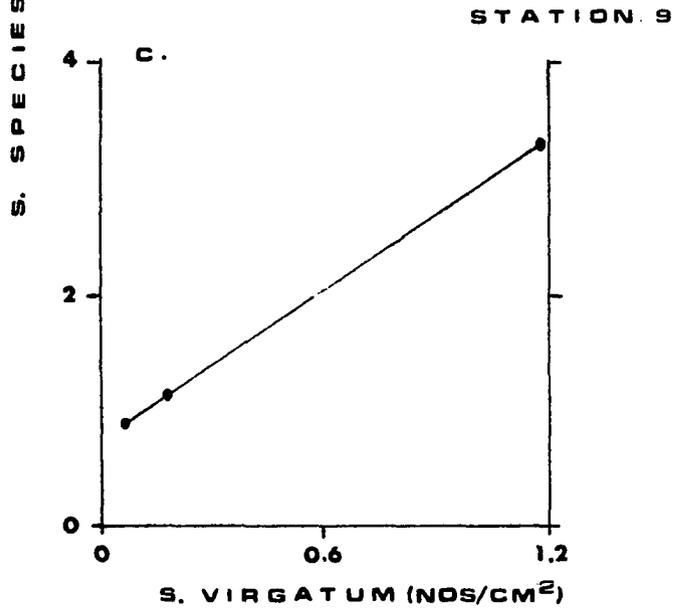
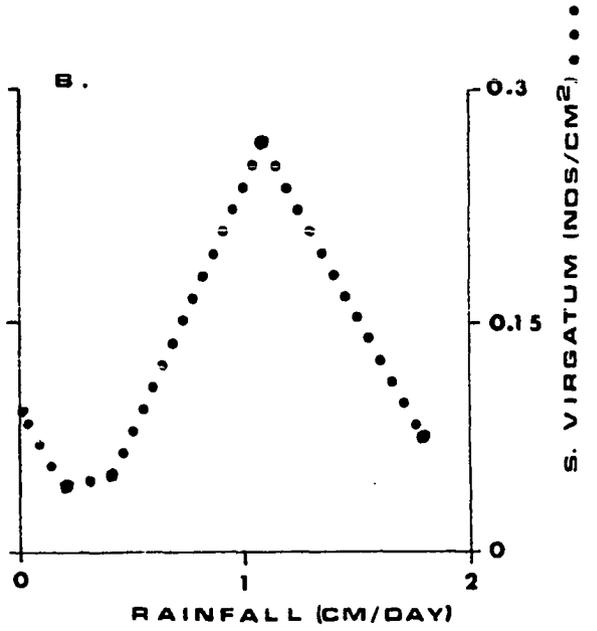
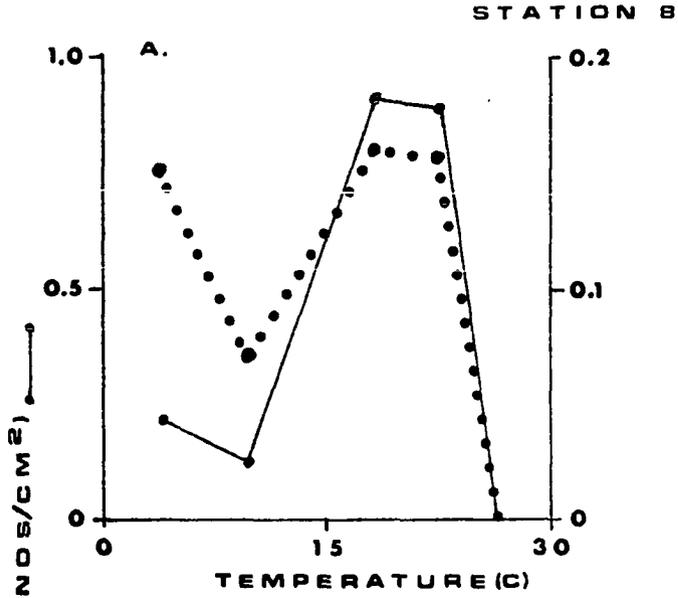


Figure 23. Seasonal changes in the trichopteran larval densities at Stations 1 and 8.

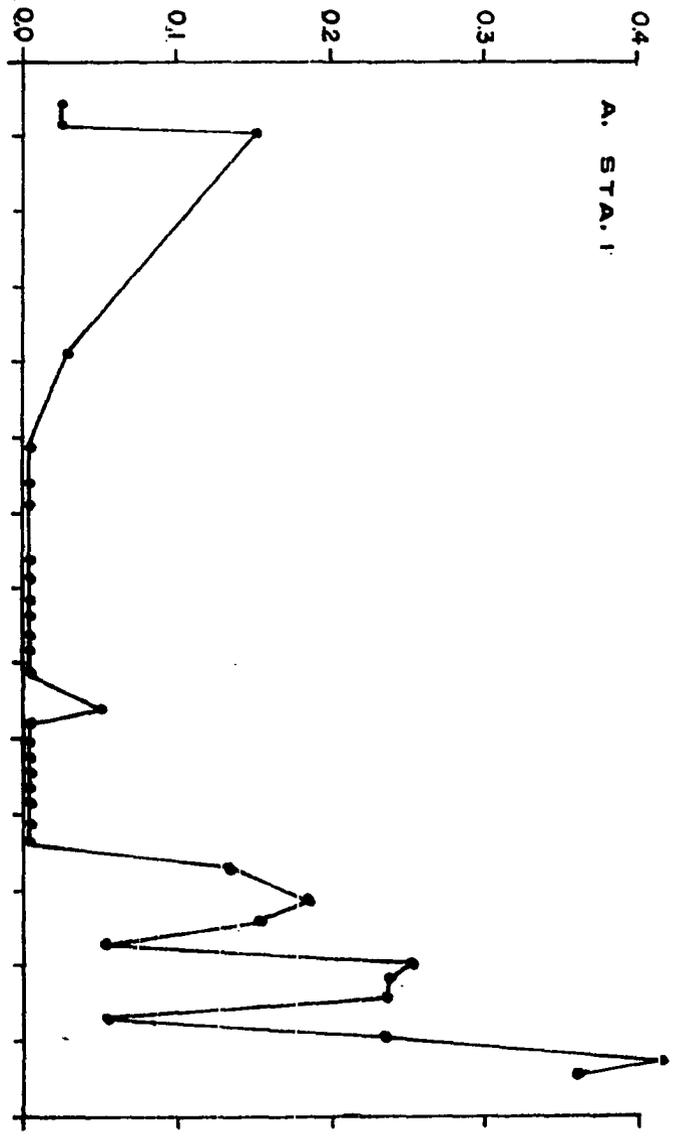
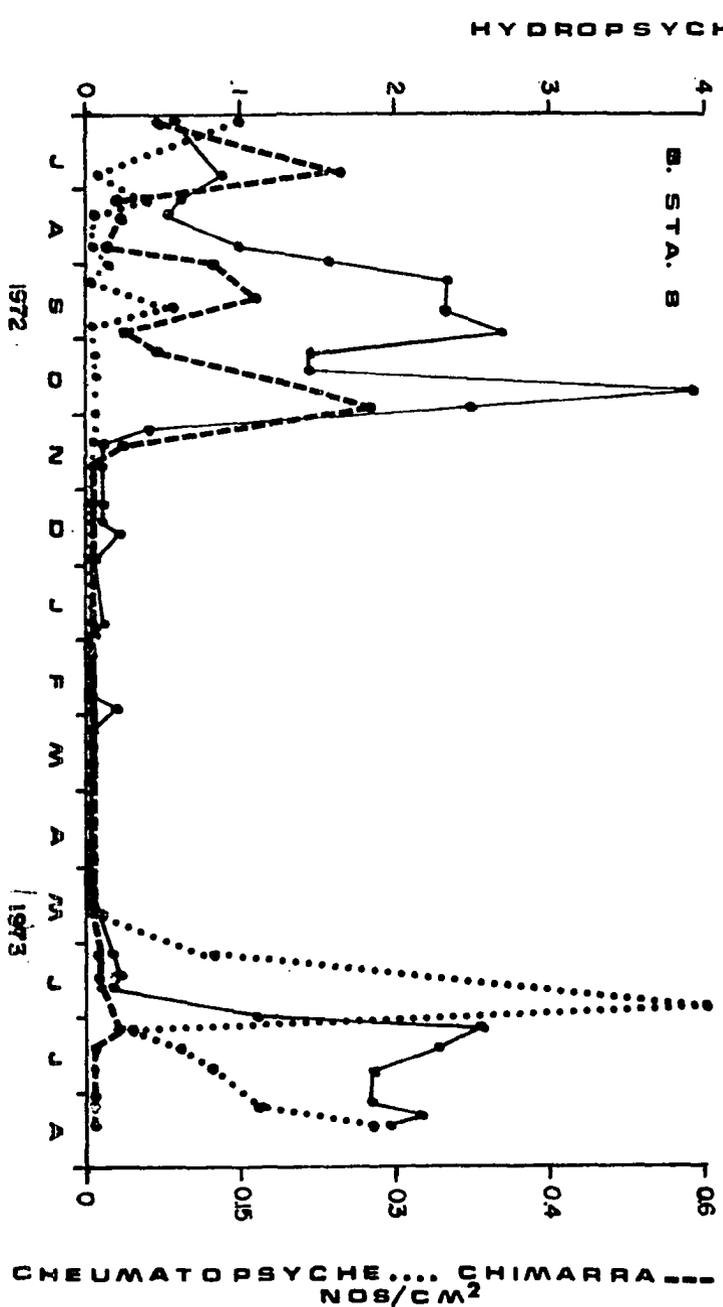


Figure 24. Seasonal fluctuations in the 24-hr drift rates of Simulium species A and virgatum immatures and adults.

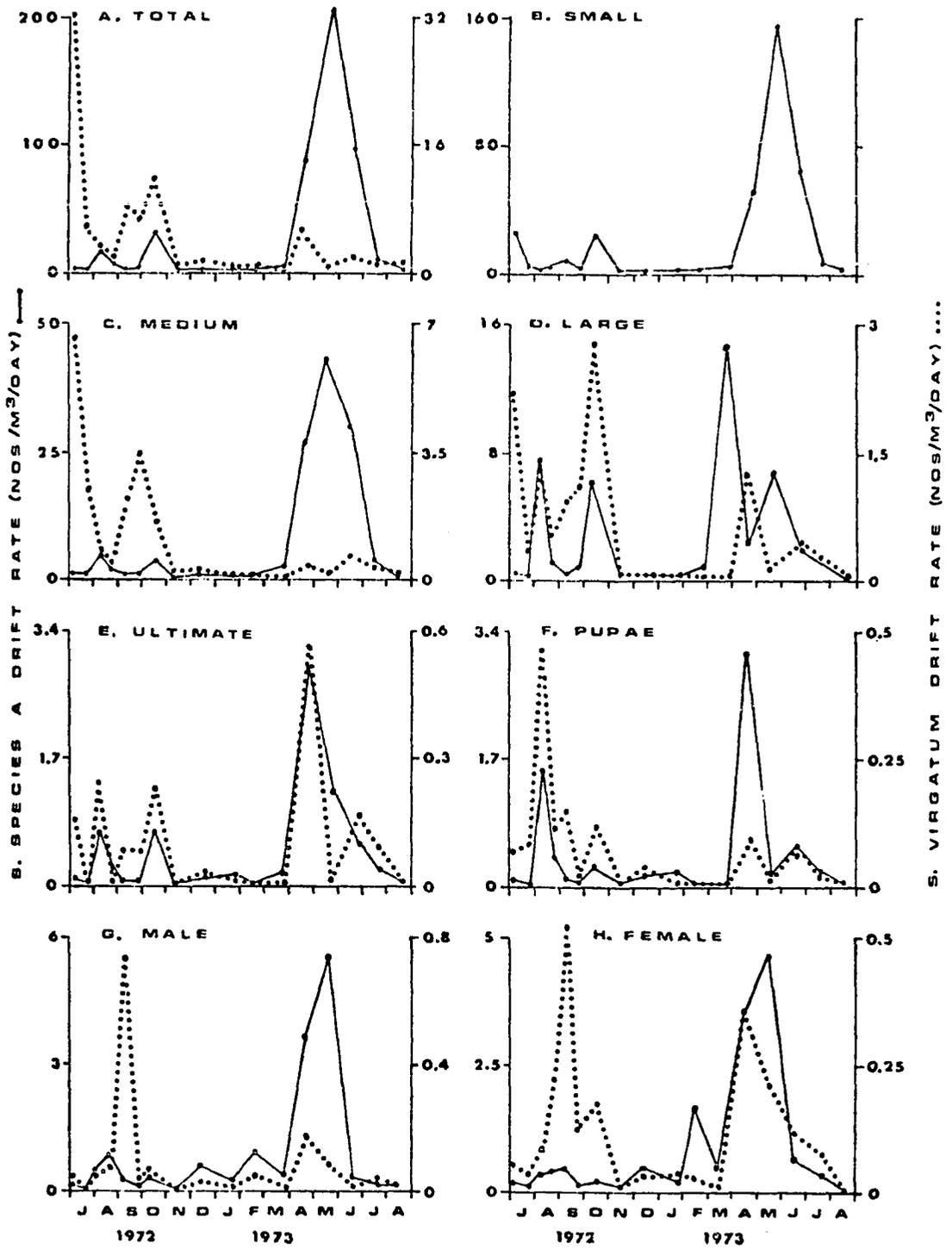


Figure 25. Seasonal fluctuations in the larval drift rates of Simulium trivittatum.

DRIFT RATE (NOS/M³/DAY)

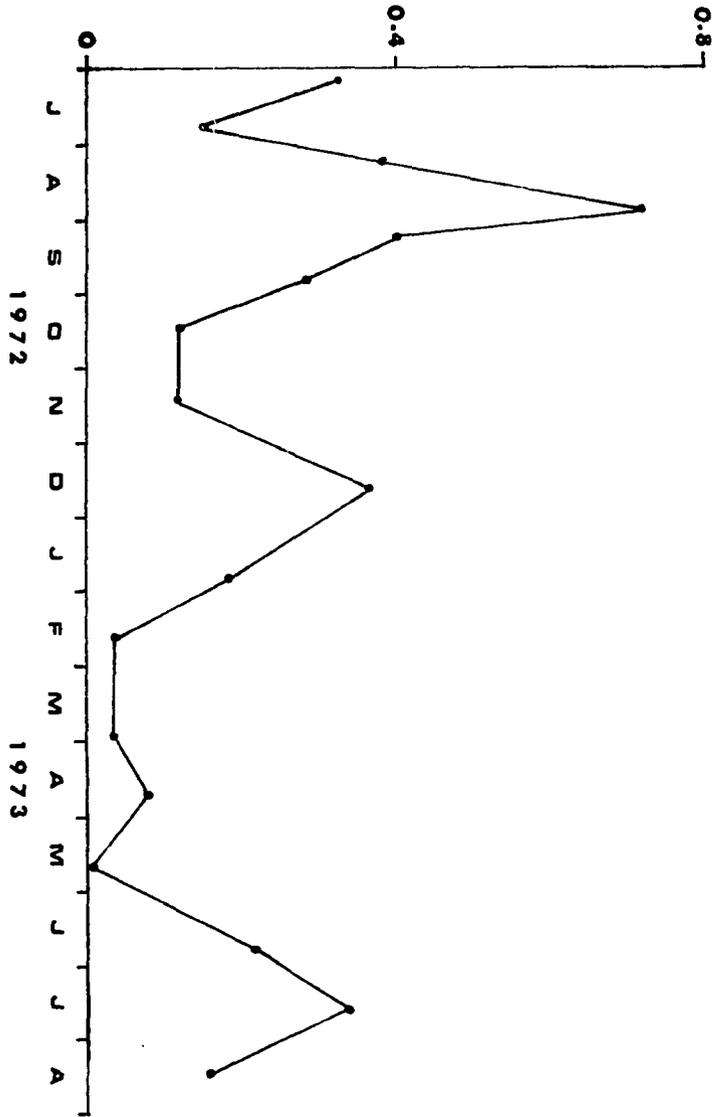


Figure 26. Depth and current velocity estimates at drift nets A and B for each 24-hr study. Net A (____); Net B (. . . .)

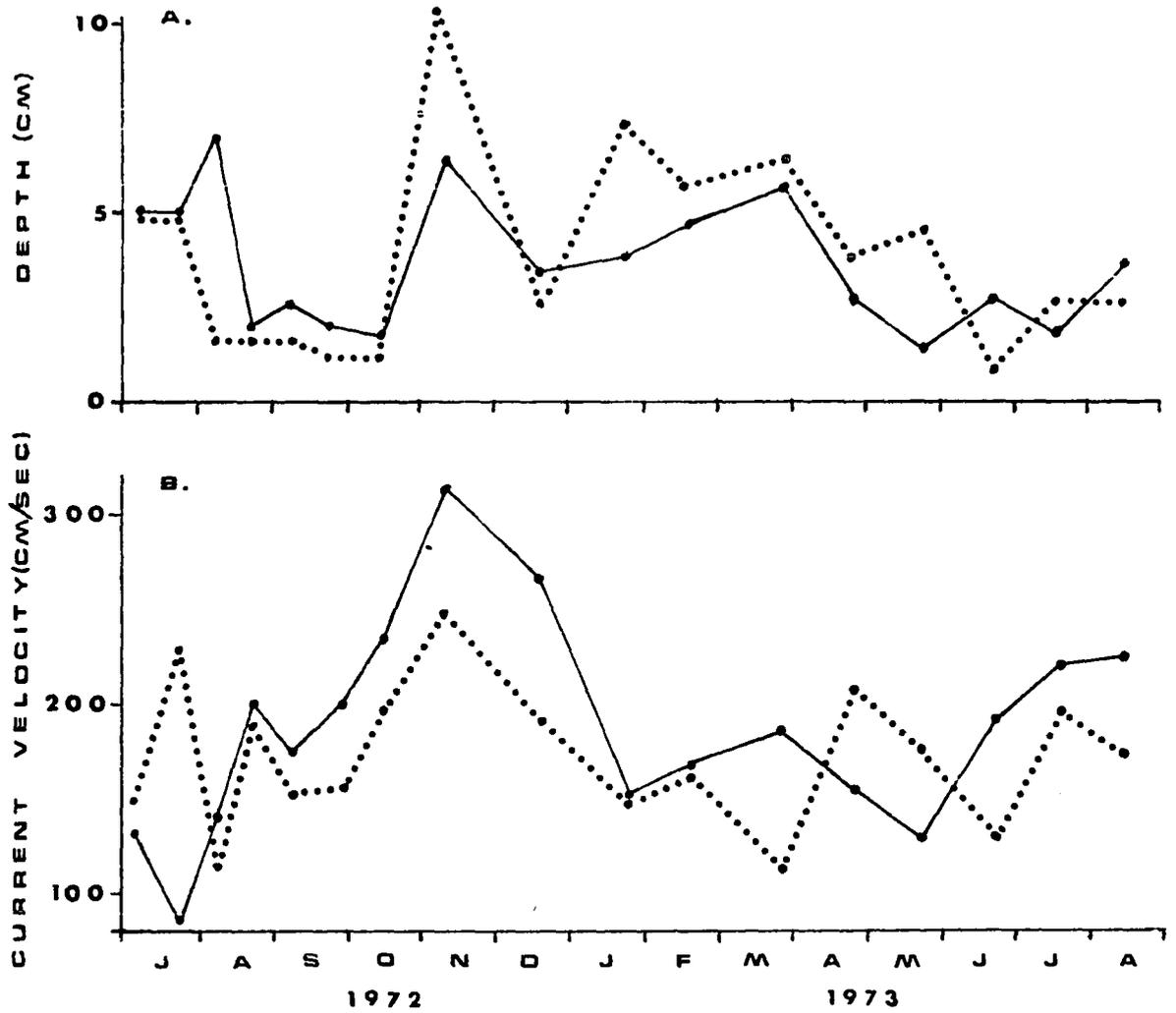
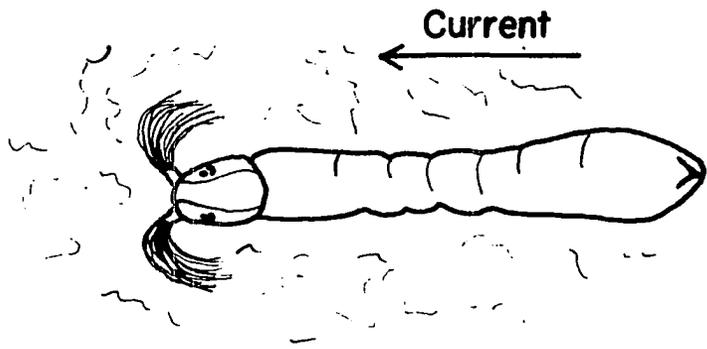
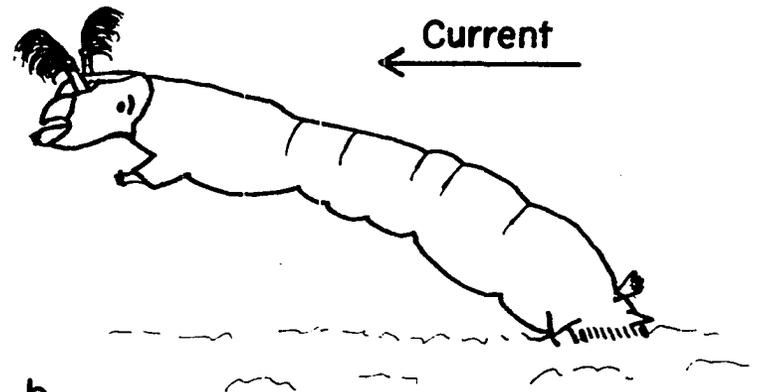


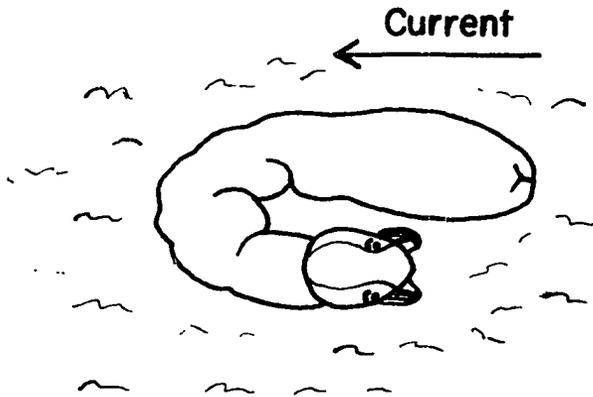
Figure 27. Substrate appression exhibited by Simulium species A and virgatum at Honey Creek. A. Normal feeding position, dorsal view; B. Normal feeding position, lateral view; C. Substrate appression, dorsal view; D. Substrate appression, lateral view. Drawings were sketched from actual photographs.



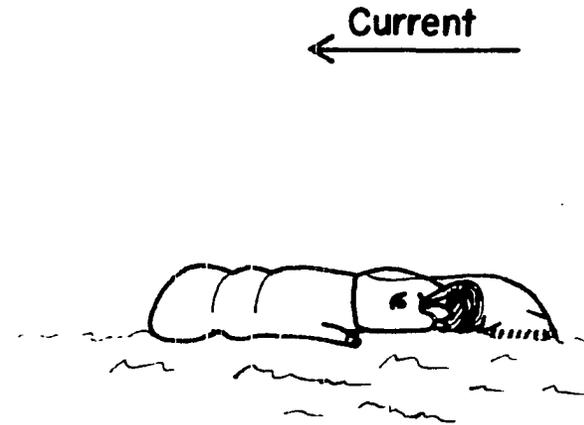
a.



b.



c.



d.

Figure 28. Significant polynomial regressions of larval drift rates on benthic density. Simulium species A (____); Simulium virgatum (. . . .)

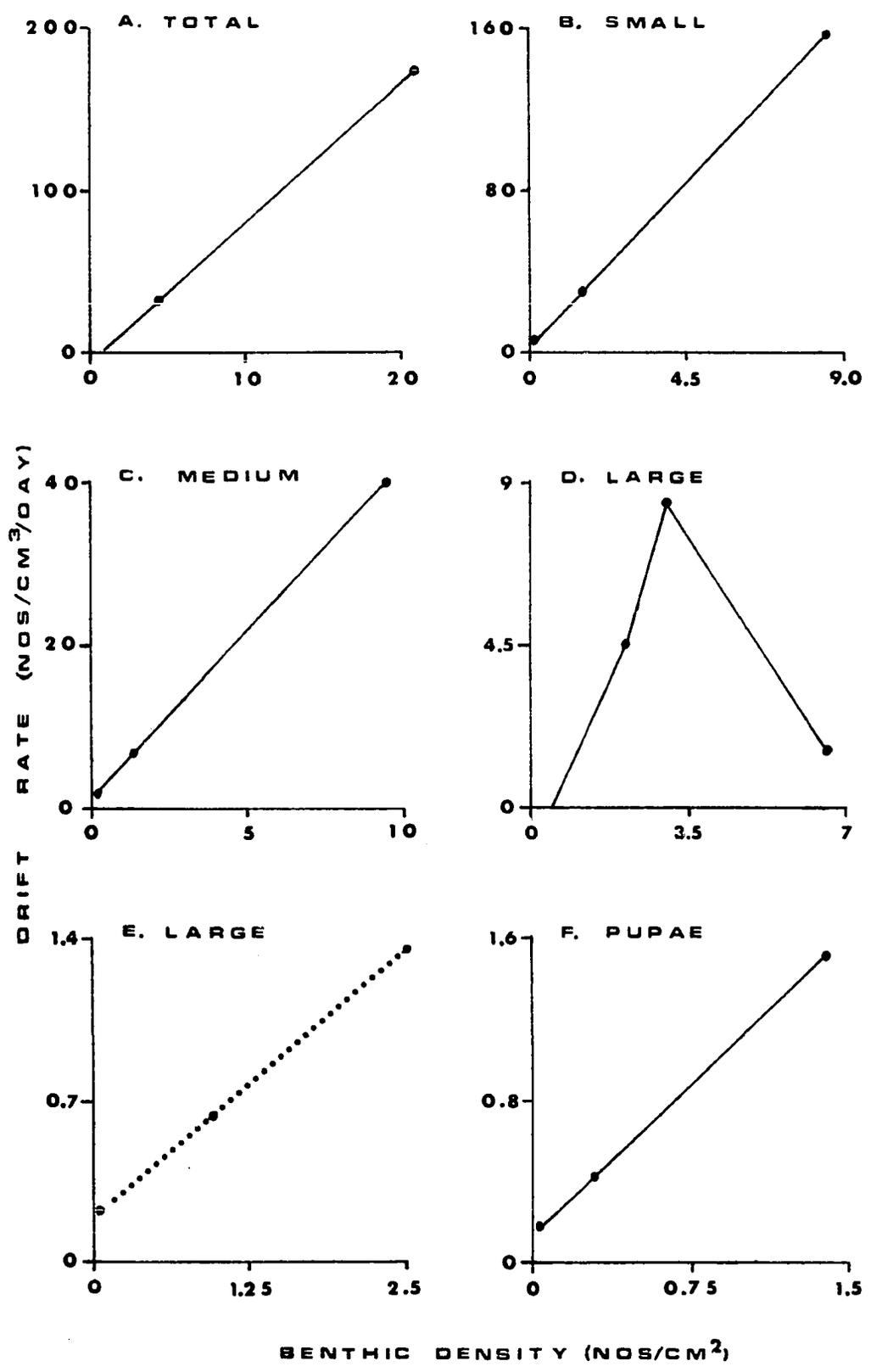
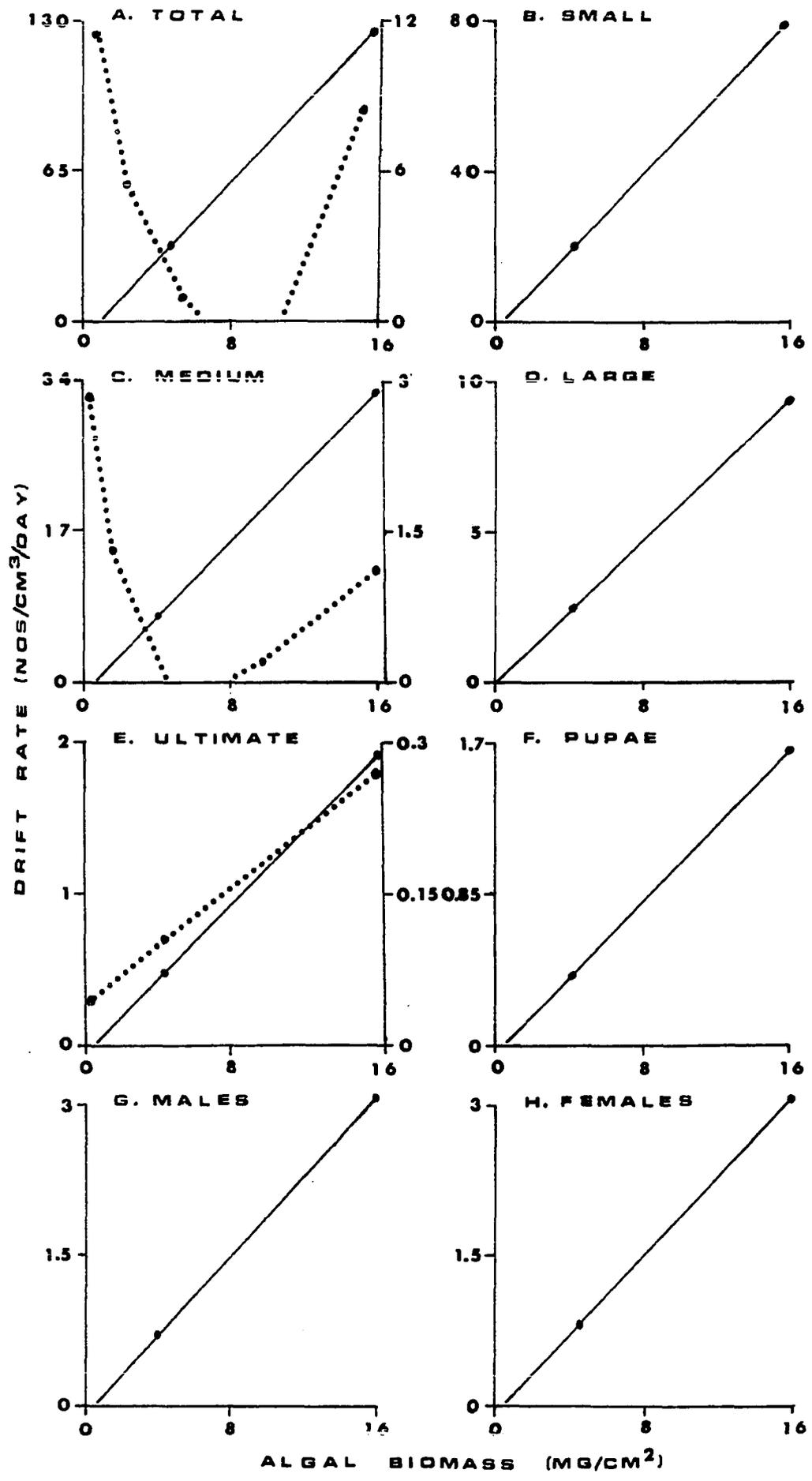


Figure 29. Significant regression of immature Simuliidae drift rates on algal biomass. Simulium species A (____); S. virgatum (. . . .).



ALGAL BIOMASS (MG/CM²)

Figure 30. Significant polynomial regression of Simulium drift rates on selected limnological parameters. Simulium species A (____); S. virgatum (. . . .).

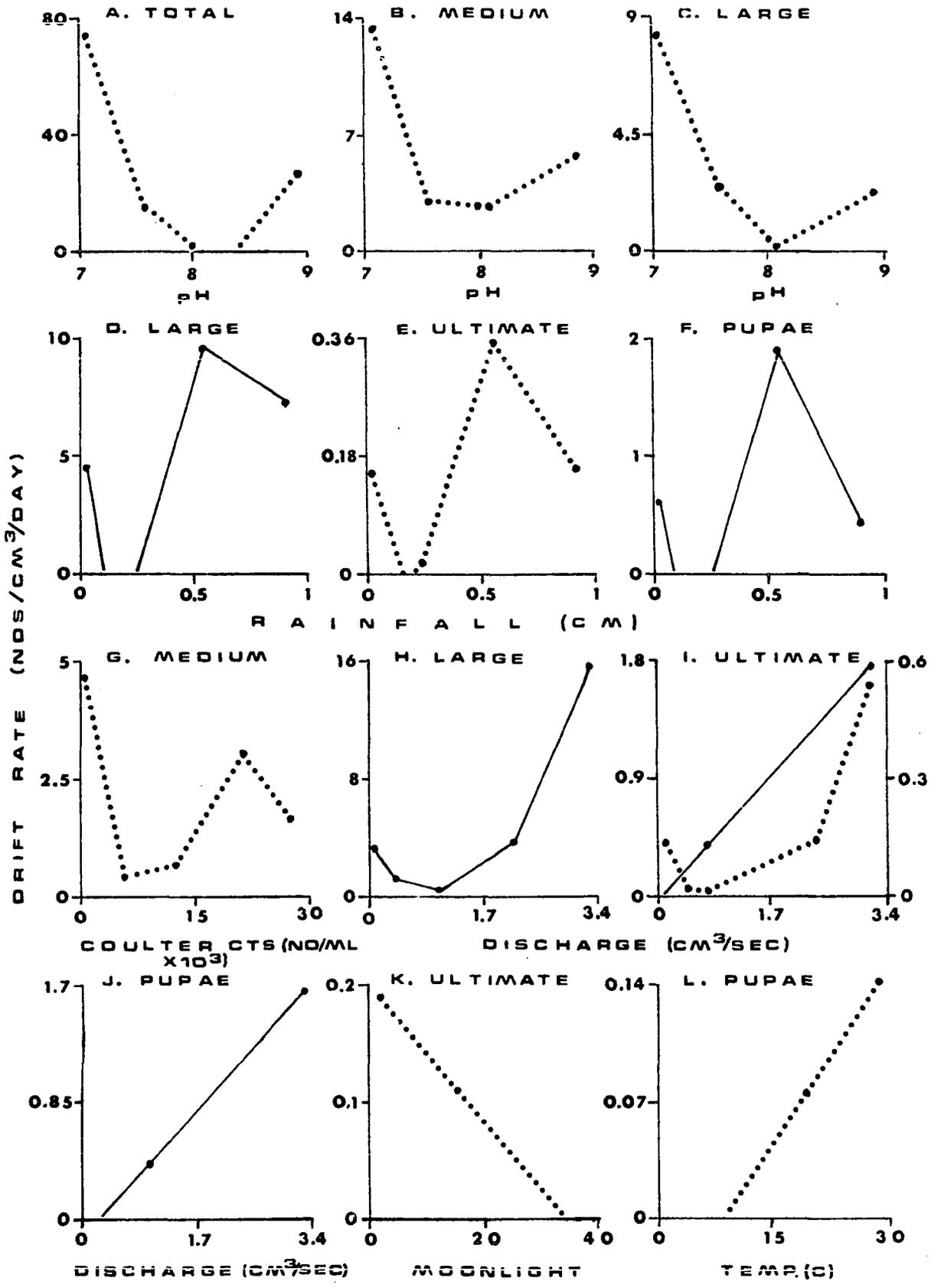


Figure 31. Significant polynomial regressions of Simulium drift rates on selected limnological parameters. Simulium species A (____); S. virgatum (. . . .).

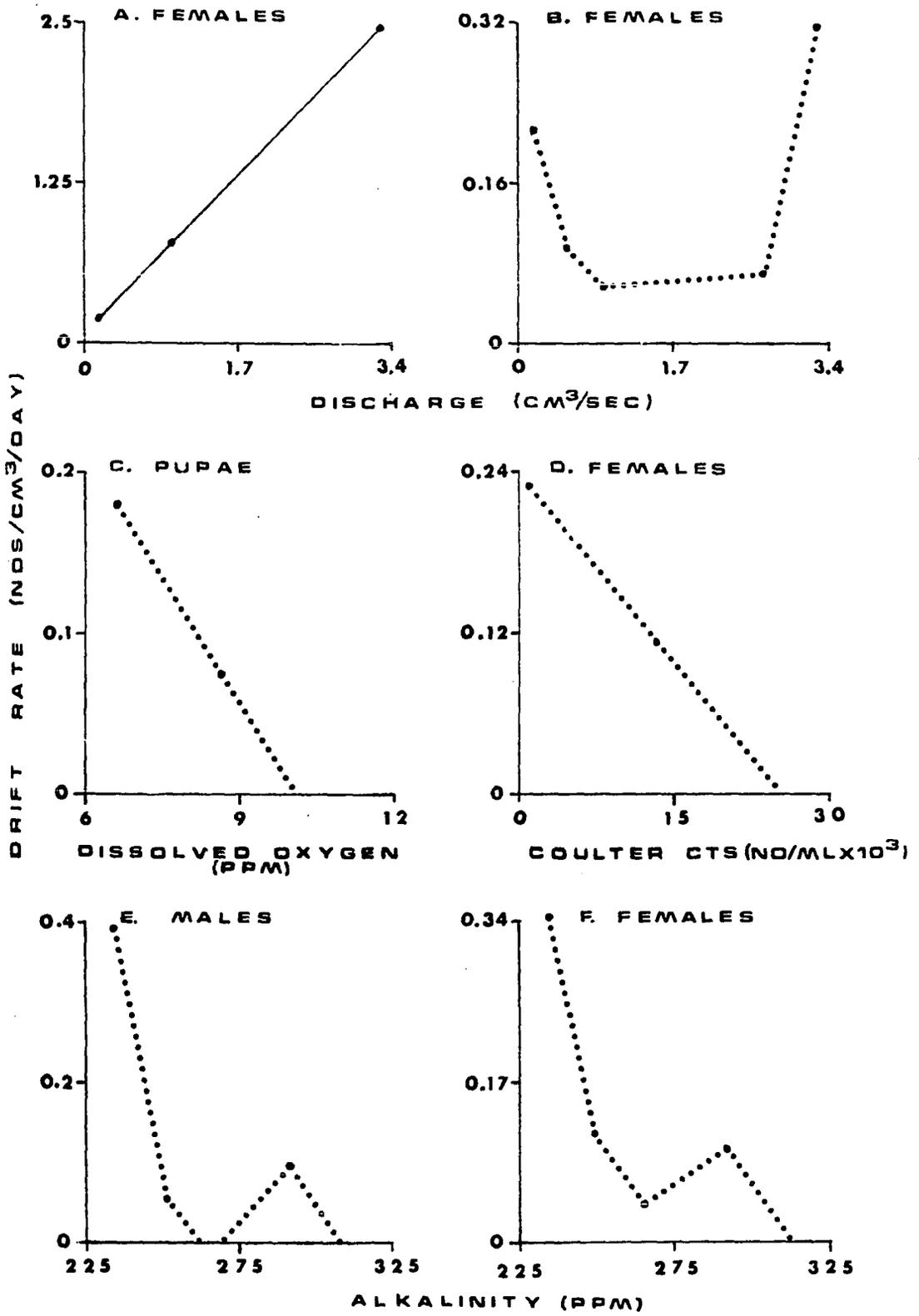


Figure 32. Significant polynomial regressions of Simulium trivittatum larval drift on dissolved oxygen and discharge.

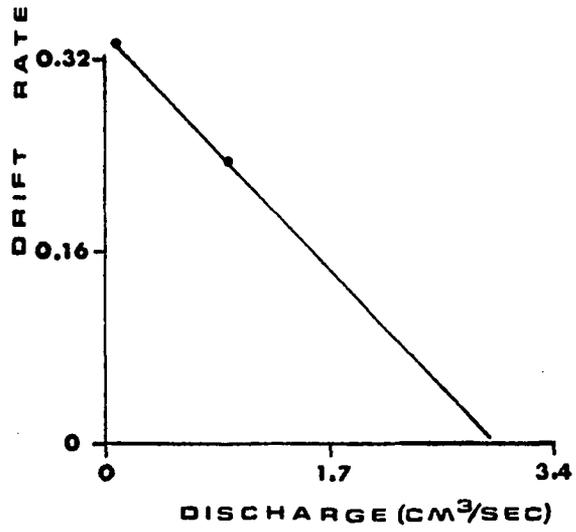
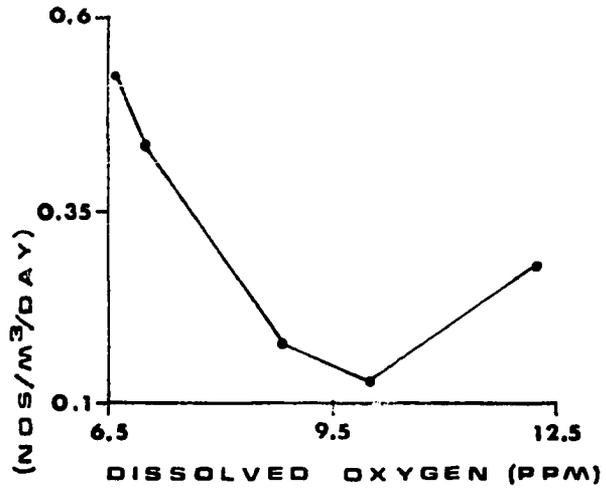


Figure 33. Diel drift patterns for Simulium species A larvae and adults. N = Number of 24-hr studies included.

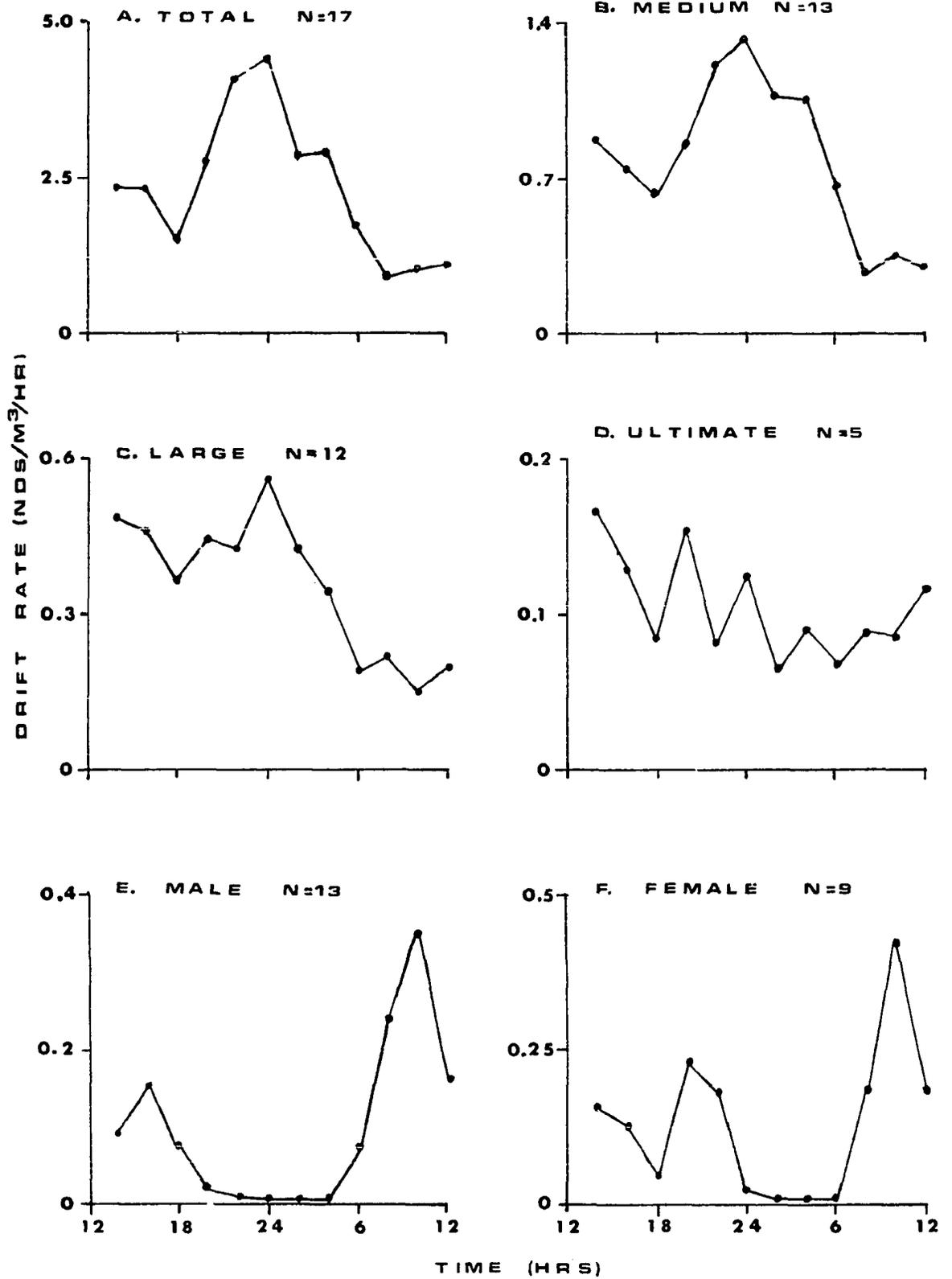


Figure 34. Diel drift patterns for Simulium virgatum larvae and adults and Simulium small larvae. N = Number of 24-hr studies included.

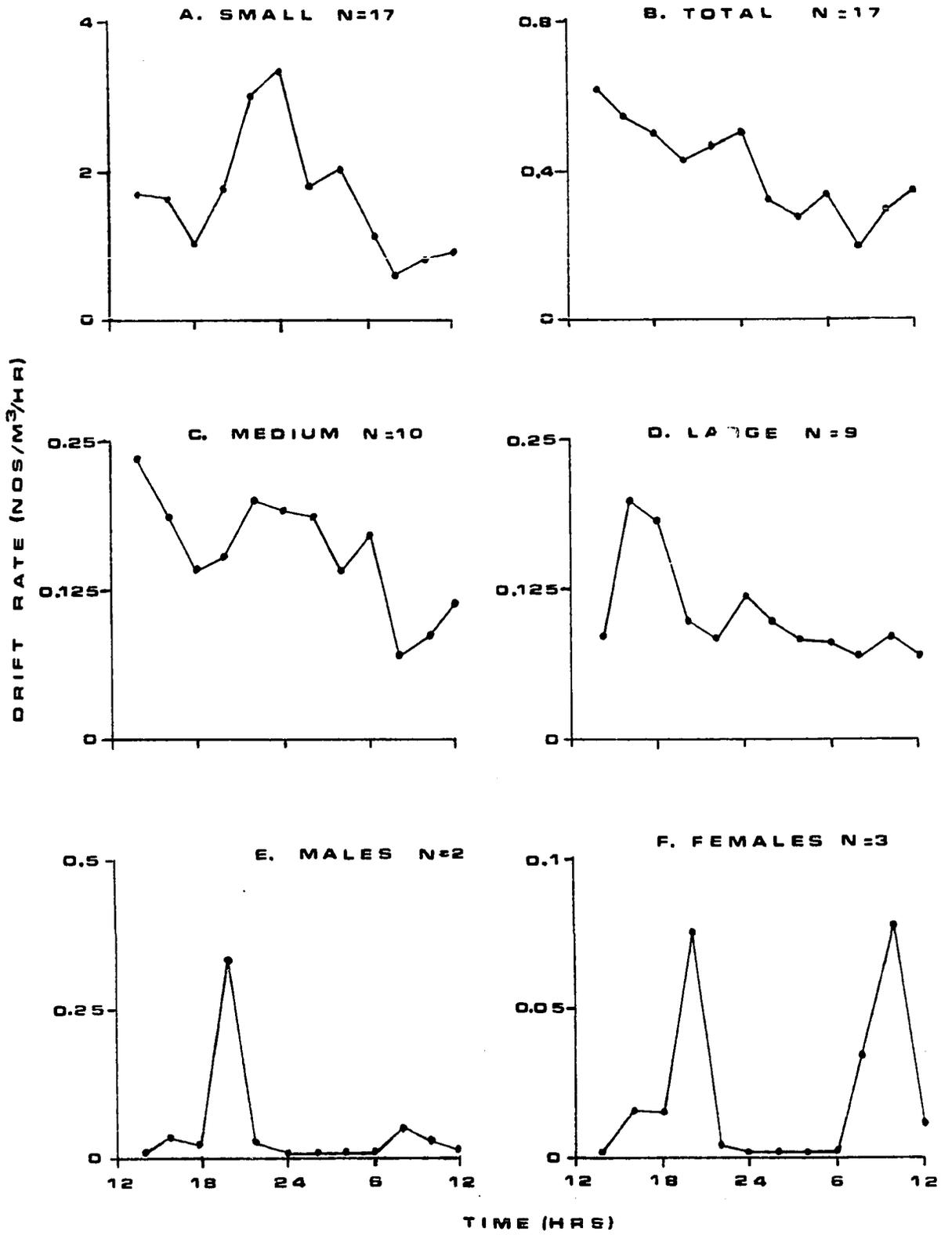


Figure 35. Diel drift patterns for Simulium trivittatum larvae

N = Number of 24-hr studies included.

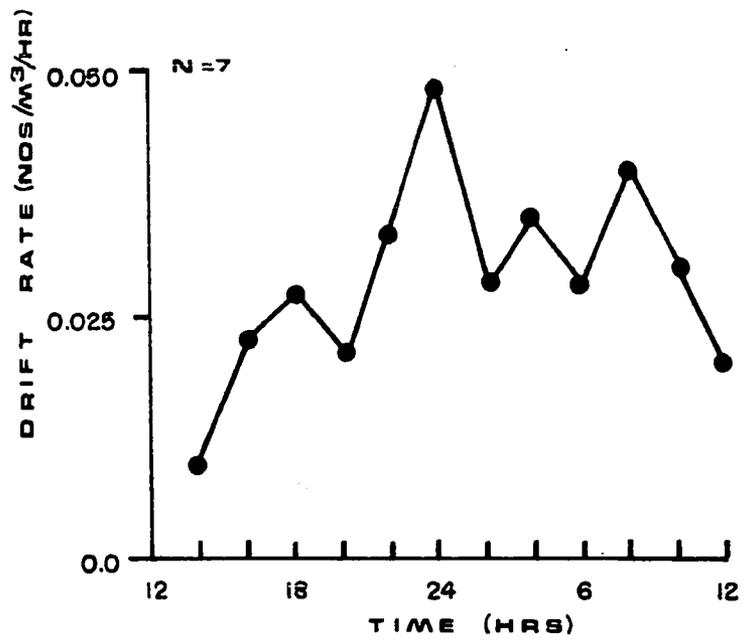


Figure 36. Diel patterns for the yearly means of the selected abiotic variables measured below Station 4. N = 17.

