EMERGENCE, GROWTH, DRIFT AND MICRODISTRIBUTION OF STONEFLIES (PLECOPTERA) IN AN OZARK FOOTHILLS STREAM, DELAWARE COUNTY, OKLAHOMA

THESIS

Presented to the Graduate Council of the
North Texas State University in Partial
Fulfillment of the Requirements

For the Degree of

MASTER OF SCIENCE

by

Mark R. Ernst, B.S.

Denton, Texas

May, 1985

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Adult stonefly emergence, nymphal growth, drift and microdistribution were examined in Battle Branch, a second-order, spring-fed stream, from November, 1982 to May, 1984. Adults of 22 species emerged successionally, with specific adults present every month. Searching emergent objects and the stream margin was best for collection of winter and early spring emerging species. Sweeping the streamside and light trapping were most efficient for late spring and summer emerging species. Nymphal growth for nine abundant species generally fit double log or semilog models. Drift was low, but did show a post-sunset pulse. Generally, leaf material was found to be significantly related ($p<0.001$) to density, diversity and biomass of stoneflies in Battle Branch.

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CHAPTER I

INTRODUCTION

Stoneflies have long been a focus of stream ecologists because of their importance as indicators of water quality, contributors to secondary production, processors of organic matter and demonstrators of ecological phenomena such as successional emergence, flexible life cycles, drift and microdistribution. Studies of adult stonefly emergence (Sheldon and Jewett 1969, Harper and Pilon 1970, Hartland-Rowe 1971, Harper 1973a, Harper 1973b, Narf and Hilsenhoff 1974, Kerst and Anderson 1975, Neves 1978, White et al. 1979), nymphal growth (Harper and Magnin 1969, Coleman and Hynes 1970, Harper 1973a, Harper 1973b, Brittain 1980, Feminella 1983, Jop and Szczytko 1984), drift (Elliot 1967a, Anderson and Lehmkuhl 1968, Walton et al. 1977, Walton 1980, Stewart and Szczytko 1983) and microdistribution (Minshall and Minshall 1977, Rabeni and Minshall 1977, Peckarsky 1984, Williams 1983, Minshall 1984) have generated much information on the ecology of stoneflies. However, there is little information on stoneflies for the Ozark area of central United States. Other than the distributional studies of Ross and Ricker (1971) and Stark and Stewart (1973) and the ecological studies of Feminella (1983) and Brown and Ricker (1982) there are no detailed studies on stoneflies for this region.

I conducted a nineteen month study on a diverse stonefly community in Battle Branch, a second order, Ozark foothill stream. Battle Branch is a typical spring-fed, unregulated Ozark stream with fast, gravel riffles and slow pool habitats, traversing a primarily wooded watershed. Specific objectives of this study were to

1. Elucidate emergence periods and patterns for the entire stonefly community;
2. Assess the effectiveness of five concurrently employed adult collecting methods: pit traps, sticky traps, sweeping, searching and light trapping;
3. Describe the relationships between numbers of adults collected by the methods and benthic nymphal densities;
4. Describe and model the growth and drift of the nine most abundant species;
5. Describe the relationships between nymphal density and biomass of eight species with organic matter;

CHAPTER II

EMERGENCE AND COLLECTING METHODS

Introduction

Successional stonefly emergence in North America has been reported from some streams of the eastern United States (Neves 1978, White et al. 1979), upper midwest (Narf and Hilsenhoff 1974), western United States (Sheldon and Jewett 1969, Kerst and Anderson 1975) and Canada (Harper and Pilon 1970, Radford and Hartland-Rowe 1971, Harper 1973a, 1973b, Harper and Hynes 1972). Similar studies have not been conducted on any Ozark stream, although some general knowledge of stonefly emergence in the region has come from ecological and distributional studies (Ross and Ricker 1971, Stark and Stewart 1973, Feminella 1983).

Most assessments of stonefly emergence have been based on limited collecting methods such as sweeping (Radford and Hartland-Rowe 1971), sweeping and handpicking (Sheldon and Jewett 1967), handpicking and intensive rearing (Narf and Hilsenhoff 1974), tent traps (White et al. 1979), emergence traps (Kerst and Anderson 1974, Harper and Pilon 1970), sticky traps (Harris and McCafferty 1977), sticky traps and emergence traps (Harper 1973a), or pitfalls (Muller 1973, Stanford 1975). Neves (1978) used various combinations of handpicking, sweeping, blacklighting and adhesive traps to monitor emergence, and briefly discussed these effectiveness of the methods for different families.

This study elucidates emergence patterns for the diverse stonefly community of a second-order Ozark stream, and assesses the applicability of five concurrently employed collecting methods: pit traps, sticky traps, sweeping, searching and light trapping. Harper and Pilon (1970) suggested emergence traps yield the only reliable results of stonefly emergence periods. Other methods are primarily indicative of species presence. The relationship of emergence to presence is complicated by variable specific adult life-spans. Since emergence traps were not used in this study due to two week sampling periodicity and probable disturbance, my data suggests stonefly presence more than emergence. Understanding this limitation, I use the term "emergence" to be consistent with previous stonefly literature using various adult collecting methods.

Study Site

Battle Branch is a 3.9 Km, spring-fed, 2nd-order stream of the Illinois River drainage in Delaware County (36° 12' N 94° 41' W), northeastern Oklahoma. The study site was established along 300 m of the stream, approximately 730 m above its confluence with Flint Creek. The stretch included seven riffles and seven pools, with riffle substratum composed of gravel, pebbles and a scattering of cobbles (after Cummins 1962), and pool substratum of fine gravel with several sections of exposed bedrock. Riparian vegetation was predominantly sycamore (*Platanus occidentales*), oak (*Quercus* sp.), and maple (*Acer* sp.). Emergent beds of watercress (*Nasturtium* sp.) were abundant along stream margins and jewelweed (*Impatiens* sp.) became dense along the gravel banks during spring and early summer. A few scattered clumps of emergent waterwillow (*Dianthera americana*) were present in the lower section of the study area.

Materials and Methods

Sampling for adults began Nov. 1982, and continued for one year, through Nov. 1983. Two and a half days were spent on the site twice monthly during this period, except Oct. when one midmonth visit was made. Additional collections of adults were obtained by searching the stream margin during Sep., 1982, and monthly from Dec., 1983 to May, 1984, to supplement the species list and corroborate some emergence periods. Ten Surber samples (0.1 m^2, mesh= 150 um) were taken monthly to compare benthic collections with adult collections. The five adult collecting methods and timing of their application during site visits were as follows:

Pit traps. Twelve pit traps consisting of 857 ml tin cans (10 cm dia.) were embedded flush within the rocky substratum, no more than 0.5 m from the margin of 4 riffle areas. They were half filled with 50% isopropanol and capped with a thin layer of diesel fuel to retard isopropanol evaporation. A flat rock was placed in a raised position over each, to simulate a minuscule cave and protect the trap from rain and leaves (after Stanford 1975). Traps remained in place the entire year. Stoneflies falling into the traps were removed with an aquarium net the first and third day of each collecting period.

Sticky traps. Four 4.0 x 59.0 cm, painted flat black strips of wood were secured horizontally by two metal stakes and stones, parallel to the pit trapped riffles. Tangle Trap (The Tanglefoot Company, Grand Rapids, MI) was spread on their entire underside.

Stoneflies adhereing to the board were gently scraped free with a small, flat, stick and submerged for ca. 15 minutes in a vial of Turpentine to dissolve residual adhesive. The surface area of the sticky traps equaled that of the pit traps. The traps were inspected the first and third day of each sampling period.

Light trapping. A Bioquip Universal Light Trap with an 8 watt fluorescent blacklight was run for one hr, beginning 0.5 hr before dark, on the first and second night of each sampling period. The location was randomly alternated between an upstream and a downstream riffle within the sampling site during the successive nights. Riffles with pit traps or sticky traps were avoided to prevent biased concentrations of adults in these areas. Since many stoneflies did not fly directly into the light trap I constantly collected the adjacent, lighted area with an aspirator.

Searching. The entire study section was searched for a 2 hr period on the first and third days of each sampling period. Searching entailed careful scrutiny of emergent logs, leaf packs and vegetation, debris accumulations, streamside and emergent rocks, tree trunks and a bridge foundation in a zone up to 10 m wide on each side of the stream. Adults and exuvia were collected with an aspirator and forceps.

Sweeping. One hr was spent sweeping emergent watercress or waterwillow and streamside jewelweed or trees up to 20 m from the stream margin. The sweep net was also used to rap trees and limbs as high as 3 m, to dislodge adults. Sweeping was conducted on the first and third days of each sampling period. Searching and sweeping were conducted during the afternoon (1200 to 1500 hr) in winter and fall, and morning (700 to 1000 hr) in spring and summer to coincide with observed periods of adult stonefly presence. Additional adults were collected by periodic searching in areas adjacent to the 300 m study area and used to substantiate emergence periods: they were not used in the comparison of methods, assessment of emergence patterns, or evaluation of sex ratios.

The five adult collecting methods were compared for individual species, total species and for the relationship with ranked benthic densities. Comparisons are based on total numbers or percentages captured by each method (Fig. 3). The inherent disparity of the methods made it unfeasible to attempt to reduce them to a comparable unit of effort (e.g. time or area) for statistical analysis. Comparisons of percentages can be misleading when sample sizes are small and probably do not reflect effectiveness of individual methods. However, given the regimented methods and sample size collected, percentages do suggest methods which sould be employed in future studies. The relationship between adults collected and the benthic densities involved Spearman Rank correlation (r_s) of the average monthly benthic density of each species and the respective number of adults collected by each method. Nymphs of two species of *Zealeuctra* and four species of *Neoperla* could not be identified below the generic level, so adults were similarly grouped by genus. *Perlinella* adults were also treated at the generic level, since nymphs of the two species were not found in benthic samples. The benthic density of *Perlinella* was set at zero for ranking and subsequent analysis, although nymphs were present in the benthos since a *P. drymo* exuvium was found.

Emergence patterns for species providing sufficient sample sizes were tested for skewness using the g statistic (Zar 1974) via a computerized Statistic Analysis System (SAS 1982). Only those individuals collected by the regimented 5 collecting methods from Nov., 1982, to Nov., 1983, were used.

Sex ratios were tested for evenness by chi-square with the application of Yates correction for continuity (Zar 1974). Observed numbers of males and females were those collected by the 5 methods, expected numbers were the mean of the sexes combined.

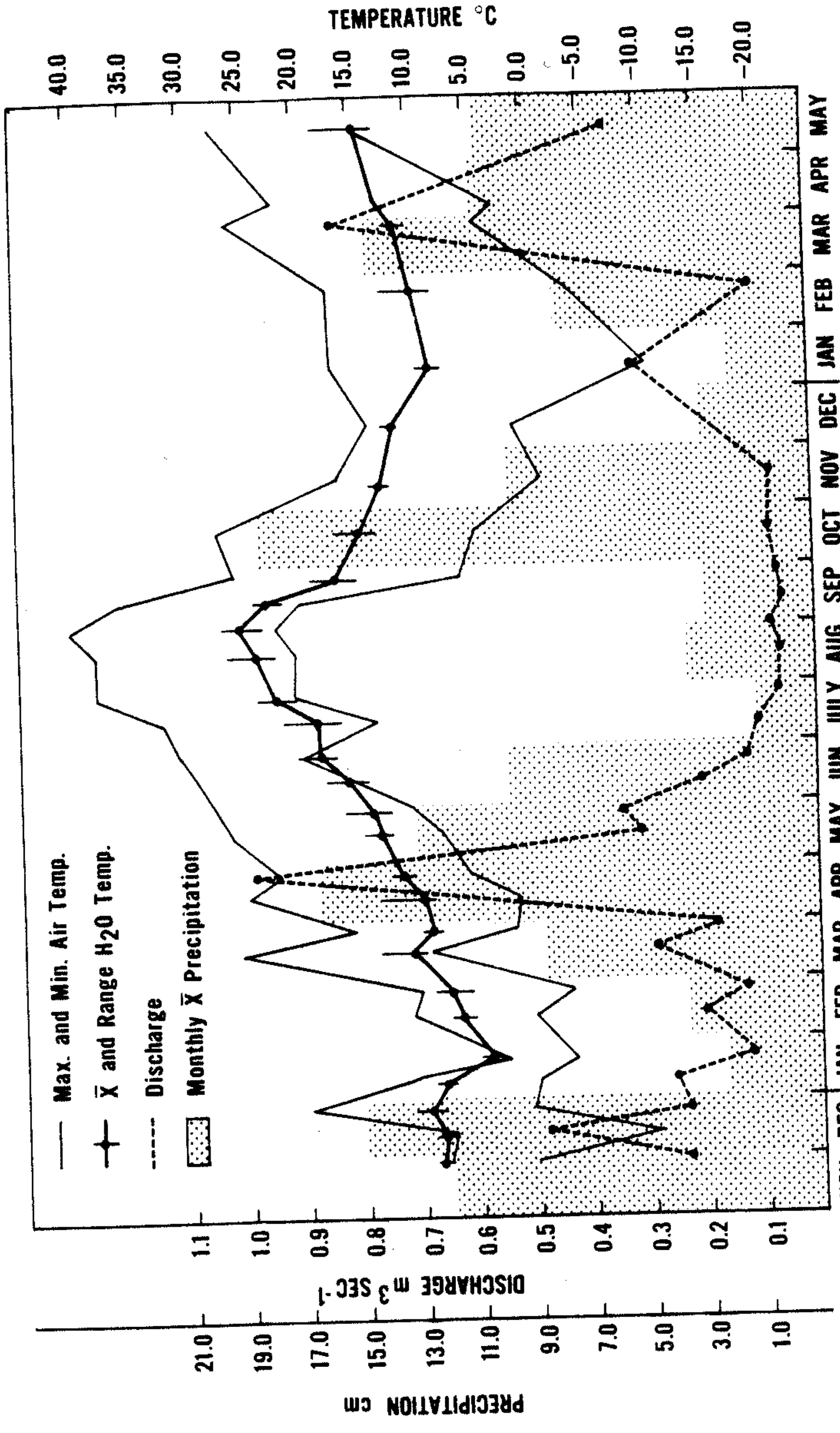
The following physiochemical data were collected each sampling period: 1) Total alkalinity, hardness and pH with a Hach Kit, 2) dissolved oxygen with a Model 54 YSI Oxygen Meter, 3) water temperature in the morning, afternoon and evening with a total immersion°C thermometer and 4) current velocity (for discharge) with a Kahl Pigmy Flow Meter. Maximum-minimum air temperatures and total monthly precipitation were obtained from the Kansas (town), Oklahoma weather station ca. 10 km from the study site.

Results and Discussion

During the study period, air and water temperature ranged from -11 to 40°C and 3.9 to 27.0°C, respectively, and mean discharge was 0.26 m^3 sec with maxima occurring in spring and fall (Fig. 1). Percent O_2 saturation ranged from 87% in spring to 108% in winter, averaging 95%. Ranges and means for chemical parameters were: pH, 7.1 to 7.9 ($\overline{X}$= 7.3); hardness, 77 to 137 mg/l $CaCO_3$ ($\overline{X}$= 110); and alkalinity, 34 to 96 mg/l $CaCO_3$ ($\overline{X}$= 69).

A total of 7219 adult stoneflies, representing 6 families and 22 species were collected during the study. One species, <u>Helopicus</u> <u>nalatus</u> (Frison), was

Fig. 1. Battle Branch water temperature, discharge, area air temperature and precipitation; Nov. 1982 to May 1984, Delaware County, Oklahoma.

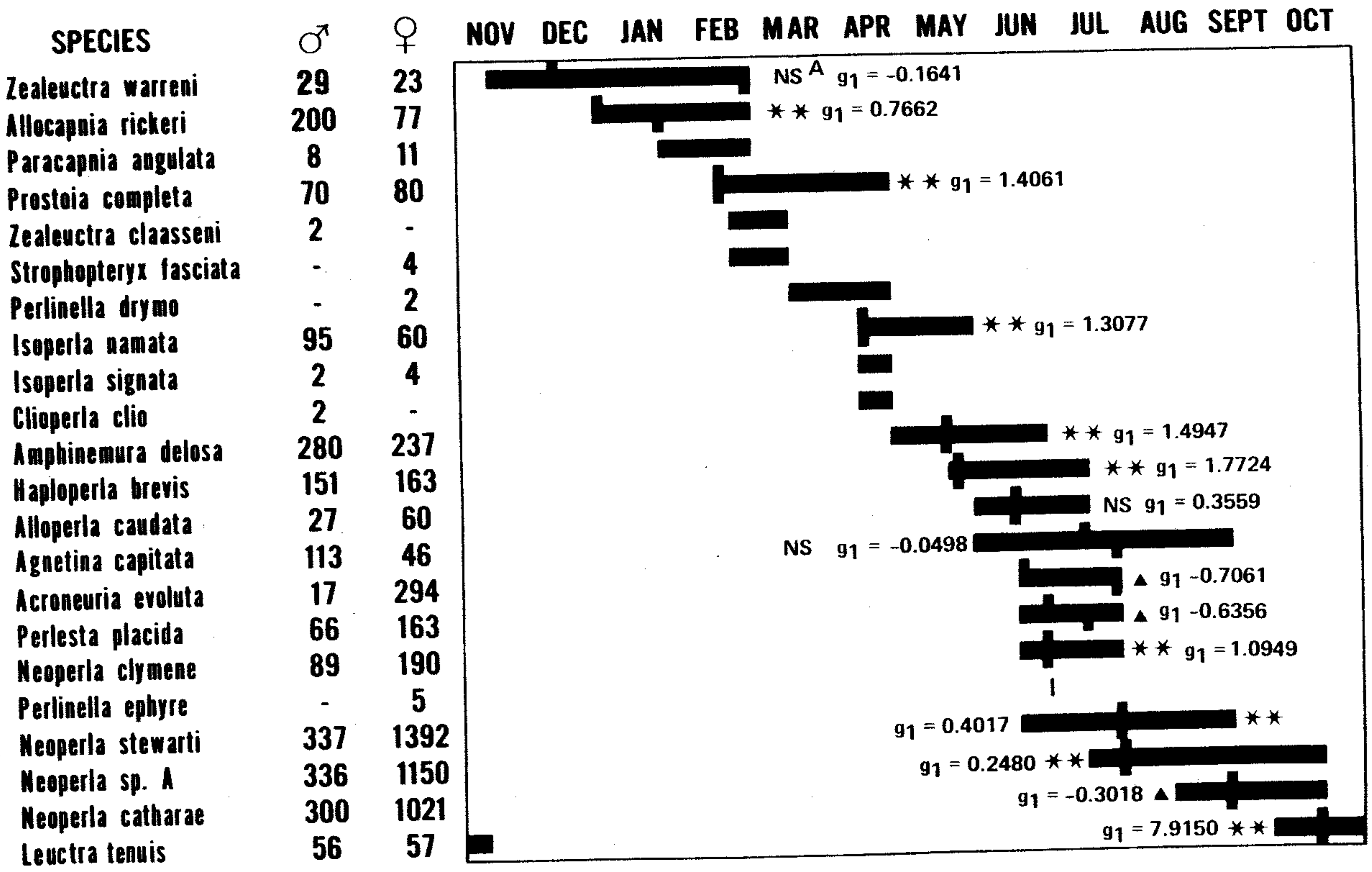

Max. and Min. Air Temp.
X̄ and Range H2O Temp.
Discharge
Monthly X̄ Precipitation
TEMPERATURE °C
40.0
35.0
30.0
25.0
20.0
15.0
10.0
5.0
0.0
-5.0
-10.0
-15.0
-20.0
DISCHARGE m3 SEC-1
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
PRECIPITATION cm
21.0
19.0
17.0
15.0
13.0
11.0
9.0
7.0
5.0
3.0
1.0
NOV
DEC
1982
JAN
FEB
MAR
APR
MAY
JUN
JULY
AUG
SEP
OCT
NOV
DEC
1983
JAN
FEB
MAR
APR
MAY
1984

found in low benthic abundance and never collected as adults.

Neves (1978) suggested there was a general trend in North America for maximum stonefly diversity to occur in north temperate streams, with fewer species occurring at more extreme northern or southern latitudes. Based on extensive collecting in the region (Poulton and Stewart, unpublished) I consider the 23 species found in Battle Branch (Fig. 2 or 3 plus H. nalatus) to represent a high diversity for an Ozark stream. This diversity is less than that reported for several north temperate streams: L'Achigan River, Quebec (34 spp., 46° 36' N, Harper 1976), Pine-Popple River, Wisconsin (34 spp., 45° 50' N, Hilsenhoff et al. 1972), Factory Brook,Massachusetts (45 spp., 42° 20' N, Neves 1978). These studies tend to generally support Neves' hypothesis, however, this is an over simplification since altitude, stream size, pollution, perturbation, hydrology and the energy base greatly influence stonefly diversity at particular latitudes (e.g. 16 spp., Otter Creek, ca. 43° N, Narf and Hilsenhoff 1974).

Battle Branch stoneflies displayed a temporal emergence succession covering the whole year (Fig. 2). Since emergence periods generally vary little within a region despite yearly climatic variability these

Fig. 2. Plecoptera emergence periods and patterns, all methods combined; Nov. 1982 to May 1984, Battle Branch, Delaware County, Oklahoma. Horizontal bar = emergence period; upper vertical bar = peak male emergence; lower vertical bar = peak female emergence; g_1 = measure of emergence pattern; NS = not significantly skewed ($p>0.01$); ** = positively skewed ($p<0.01$); ▲ = negatively skewed ($p<0.01$); A = females only, sexes combined for all others.


SPECIES
♂
♀
NOV DEC JAN FEB MAR APR MAY JUN JUL AUG SEPT OCT
Zealeuctra warreni 29 23 NS A $g_1 = -0.1641$
Allocapnia rickeri 200 77 ✶✶ $g_1 = 0.7662$
Paracapnia angulata 8 11
Prostoia completa 70 80 ✶✶ $g_1 = 1.4061$
Zealeuctra claasseni 2 -
Strophopteryx fasciata - 4
Perlinella drymo - 2
Isoperla namata 95 60 ✶✶ $g_1 = 1.3077$
Isoperla signata 2 4
Clioperla clio 2 -
Amphinemura delosa 280 237 ✶✶ $g_1 = 1.4947$
Haploperla brevis 151 163 ✶✶ $g_1 = 1.7724$
Alloperla caudata 27 60 NS $g_1 = 0.3559$
Agnetina capitata 113 46 NS $g_1 = -0.0498$
Acroneuria evoluta 17 294 ▲ g_1 -0.7061
Perlesta placida 66 163 ▲ g_1 -0.6356
Neoperla clymene 89 190 ✶✶ $g_1 = 1.0949$
Perlinella ephyre - 5
Neoperla stewarti 337 1392 $g_1 = 0.4017$ ✶✶
Neoperla sp. A 336 1150 $g_1 = 0.2480$ ✶✶
Neoperla catharae 300 1021 $g_1 = -0.3018$ ▲
Leuctra tenuis 56 57 $g_1 = 7.9150$ ✶✶

periods should be representative, within about a two week period for this area (Harper and Pilon 1970, Kerst and Anderson 1974). Emergence periods for winter and spring species in Battle Branch began a month to two weeks earlier than for more northern latitudes, while late spring and summer species had emergence periods that began at similar times. Conversely, the autumnal species, *Leuctra tenuis* emerged up to four months later than reported for more northern latitudes.

The succession of emergence periods for congeneric species has been attributed largely to evolutionary divergence of life histories, which minimizes interspecific competition and provides genetic isolation (Illies 1952, Harper and Pilon 1970). In this study, the temporally staggered emergence periods of *Zealeuctra warreni* and *Z. claasseni*, and *Perlinella drymo* and *P. ephyre* suggest segregation (Fig. 2). *Isoperla* and *Neoperla* emergence periods strongly overlap. Two species of *Isoperla* in Quebec were found to have identical emergence periods (Harper and Pilon 1970), and Kerst and Anderson (1974) found temporal separation of emergence within the suborder Holognatha, but not in Systellognatha, in an Oregon stream.

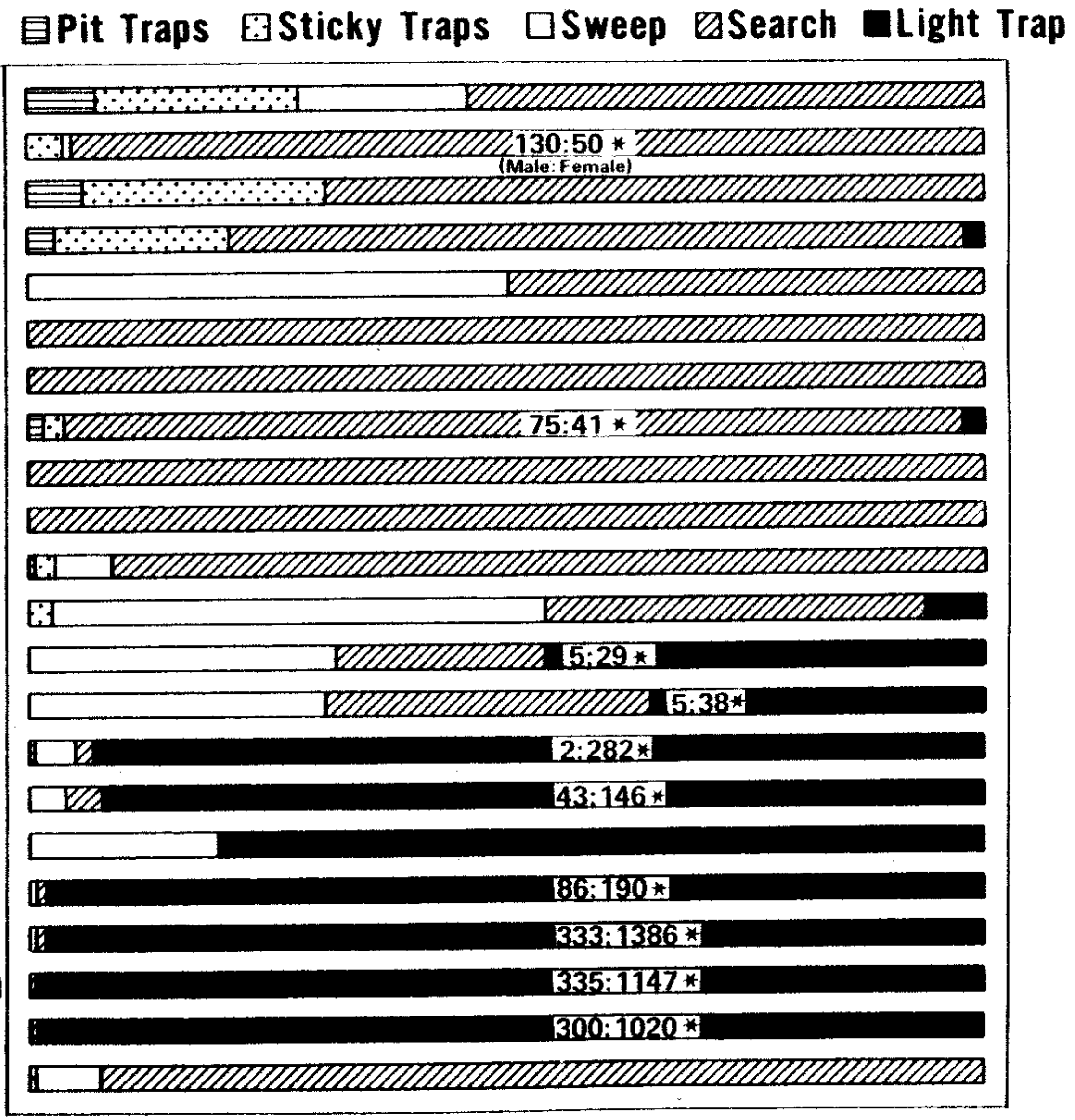
Harper and Pilon (1970) distinguished between synchronous and extended emergence patterns, based on the intensity of emergence during the emergence period.

In the synchronous pattern, emergence is concentrated at the beginning of the emergence period, indicative of a positively skewed distribution. In the extended pattern, emergence increases gradually to a median maximum and then slowly recedes, resembling a symmetrical or normal distribution. Emergence patterns for most species in Battle Branch generally resemble those reported for other streams, but one additional pattern is apparent; collections of *Acroneuria evoluta* and *Perlesta placida* were negatively skewed ($p<0.01$, Fig.2). Since these species were readily attracted to the light trap (Fig. 3) and collections contained significantly more females than males ($p<0.05$, Fig. 3) I believe the negative skewness reflects oviposition flights of females after a period of maturation in the riparian canopy. Differences due to sex in emergence patterns are discussed under each species.

Searching emergent leaf packs, logs, rocks and the stream margin resulted in collection of 21 of the 23 species (91%), omitting only *H. nalatus* and *P. ephyre*. Sweeping and light trapping collected 13 (57%) and 12 (52%) species represented, respectively. Sticky trap and pit trap collections were relatively low, with only 8 (35%) and 6 (26%) of the total species list, respectively. Generally, searching was most applicable to cryptic fall, winter and early spring emerging

Fig. 3. Percentages of total adults caught by various methods; Nov. 1982 - Nov. 1983, Battle Branch, Delaware Co. Oklahoma. Bar = 100%, numbers within bars = method specific sex ratio; NS = ratio not significantly different from 1:1 ($p>0.05$), * = significant deviation ($p<0.05$).

SPECIES	♂		♀
Zealeuctra warreni	13	NS	15
Allocapnia rickeri	136	✶	52
Paracapnia angulata	7	NS	9
Prostoia completa	32	NS	33
Zealeuctra claasseni	2		-
Strophopteryx fasciata	-		2
Perlinella drymo	-		1
Isoperla namata	77	✶	44
Isoperla signata	1		2
Clioperla clio	2		-
Amphinemura delosa	234	NS	208
Haploperla brevis	111	NS	122
Alloperla caudata	22	✶	52
Agnetina capitata	76	✶	45
Acroneuria evoluta	10	✶	292
Perlesta placida	56	✶	151
Perlinella ephyre	-		5
Neoperla clymene	89	✶	190
Neoperla stewarti	337	✶	1391
Neoperla sp. A	336	✶	1150
Neoperla catharae	300	✶	1021
Leuctra tenuis	38	NS	38



species, sweeping became more useful for actively flying, late spring and early summer species and light trapping was the most effective method for summer emerging, crepuscular species, specifically the perlids (Fig. 3). These results are similar to those of Frison (1935) and Neves (1978) for different species assemblages.

Low numbers and diversity of adults in pit and sticky traps on Battle Branch (Fig. 3) appears to be at least partially due to the behavior of these species. The majority of species either remained near emergence sites on emergent leaf packs, logs or vegetation, or flew into streamside vegetation. Few adults inhabited the rocky streamside, as is often the case with species of open canopied western streams. It is also probable that alcohol and/or diesel fuel vapor evokes some avoidance behavior in adult stoneflies. However, the success of similar pit traps for collecting adults by Müller (1973) and Stanford (1975) suggests that pit trap ineffectiveness on Battle Branch is more likely a result of emergence behavior of the particular stoneflies, rather than trap avoidance. Given the relatively low numbers collected in pit traps and the time necessary for installation and maintenance, their use is not recommended for monitoring Ozark stonefly emergence.

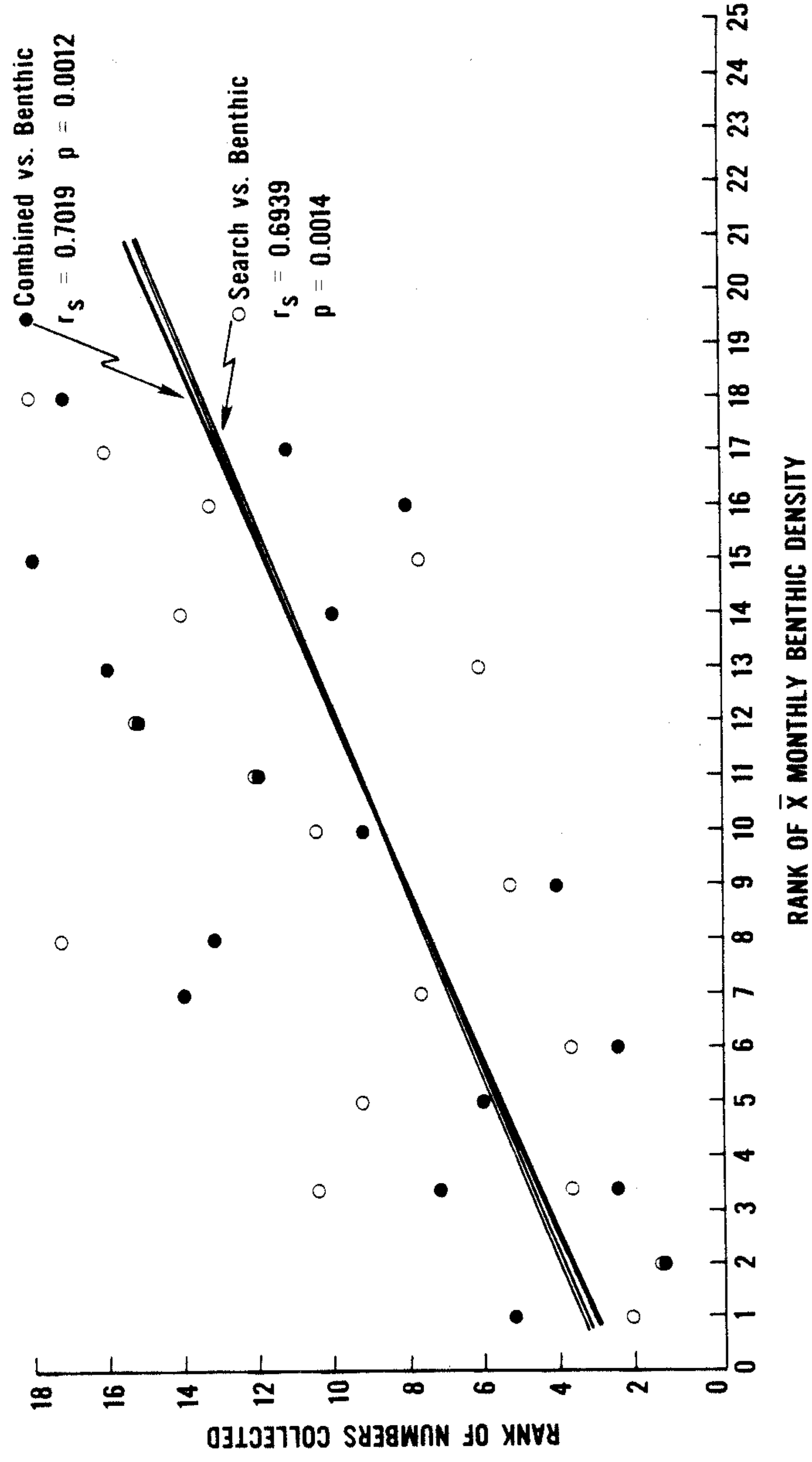
Sticky traps, although similarly ineffective in percentage of total or specific adults captured, required only seasonal maintenance and about 15 minutes of collection time per day. Calculation of catch rates based on this 15 minute effort vs. the longer time spent searching or sweeping indicates sticky traps were relatively efficient for winter and early spring emerging species, particularly Z. warreni, Paracapnia angulata and Prostoia completa. The Tanglefoot method might be even more effective if used above water on emergent objects and vegetation. Harper (1973a) monitored P. completa emergence with "adhesive traps". Alterations of my trap design to concentrate efforts on emergent leaf packs, logs or vegetation would probably be advantageous, but the absence of Perlidae in sticky trap collections suggests their limited use, as these larger species can pull through the material.

Sex ratios of adults often deviated from an expected 1:1 ratio (Fig. 3). Significantly more males ($p<0.05$) of the active Allocapnia rickeri and Isoperla namata were collected while searching (Fig. 3). Conversely, sex ratios revealed significantly greater numbers of females for species attracted to the light trap ($p<0.05$, Fig. 3). Vaught and Stewart (1974) reported one male to five females in peak light trap collections of Neoperla clymene in Texas. The greater number of females attracted to the light may be a result of their generally longer life-span (Narf and Hilsenhoff 1974) and/or crepuscular oviposition habits within the families Chloroperlidae and Perlidae, during which the light is mistaken for water.

Mean monthly benthic density ranged from $698/m^2$ for Amphinemura delosa to $0.25/m^2$ for Helopicus nalatus. Correlating the ranks of the benthic density on the ranks of the total numbers collected for each species, by method, reveals a significant relationship between benthic density and search collections (r_s=0.6939, p=0.0014, Fig. 4). Correlation coefficients for benthic populations on the other four methods were not significant (r_s ranged from 0.4262 to 0.3157; p ranged from 0.0778 to 0.2019). Correlating ranked benthic densities of each species on the respective ranked total number collected by summing the five methods reveals a relationship that is only slightly more significant than for search alone (r_s=0.7019, p=0.0012, Fig. 4).

Positive trends between ranks of species caught searching vs. sticky traps (r_s=0.7766, p=0.0002), searching vs. pit traps (r_s=0.4018, p=0.0983) and search vs. sweeping (r_s=0.3833, p=0.1164) indicate the corroborative interaction of these methods. Light trapping was negatively associated to searching (r_s

Fig. 4. Spearman rank correlation of search method for adults with benthic density and combined collection methods with benthic density. Each circle represents a different species. Nov. 1982 - Feb. 1984, Battle Branch, Delaware Co., Oklahoma. Lines drawn from least squares regression to demonstrate trend.


● Combined vs. Benthic
$r_s = 0.7019$ $p = 0.0012$
○ Search vs. Benthic
$r_s = 0.6939$
$p = 0.0014$
RANK OF NUMBERS COLLECTED
0
2
4
6
8
10
12
14
16
18
RANK OF $\bar{X}$ MONTHLY BENTHIC DENSITY
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25

=-0.0210, p=0.9341). Large numbers of Neoperla, Perlesta and Acroneuria were collected by the light, but only infrequently by the other methods.

The details of emergence periods, patterns and methods of each species are discussed below in order of their emergence time.

Zealeuctra warreni Ricker and Ross: The small sample size of males showed a synchronous emergence pattern with a peak in early Dec. Females had an extended emergence pattern (g_1 =-0.1641, p>0.20) with specimens being found two months after the last males were collected. Adults were found in the greatest abundance on emergent leaf packs, logs and streamside vegetation during warm afternoons, and under stones during cool morning hours.

Allocapnia rickeri Frison: Adults on Battle Branch appeared in late Dec., about two weeks earlier than in Wisconsin (Narf and Hilsenhoff 1974). The emergence pattern for sexes combined is synchronous (Fig. 2). Males alone demonstrated a synchronous pattern (g_1 =1.0961, p<0.01) and were collected in significantly greater numbers (Fig. 3). Females exhibited a more symmetrical, extended emergence pattern (g_1 =0.4600, 0.20>p>0.10). The greatest number of adults were collected by searching emergent leaf packs, logs and fence posts. Adult attraction to vertical surfaces and their active movement permits quick collections of many specimens with an aspirator.

Paracapnia angulata Hanson: This study extends the western range of this eastern species. Emergence began in mid-Jan., about one month earlier than reported for Wisconsin (Narf and Hilsenhoff 1974) or Massachusetts (Neves 1978), and three months earlier than Quebec (Harper and Magnin 1969). Unlike *A. rickeri*, this species often inhabits the rocky bank where it can be collected by searching or sticky traps (Fig. 3).

Prostoia completa (Walker): Emergence began in mid-Feb, about 1.5 months earlier than reported for southern Ontario (Harper 1973a) and Massachusetts (Neves 1978). Both sexes demonstrated positively skewed emergence periods (male: $g_1 = 1.8252$, female: $g_1 = 1.0375$, $p < 0.01$, Fig. 2), resembling the pattern observed by Harper (1973a). Emergent leaf packs were a productive place to search, but this ubiquitous species was collected with a variety of methods (Fig. 3).

Zealeuctra claasseni (Frison): A male specimen collected on Feb 27,983, indicated their presence about three weeks later than reported for northern Texas (Snellen and Stewart 1979a).

Strophopteryx fasciata (Burmeister): Collections of two females on Mar. 14, 1983 and Feb. 20, 1984, respectively, indicate at least a portion of the general emergence period (Fig. 2). Frison (1935) reported emergence from Feb. through Apr., with the greatest intensity toward the end of Mar.

Perlinella drymo (Newman) and *Perlinella ephyre* (Newman): These temporally segregated congeners were never collected in benthic samples, yet an exuvium of *P. drymo* was found. Although samples sizes are small, collections of *Perlinella* from other Ozark streams also suggest spring emerging *P. drymo* to be frequently collected by searching streamside gravel and debris, while *P. ephyre* is common in summer light trap collections (B. Poulton and K. Stewart, unpublished data). This study extends the western range of *P. ephyre*.

Isoperla namata Frison: Emergence began in early Apr., coinciding with deciduous tree budding. Sexes combined reveal a synchronous emergence pattern (Fig. 2), but, the significantly greater number of males ($p<0.05$) bias the distribution ($g_1=2.3481$, $p<0.01$) as females exhibit an extended emergence pattern ($g_1=0.4584$, $0.20>p>0.10$). Most adults (96%) were captured by searching emergent logs and leaf packs during the morning. Adults were scarce during the afternoon, suggesting they leave the stream and fly into streamside brush. Females were observed ovipositing over riffles at dusk.

Isoperla signata (Banks): This study extends the southwestern range of this species. A small sample of adults and collections of exuvia from the bridge foundation indicate that *I. signata* maintains the synchronous emergence pattern reported for Wisconsin (Jop and Szczytko 1984).

Clioperla clio (Newman): Two males collected while searching on Apr. 9,1983 indicate emergence in Battle Branch begins at about the same time as repoted for Morgan Creek, Kentucky (Minshall and Minshall 1966), but one to 1.5 months earlier than reported for Wisconsin (Narf and Hilsenhoff 1974), Massachusetts (Neves 1978) or southern Ontario (Harper 1973b). Feminella (1983) found emergence in mid-Mar. in the Little Missouri River, Arkansas and concluded that temperature and/or photoperiod differences in lower latitudes shortened total *C. clio* nymphal development.

Amphinemura delosa (Ricker): Emergence began in late Apr., about 2 weeks earlier than southern Ontario (Harper 1973a) and 3 weeks earlier than Wisconsin (Narfnd Hilsenhoff 1974). Both sexes showed a positively skewed emergence patterns (male: g_1=1.6984, female: g_1=1.3669, $P<0.01$, Fig. 2). Harper (1973a) also reported a positively skewed pattern with superficial resemblance to an extended pattern. Adults were readily collected by searching leaf packs, emergent logs and watercress during the morning.

Haploperla brevis (Banks): Emergence began in mid May when when trees were fully leaved. Emergence began in Quebec (Harper and Magnin 1969) and Massachusetts (Neves 1978) in late May. Males ($g_1 = 2.4150$) and females ($g_1 = 1.3036$) had significantly skewed emergence patterns ($p < 0.01$, Fig. 2). Most individuals (51%) were collected by sweeping streamside sycamore, oak and maple limbs. Teneral adults were found early in the morning. This is the earliest emerging species attracted to the light in reasonable numbers (one male and 14 females, Fig. 3).

Alloperla caudata Frison: Emergence began shortly after H. brevis (Fig. 2). Neves (1978) reported a similar time of emergence for Factory Brook, Massachusetts. The emergence pattern of neither males ($g_1 = 0.5378$) nor females ($g_1 = 0.1843$) was significantly skewed ($p > 0.20$, Fig. 2). Collection was similar to that of H. brevis, with the exception of a greater percentage of adults light trapped (Fig. 3). Chloroperlids that were collected at the light trap generally appeared at dusk, earlier than the Perlidae.

Agnetina capitata (Pictet): This species initiated Perlidae emergence in late May, when three males were collected by sweeping streamside jewelweed. This is the only species in which my sampling regime detected protandry. Harper (1973b) and Neves (1978) record emergence beginning in early Jun. and mid Jun., respectively. The emergence pattern of males (g_1 =-0.1559) and females (g_1=-0.2135) were not significantly skewed (p>0.20, Fig. 2). Harper (1973b) also reported an extended emergence pattern, suggesting this to be manifested by a large spread of nymphal sizes. Males were primarily collected by search and sweep, but females were significantly more common in light trap collections (Fig. 3).

Acroneuria evoluta Klapalek: Emergence began in Jun. with a similar number of males and females collected. No males were collected during Jul. when large numbers of crepuscular females were collected in the light trap (Fig. 3), yielding a negatively skewed emergence pattern for females (g_1=-0.7009, p<0.01) and sexes combined (Fig. 2). As found for *A. capitata*, males were most often collected by search or sweeping jewelweed and watercress.

Perlesta placida (Hagen): Since *P. placida* probably represents a species in a taxonomically uncertain complex, comparisons to the work of Snellen and Stewart (1979b) and Frison (1935) are inappropriate at this time (B. P. Stark, personal communication). My males exhibited a synchronous emergence pattern beginning in early Jun. (g_1=1.1289, P<0.02), while the significantly more abundant females ($p<0.05$) were negatively skewed (g_1=-0.9927, $p<0.01$). Most adults were collected by the light trap (Fig. 3). Adults could also be collected by searching or sweeping emergent waterwillow in the pool areas of the stream.

Neoperla clymene (Newman), *Neoperla stewarti* Stark and Baumann, *Neoperla* sp. A and *Neoperla catharae* Stark and Baumann: This group of morphologically similar species show much overlap in emergence periods (Fig. 2). *Neoperla clymene* began emerging in early Jun., approximately the same time as reported for the Brazos River, Texas (Vaught and Stewart 1974). Sexes combined (Fig. 2) and females (g_1=1.2551) reveal a synchronous emergence pattern, while the smaller sample size of males demonstrated an extended pattern (g_1=0.4914, $p>0.05$). *Neoperla stewarti* had a synchronous emergence pattern for both males (g_1=0.4161) and females (g_1 =0.3751). *Neoperla* sp. A demonstrated a synchronous emergence for sexes combined (Fig. 2) and males (g_1 =1.0595, $p<0.01$), but females displayed an extended pattern (g_1=-0.0582, $p>0.05$). The last member to emerge, *N. catharae*, demonstrated a negatively skewed pattern. Separating sexes revealed females to have an extended pattern (g_1=-0.0373, $p>0.20$), but males were negatively skewed (g_1=-1.4621, $p<0.01$). Unlike the negatively skewed patterns for *A. evoluta* and *P.*

placida resulting from a female maturation period and delayed oviposition flight, the negatively skewed pattern of *N. catharae* is a result of the males. Possibly the cool air temperatures of late Sep. (Fig. 1) killed many of the adults or decreased the effectiveness of the light trap (17 to 18°C at trap time), resulting in a male distribution without a right-hand tail. Pre-emergent nymphs in Sep. Surber samples probably produced the females collected in Oct. *N. catharae* is a new state record. Significantly more females were collected for all *Neoperla* species ($P<0.05$, Fig. 3).

Neoperla nymphs averaged 84/m^2 annually, yet adults were rarely collected by any method other than light trapping (Fig. 3), demonstrating the importance of light trapping for assessing this genus.

Leuctra tenuis (Walker): This new state record represents the only true fall emerging species in Battle Branch (Fig. 2). Emergence has been reported to begin in May in Wisconsin under field simulated laboratory conditions (Narf and Hilsenhoff 1974) and Jul. in Massachusetts (Neves 1978) and southern Ontario (Harper and Pilon 1970). Emergence extended into Aug. (Harper and Pilon 1970, Harper 1973a) or early Sep. (Narf and Hilsenhoff 1974, Neves 1978). Harper and Pilon (1970) categorized the emergence pattern of *L.*

tenuis as extended in Quebec. During 1983, I found a synchronous emergence pattern for females ($g_1 = 5.9828$, $p < 0.01$) and males were collected on only one sampling date. This autumnal species was collected most often by searching recently formed leaf packs, emergent logs or the bridge foundation.

CHAPTER III

GROWTH, DRIFT AND APPLICATION OF REGRESSION MODELS

Introduction

The nymphal growth and drift of nine abundant stonefly species, *Amphinemura delosa* (Ricker), *Prostoia completa* (Walker), *Allocapnia rickeri* Ricker, *Leuctra tenuis* (Walker), *Isoperla namata* Frison, *Isoperla signata* (Banks), *Haploperla brevis* (Banks), *Acroneuria evoluta* Klapalek and *Agnetina capitata* (Pictet), were studied in Battle Branch, a second-order Ozark steam in Delaware Co., Oklahoma. These aspects have not been previously reported for *Acroneuria evoluta*. Life histories of the other eight species have been studied in other regions (Coleman and Hynes 1970, Feminella 1983, Harper 1973a, 1973b, Harper and Magnin 1969, Jop and Szczytko 1984, Krueger and Cook 1981), and categorized according to Hynes (1961) classification system.

In addition to characterizing nymphal growth and drift, another major objective was to assess the fit of observed nymphal growth of the 9 species to 5 different mathematical models. Branham et al. (1975), Humpesch (1979, 1981), Brittain (1983), Heiman and Knight (1975) and Knight et al. (1976) have used mathematical models to quantify growth rates for aquatic insects with fast or slow cycles. Such modeling allows critical comparison of the growth rates of different species.

The drift of stoneflies has received little attention in relation to other aquatic orders (Elliot 1967a), probably reflecting their low drift propensity (Brusven 1970, Stewart and Szczytko 1983). Most stoneflies drift in pre-emergent instars, primarily just after sunset (Elliot 1967a, Stewart and Szczytko 1983). Anderson and Lehmkuhl (1968) found large numbers of Capnia and Nemoura succumbing to fall freshets. Walton (1980) and Walton et al. (1977) reported substrate, density, current velocity and/or predators variously influenced the drift of Acroneuria abnormis (Newman) and Taeniopteryx spp. in laboratory streams.

Materials and Methods

Benthic sampling was conducted for 19 months, Nov. 1982 - May 1984. During the first 4 months, only qualitative samples were taken,consisting of several kicks of leaf packs and mineral substrates in riffle areas with a 2-stage net having 1.0 and 0.153 mm mesh openings, respectively. For the remaining period, 10 samples/month were taken across a continuum of visible organic matter (leaf) with a modified Surber sampler ($0.1\ m^2$, mesh= 0.153 mm), except Mar. - May, 1984, when five samples/month were taken. Additional qualitative sampling during his period was done with the kick net to assure sufficient sampling of less common species.

Samples were preserved in 70% isopropanol. In the laboratory all insects were separated from large debris by washing over a 0.150 mm sieve, then hand picked from the fine debris under a dissecting microscope. Interocular width (head capsule width = HCW) of identified stonefly nymphs were measured to the nearest 0.04 mm with an ocular micrometer. Mean benthic densities ($No./m^2$) were calculated from Surber samples over the Mar. 1983 to May 1984 period.

The observed growth of each stonefly species was compared to the following five growth models, with HCW and time in days as the dependent and independent variables, respectively:

1) Least squares regression,

$$HCW = b + a(DATE)$$

2) Semilog or exponential least squares regression,

$$\ln HCW = b + a(DATE)$$

3) Double log or power curve least squares regression,

$$\ln HCW = b + a(\ln DATE) \quad \text{or} \quad HCW = c(DATE)^a$$

4) Exponential asymptotic nonlinear regression,

$$HCW_{DATE} = HCW_{I}\ e^{a(DATE)}$$

5) Exponential asymptotic nonlinear regression,

$$HCW_{DATE} = HCW_{E}\ e^{a(DATE)}$$

where: HCW = head capsule width in mm, HCW_{DATE} = head capsule width at specified date, HCW_{I} = measured initial head capsule width, HCW_{E} = estimated initial head capsule width, DATE = Date, standardized by setting the first collection of nymphs as day 1 and adding subsequent days until the end of the growth period, b = y intercept, c = natural antilog of b, a = growth rate or growth coefficient.

Equations 1-3 are ordinary least squares regressions with various natural log transformations to reduce heteroscedasticity (Zar 1974) and/or linearize observed growth curves. Equations 4 and 5 are both nonlinear exponential regression equations. They differ in the assignment of a constant for initial HCW in equation 4 based on the mean of the sample, whereas in equation 5 the computer estimates initial HCW. Initial HCW estimation is within the range of measurements for DAY = 1. Growth data were not included from months when there was a negative change in the size distribution of nymphs due to emergence. A comparison of growth rates (coefficients) from two regression equations was accomplished by utilizing a "dummy" variable (Hanushek and Jackson 1977). Only slopes from equation 2 were statistically compared.

Drift was measured each month, Apr. 1983 - May 1984, except Apr. 1984, with a modified Muller sampler described by Cloud and Stewart (1974a, b) and Stewart and Szczytko (1983). Two samplers with 0.471 mm mesh Nitex bags were placed in the main thalweg 60 min. before sunset and 30 min. after sunset each month. They were left in position for 30 min. after which contents were preserved in 70% isopropanol. All insects were hand picked under 6x from samples, identified to lowest possible taxon and counted. Remaining organic matter was dried at 50^{o}C in preweighted tin pans for ca. 24 hrs or until constant weight on a Mettler analytical balance was achieved. Current velocity was measured with a Kahl Pigmy Flow Meter before each drift sample period and used to calculate volume of water sampled over the 30 min periods. Drift was then expressed as drift density, i.e. number of animals per 10 m^3 of water, (Elliot 1970, Stewart and Szczytko 1983). Drift density pre-sunset and post-sunset was compared by a Wilcoxon sign rank test (Mann Whitney U, Zar 1974). Drift density differences between insect orders were analyzed with a

Student-Newman-Keuls (SNK) multiple range test on ranked data (SAS 1982). Multivariate regression was performed on drift correlates. All data were analyzed on the North Texas State University AS/8040 computer with SAS.

Results and Discussion

Growth rates and regression statistics generated from application of each model to each stonefly species are presented in Table 1. A large sample size and intrinsic variation within each population resulted in statistical significance for equations 1-3 on each species (F test: $p<0.0001$, t-test: $p<0.0001$). The coefficient of determination (R^2) assisted in choosing the model that most accurately described my data. Nonlinear regression (equations 4, 5) on SAS (NLIN) does not produce a test of significance or R^2 to facilitate assessment of fit and comparison to other models. Similarily, transformations of data result in incongruent regression statistics for comparative purposes. Therefore, comparative measures across all equations such as plots of residuals vs. time and predicted vs. observed values were utilized to ascertain the "best fit" model for each species.

The growth of univoltine stoneflies in Battle Branch generally conformed to a power curve (equation

Table I. Regression statistics for 5 growth equations. Equations 1-3 all highly significant (F: $p<0.0001$, t: $p<0.0001$). Equations 4-5 not applicable to testing. [ ] = equation 2 growth coefficients used in comparison of species. Slopes testing only for equation 2; * $p<0.001$, ** $p<0.0001$.

Species Hynes' Class.	Equation	R^2		Error SS		Y-Intercept		Growth Coefficients ± 1 SE	
		1983	1984	1983	1984	1983	1984	1983	1984
Amphinemura delosa	1	0.39	0.51	40.71	7.07	0.1049	0.0232	0.0032±0.0001	0.0044±0.0002
univoltine, fast	2	0.47	0.52	279.53	53.67	-1.8973	-2.0400	[0.0099±0.0002**	0.0123±0.0004]
	3	0.38	0.42	329.84	65.12	-2.2203	-3.7560	0.2828±0.0059	0.6278±0.0270
	4	---	---	40.67	8.13	0.1377	0.1167	0.0110±0.0001	0.1340±0.0001
	5	---	---	40.11	7.42	0.1627	0.1609	0.0095±0.0002	0.0103±0.0004
Prostoia completa	1	0.57	0.40	4.52	21.27	0.1921	0.0873	0.0039±0.0016	0.0037±0.0001
Univoltine, fast	2	0.60	0.45	46.53	147.54	-1.7254	-1.9149	[0.0135±0.0005**	0.0110±0.0003]
	3	0.79	0.39	24.24	164.34	-2.0228	-3.4791	0.2868±0.0071	0.5710±0.0175
	4	---	---	6.98	21.74	0.1628	0.1365	0.0135±0.0002	0.0122±0.0001
	5	---	---	5.45	21.42	0.2210	0.1632	0.0098±0.0009	0.0104±0.0004
Allocapnia rickeri	1	0.56	0.41	1.48	0.33	0.3082	0.2720	0.0071±0.0004	0.0042±0.0008
Univoltine, fast	2	0.47	0.44	12.09	2.19	-1.1944	-1.3207	[0.0173±0.0012	0.0114±0.0019]
	3	0.47	0.58	12.09	1.65	-1.1770	-1.7983	0.1509±0.0101	0.2675±0.0345
	4	---	---	1.49	0.60	0.3154	0.1725	0.0167±0.0007	0.0194±0.0008
	5	---	---	1.49	0.59	0.3099	0.1750	0.0173±0.0014	0.0192±0.0052

Table I.--Continued.

Species Hynes' Class.	Equation	R^2		Error SS		Y-Intercept		Growth Coefficients ± 1 SE	
		1983	1984	1983	1984	1983	1984	1983	1984
Leuctra tenuis	1	0.47	0.47	2.32	0.20	0.2512	0.2086	0.0015±0.0001	0.0021±0.0002
Univoltine, fast	2	0.42	0.49	27.07	2.64	-1.3710	-1.5689	[0.0045±0.0002*	0.0079±0.0007]
	3	0.29	0.40	33.34	3.14	-1.4402	-1.6239	0.0951±0.0058	0.1136±0.0131
	4	---	---	3.68	0.21	0.3256	0.2136	0.0019±0.0001	0.0076±0.0003
	5	---	---	2.69	0.21	0.2631	0.2121	0.0042±0.0002	0.0077±0.0008
Isoperla signata	1	0.68	0.35	0.46	5.05	0.4760	0.4788	0.0085±0.0014	0.0064±0.0010
Univoltine, fast	2	0.72	0.32	0.51	7.70	-0.6634	-0.6673	[0.0098±0.0014	0.0074±0.0012]
	3	0.69	0.19	0.56	9.26	-0.9771	-0.6528	0.2520±0.0398	0.1093±0.0260
	4	---	---	0.60	5.01	0.4250	0.5700	0.0120±0.0004	0.0069±0.0005
	5	---	---	0.64	4.86	0.4000	0.4918	0.0127±0.0040	0.0089±0.0014
Isoperla namata	1	0.36	0.44	46.80	155.05	0.4920	0.0979	0.0039±0.0002	0.0042±0.0001
Univoltine, fast	2	0.35	0.47	113.04	533.12	-0.7656	-1.6275	[0.0059±0.0003**	0.0085±0.0001]
	3	0.43	0.39	98.35	633.51	-1.323	-3.1358	0.2500±0.0093	0.5227±0.0101
	4	---	---	75.82	149.36	0.3256	0.1938	0.0087±0.0001	0.0093±0.0001
	5	---	---	50.61	149.25	0.5250	0.2002	0.0047±0.0002	0.0090±0.0001

Table I.--*Continued*.

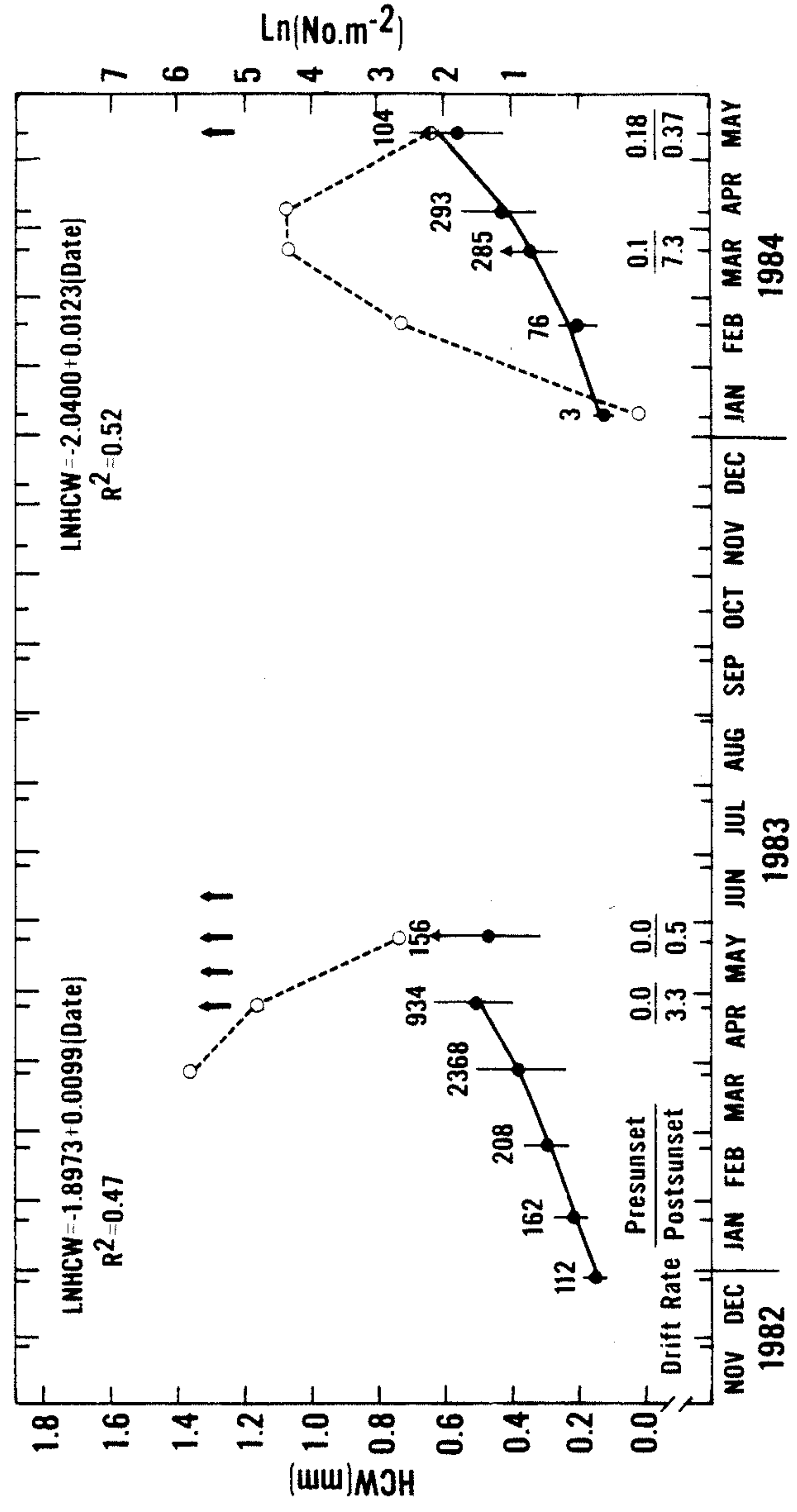
Species Hynes' Class.	Equation	R^2		Error SS		Y-Intercept		Growth Coefficients ± 1 SE	
		1983	1984	1983	1984	1983	1984	1983	1984
Haploperla brevis	1	0.39	0.65	2.00	1.65	0.2001	0.0850	0.0024±0.0002	0.0020±0.0001
Univoltine, fast	2	0.41	0.63	12.64	14.75	-1.4961	-1.8730	[0.0063±0.0005	0.0057±0.0002]
	3	0.36	0.24	13.62	30.42	-2.2066	-2.2007	0.2993±0.0279	0.2230±0.0234
	4	---	---	2.12	2.74	0.2128	0.2647	0.0068±0.0001	0.0025±0.0001
	5	---	---	2.03	2.65	0.2547	0.2008	0.0054±0.0005	0.0032±0.0003
Acroneuria evoluta	1		0.50		139.12		0.9159		0.0051±0.0001
Univoltine, slow	2		0.52		64.83		-0.105		0.0036±0.0001
	3		0.62		52.10		-1.2901		0.3669±0.0091
	4		---		2245.09		0.4848		0.0000±0.0000
	5		---		329.38		0.5610		0.0053±0.0002

3) or a semilog model (equation 2).

Amphinemura delosa growth was univoltine, fast with a probable 6 month diapause during the summer months. My interpretation of egg hatching from field studies in this and other species studied may be limited by microhabitats sampled, which make conclusions on diapause tentative and in need of laboratory validation (Harper 1973b). A similar life cycle for this species was reported by Coleman and Hynes (1970) and Harper (1973a). Harper (1973a) found laboratory incubated eggs to have a 3 month diapause with hatch occurring on a falling temperature cue. Growth in Battle Branch was best modeled with equation 2; the semi-log transformation accounted for the gradual increase in growth rate with time and the heteroscedasticity resulting from prolonged recruitment of early instars (Fig. 5). Growth rates of the two populations were similar, but the large sample size (Fig. 5) reveals statistical difference (Table 1). This species had the greatest drift densities (maximum = 7.3/10 m^3), and was the most abundant benthic species, with maximum density (2368/m^2) in Mar., 1983. Drifting nymphs had HCW's > the mean of the respective benthic samples and were most prevalent in post-sunset samples just prior to and during the emergence period (Fig. 5).

Fig. 5. *Amphinemura delosa* growth and drift. ⧫ = $\bar{X}$ head capsule width ± 1 SD, with sample size above ▲ = $\bar{X}$ head capsule width of drifting nymphs, with drift density (No./10 m^3) along lower axis; o = benthic density, (No./0.1 m^2); = adults collected; solid line is predicted growth curve from respective model, indicated along upper axis.

AMPHINEMURA DELOSA

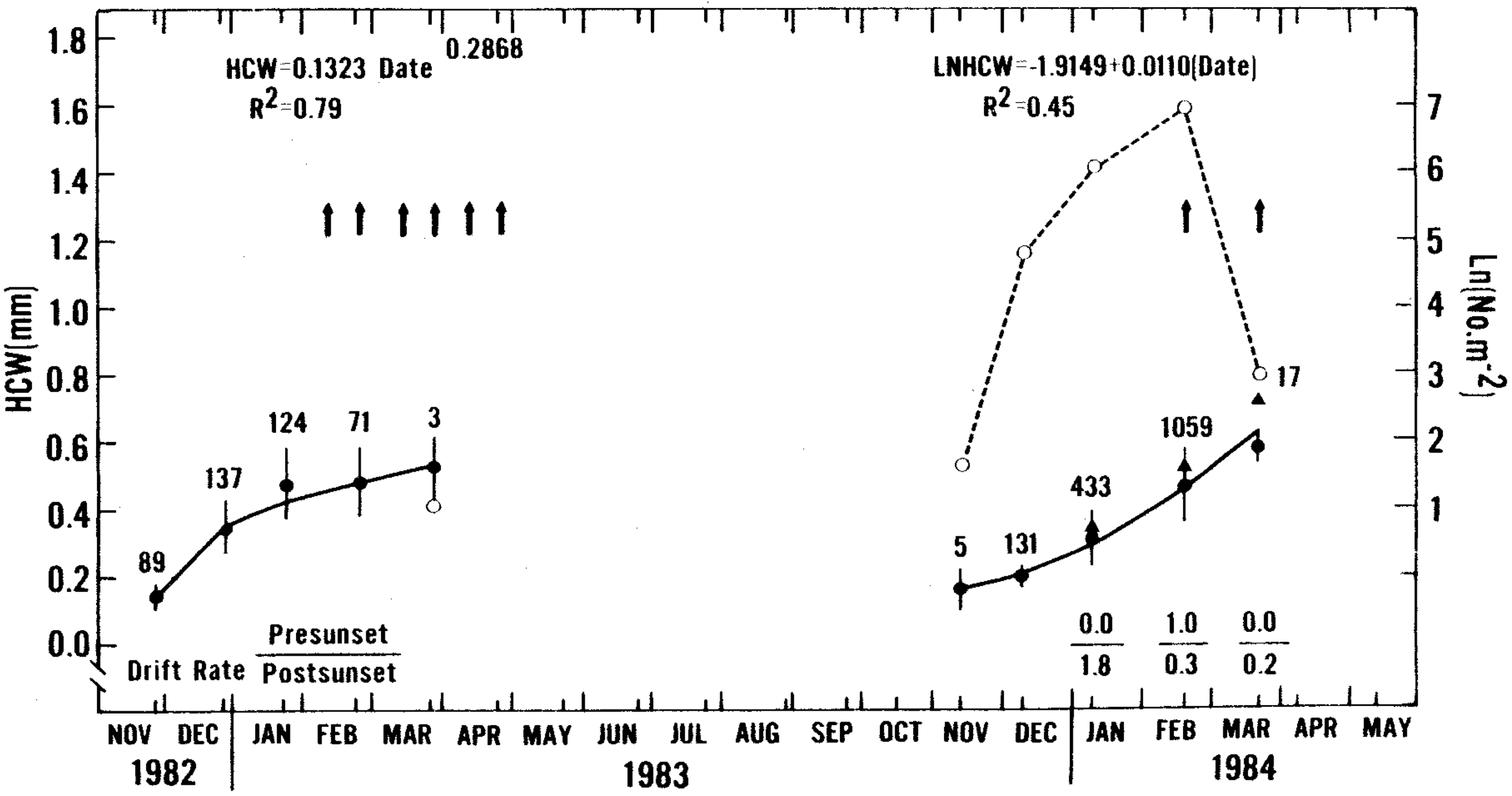


Prostoia _completa_ demonstrated a univoltine, fast life cycle with a probable egg diapause of 6 to 7 months during spring-summer (Fig. 6). A 4 month diapause was reported in laboratory eggs from southern Ontario (Harper 1973a). My 1983 cohort fit a power curve (equation 3), while the 1984 cohort was best described with a semilog regression (equation 2, Fig. 6, Table 1). These different growth patterns may have resulted from the diel temperature variability experienced, since temperature data suggest the 1984 cohort did not have the fluctuating temperature impetus during early growth stages (Sweeney 1980, Fig. 1). The relatively large growth rates during Nov., Dec. and Jan. 1983 resulted in a "waiting period" or asymptote before the emergence period. Drift was primarily during the Feb.- Mar 1984 emergence period. Size (HCW) of drifting nymphs was always > than the mean of benthic samples (Fig. 6). Maximum benthic density (1059/m^2) occurred in Feb. 1984.

Allocapnia _rickeri_ nymphal determination was based on adult collections of 277 specimens, all of this species. They exhibited a univoltine, fast life cycle with nymphs found in the stream for only 3 months (Fig. 9). Long diapause has been observed for other _Allocapnia_ spp. (Finni 1977). Krueger and Cook (1981) report a remarkably different 9 month growth period for

Fig. 6. *Prostoia completa* growth and drift. ⧫ = $\bar{X}$ head capsule width ± 1 SD, with sample size above ▲ = $\bar{X}$ head capsule width of drifting nymphs, with drift density (No./10 m^3) along lower axis; o = benthic density, (No./0.1 m^2); = adults collected; solid line is predicted growth curve from respective model, indicated along upper axis.

PROSTOIA COMPLETA



A. rickeri in northern Minnesota. Equations 1 and 3 adequately describe the fast growth of my 1983 and 1984 cohorts respectively. Two nymphs were collected in pre-sunset drift samples, at the beginning of emergence. Mean HCW was slightly greater than the respective benthic sample (Fig. 7). Maximum benthic density occurred in Dec., 1983 ($17/m^2$).

Leuctra tenuis growth was univoltine fast with an autumnal emergence and probable 4 month winter egg diapause (Fig. 8). This species is reported as univoltine, slow in southern Ontario (Harper 1973a). Equation 2 best described growth rates of the two cohorts. Growth rates were significantly different ($p=0.0006$, Table 1), however the attenuated 1984 sampling makes this comparison tentative, as the growth rate of this cohort may have slowed with maturity (Table 1). One nymph was collected in a post-sunset drift sample. Maximum benthic density occurred in May, 1983 ($223/m^2$).

Isoperla namata exhibited univoltine, fast growth with a probable 4 to 5 month diapause that was best modeled by a power curve (equation 3) in 1983 and a semilog model (equation 2) in 1984 (Fig. 9, Table 1). Feminella (1983) found populations from two sites on the Little Missouri River, Arkansas demonstrated exponential growth similar to my 1984 cohort. It is

Fig. 7. Allocapnia rickeri growth and drift. ♦ = $\bar{X}$ head capsule width ± 1 SD, with sample size above ▲ = $\bar{X}$ head capsule width of drifting nymphs, with drift density (No./10 m^3) along lower axis; o = benthic density, (No./0.1 m^2); = adults collected; solid line is predicted growth curve from respective model, indicated along upper axis.

ALLOCAPNIA RICKERI

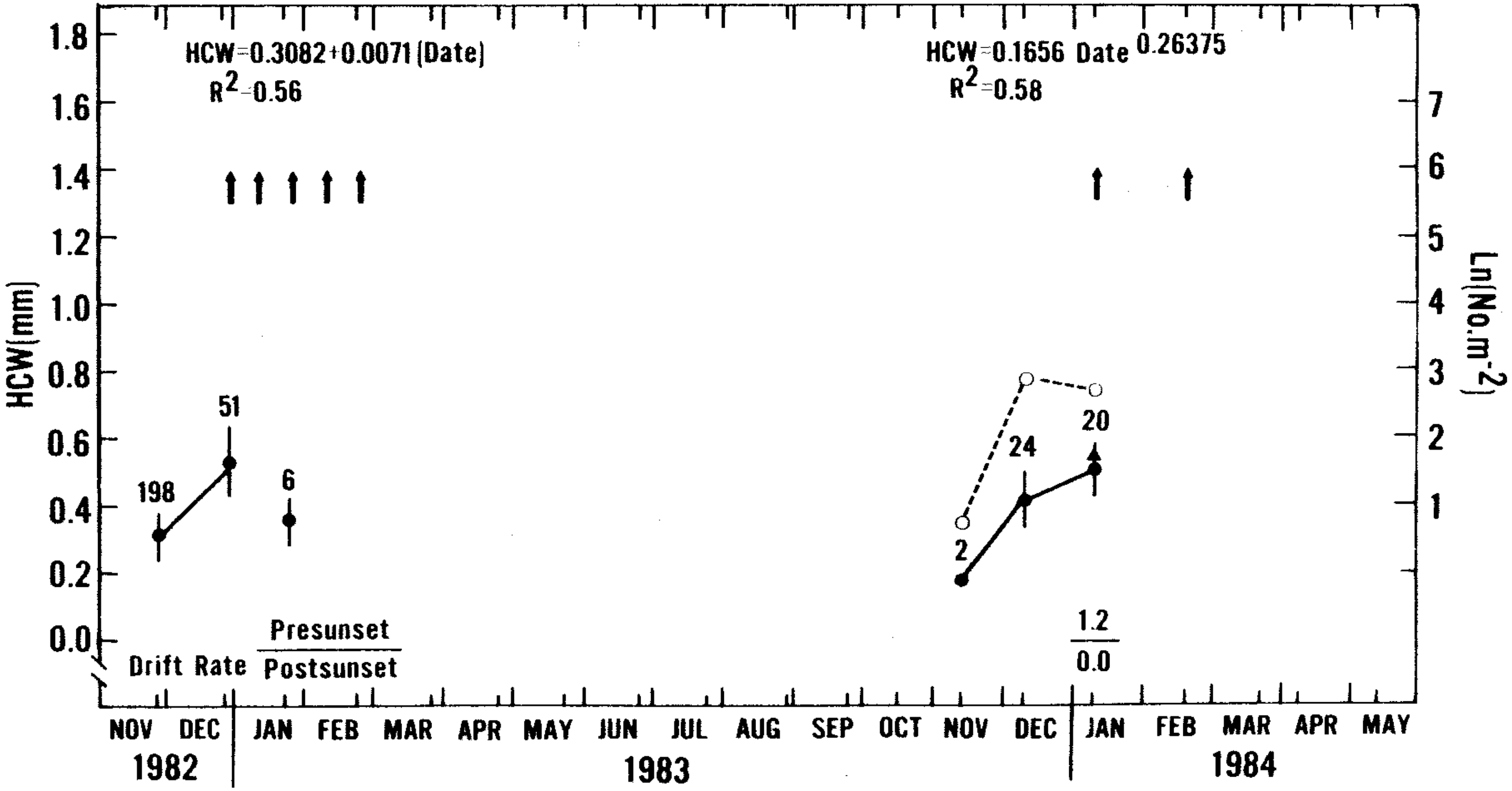


Fig. 8. *Leuctra tenuis* growth and drift. ⧫ = $\bar{X}$ head capsule width ± 1 SD, with sample size above ▲ = $\bar{X}$ head capsule width of drifting nymphs, with drift density (No./10 m^3) along lower axis; o = benthic density, (No./0.1 m^2); = adults collected; solid line is predicted growth curve from respective model, indicated along upper axis.

LEUCTRA TENUIS

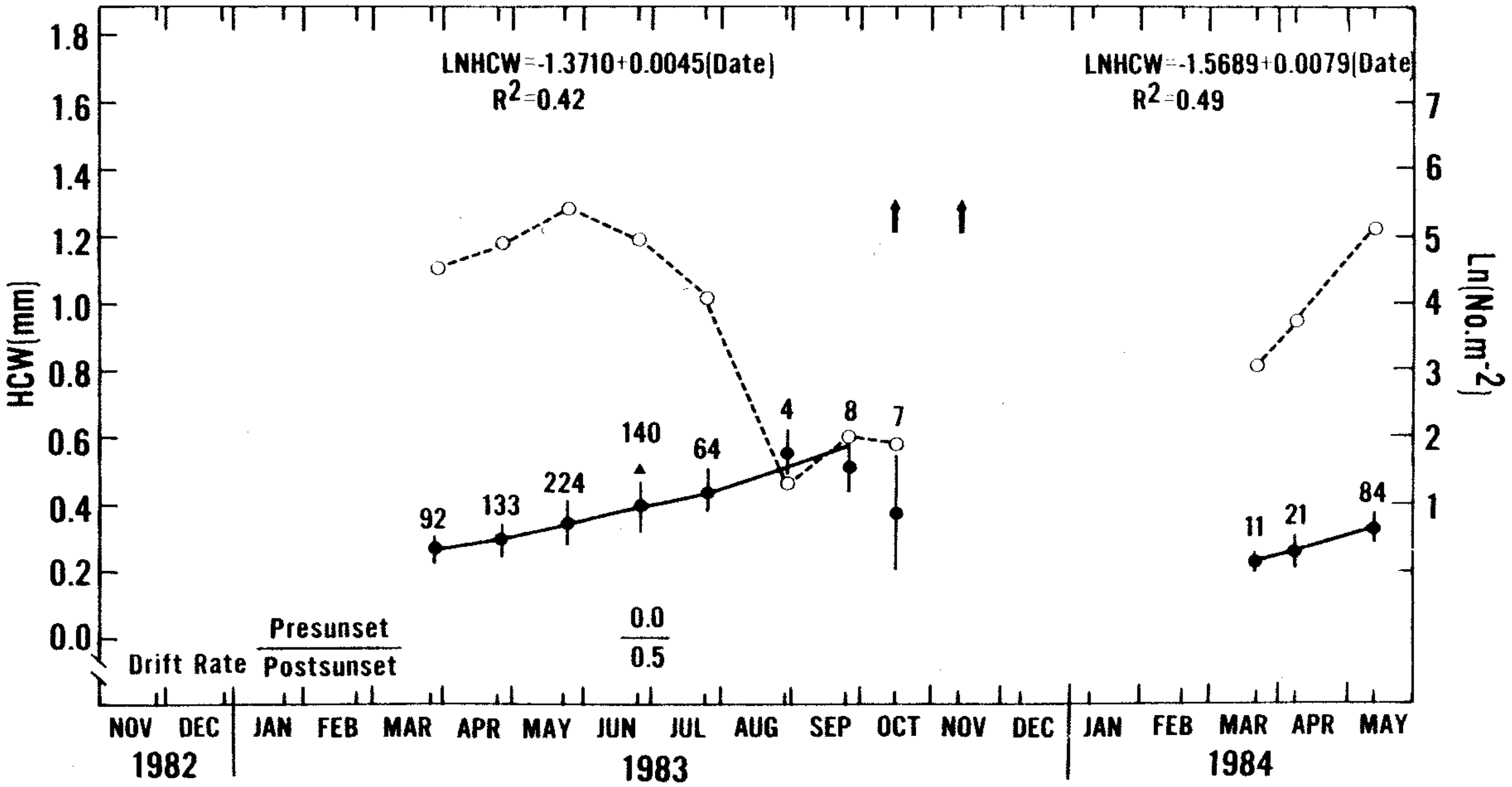
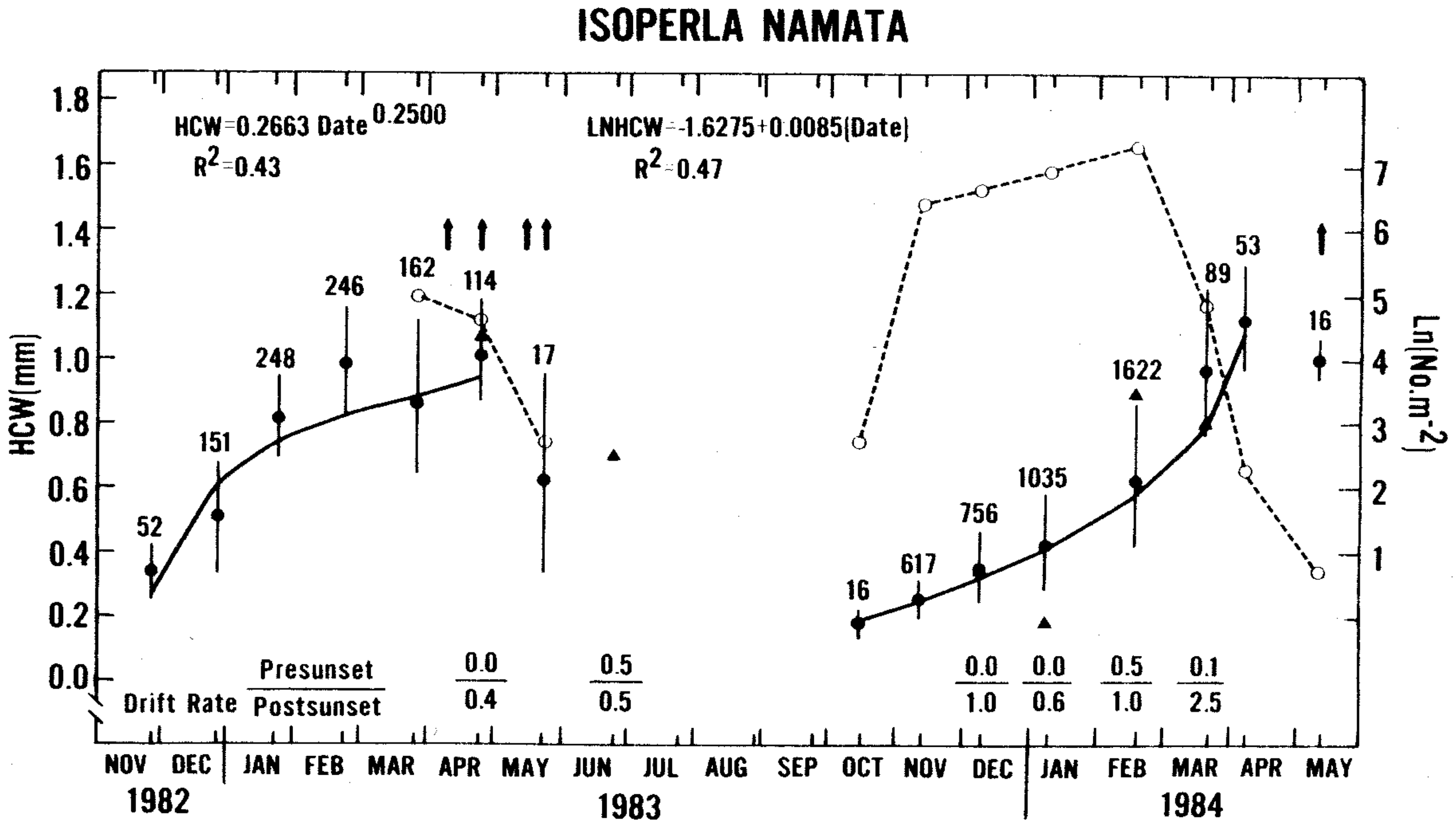


Fig. 9. Isoperla namata growth and drift. ● = $\bar{X}$ head capsule width ± 1 SD, with sample size above ▲ = $\bar{X}$ head capsule width of drifting nymphs, with drift density (No./10 m^3) along lower axis; o = benthic density, (No./0.1 m^2);   = adults collected; solid line is predicted growth curve from respective model, indicated along upper axis.

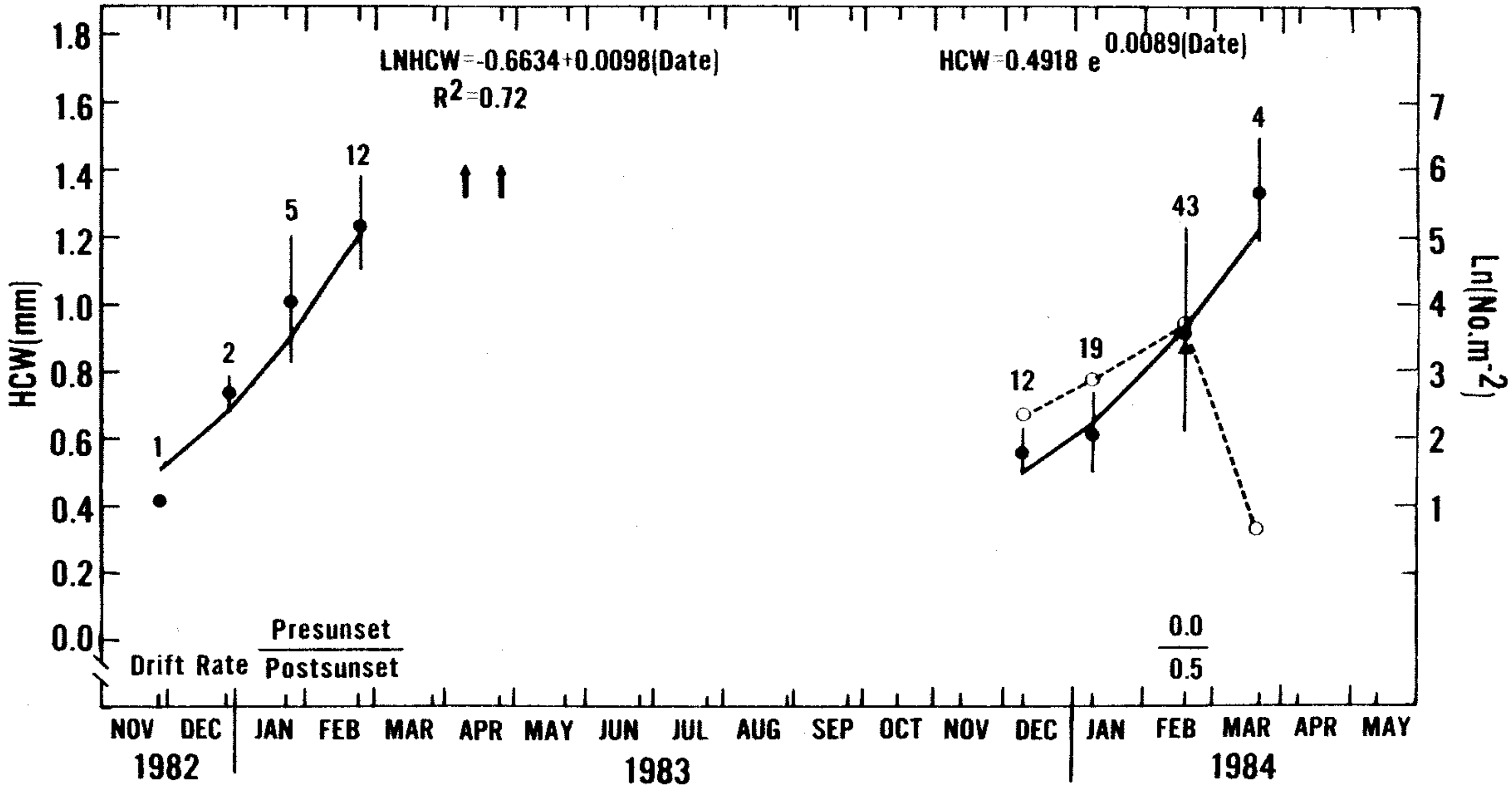

ISOPERLA NAMATA
HCW=0.2663 Date$^{0.2500}$
R^2=0.43
LNHCW=-1.6275+0.0085(Date)
R^2=0.47
HCW(mm)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Ln(No.m^{-2})
7
6
5
4
3
2
1
52
151
248
246
162
114
17
16
617
756
1035
1622
89
53
16
Drift Rate Presunset/Postsunset
0.0/0.4
0.5/0.5
0.0/1.0
0.0/0.6
0.5/1.0
0.1/2.5
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
1982
1983
1984

possible that the relatively slower initial growth of this cohort may be a response to the higher, but less variable temperature regime in Battle Branch in 1984 (Fig. 1). A similar situation exists between cohorts of *P. completa*, which experience the same nymphal thermal history as *I. namata*. Drift of *I. namata* was relatively frequent at different nymph sizes (Fig. 9) and occurred primarily during post-sunset hrs. Emergence occured in April and May, following maximum benthic density in Feb. 1984 (1622/m^2).

Isoperla signata early instars were difficult to separate from the more abundant *I. namata*; however, the growth curve of more mature, identifiable nymphs suggests a univoltine, fast life cycle with a summer egg diapause (Fig. 10). Jop and Szczytko (1984) found a near linear, slow, univoltine life cycle in a Wisconsin population of this species. In Minnesota, Krueger and Cook (1981) found *I. signata* to have an approximate 8 month life cycle in North Branch Creek and 10 or 11 months in the Caribou River. No explanation was offered for this disparity, but it seems resonable that the Caribou River's more northern latitude and cooler mean ambient temperature (4°C vs. 7 C) could prolong nymphal development. Growth in my population was strongly exponential, best modeled by equation 2 (1983) or equation 4 (1984). Growth rates

Fig. 10. *Isoperla signata* growth and drift. ● = $\bar{X}$ head capsule width ± 1 SD, with sample size above ▲ = $\bar{X}$ head capsule width of drifting nymphs, with drift density (No./10 m^3) along lower axis; o = benthic density, (No./0.1 m^2); = adults collected; solid line is predicted growth curve from respective model, indicated along upper axis.

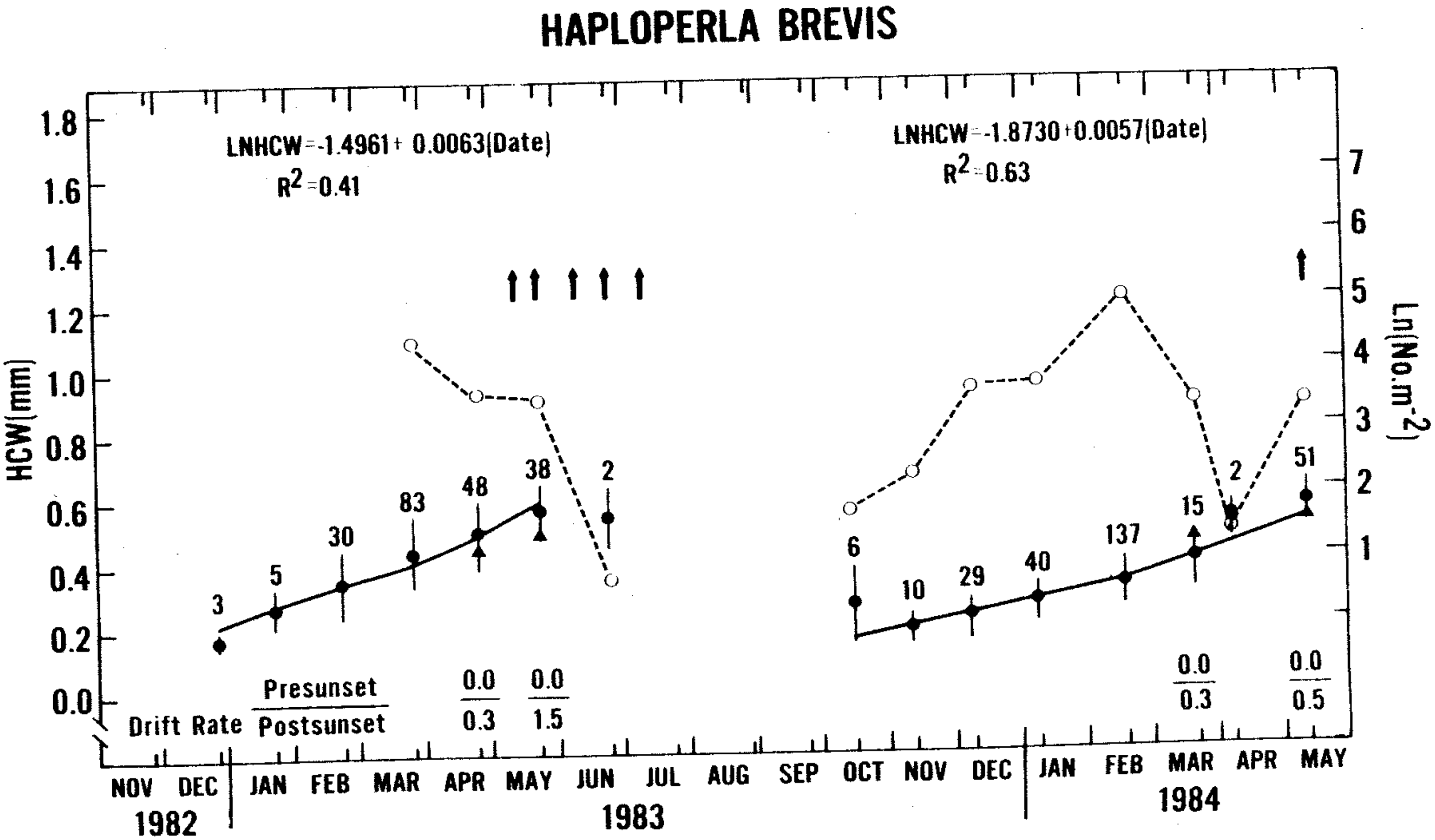
ISOPERLA SIGNATA



were not significantly different (Table 1). The greater growth rate and larger maximum size of *I.signata* may allow for its sympatry with congener, *I. namata*.

Haploperla brevis was the most abundant chloroperlidae in the stream, although 11 *Alloperla caudata* Frison nymphs were collected. The two species could be differentiated in later nymphal instars by *A. caudata* having setae only on the pronotal corners, whereas *H. brevis* have a posterior pronotal setal fringe the two were not separable in early instars. The 1983 and 1984 cohorts of *H. brevis* exhibited univoltine, fast growth with an apparent 2 to 5 month egg diapause (Fig. 11). Harper and Magnin (1969) found a 3 to 4 month diapause in a Montreal, Quebec population. Equation 2 most adequately described the statistically similar ($p=0.2598$, Table 1) growth of both cohorts. Drift density was relatively high (0.5 to 1.5/10 m^3) prior to the May - Jun. emergence and was exclusively post-sunset (Fig. 11). Drift of three other genera of Chloroperlids (1.6 to 2.6/10 m^3) was related to emergence time in the Gunnison River, Colorado by Stewart and Szczytko 1983. All drifting *H. brevis* were within one standard deviation of the benthic population mean HCW. Benthic density was maximal in Feb. 1984, at 137/m^2.

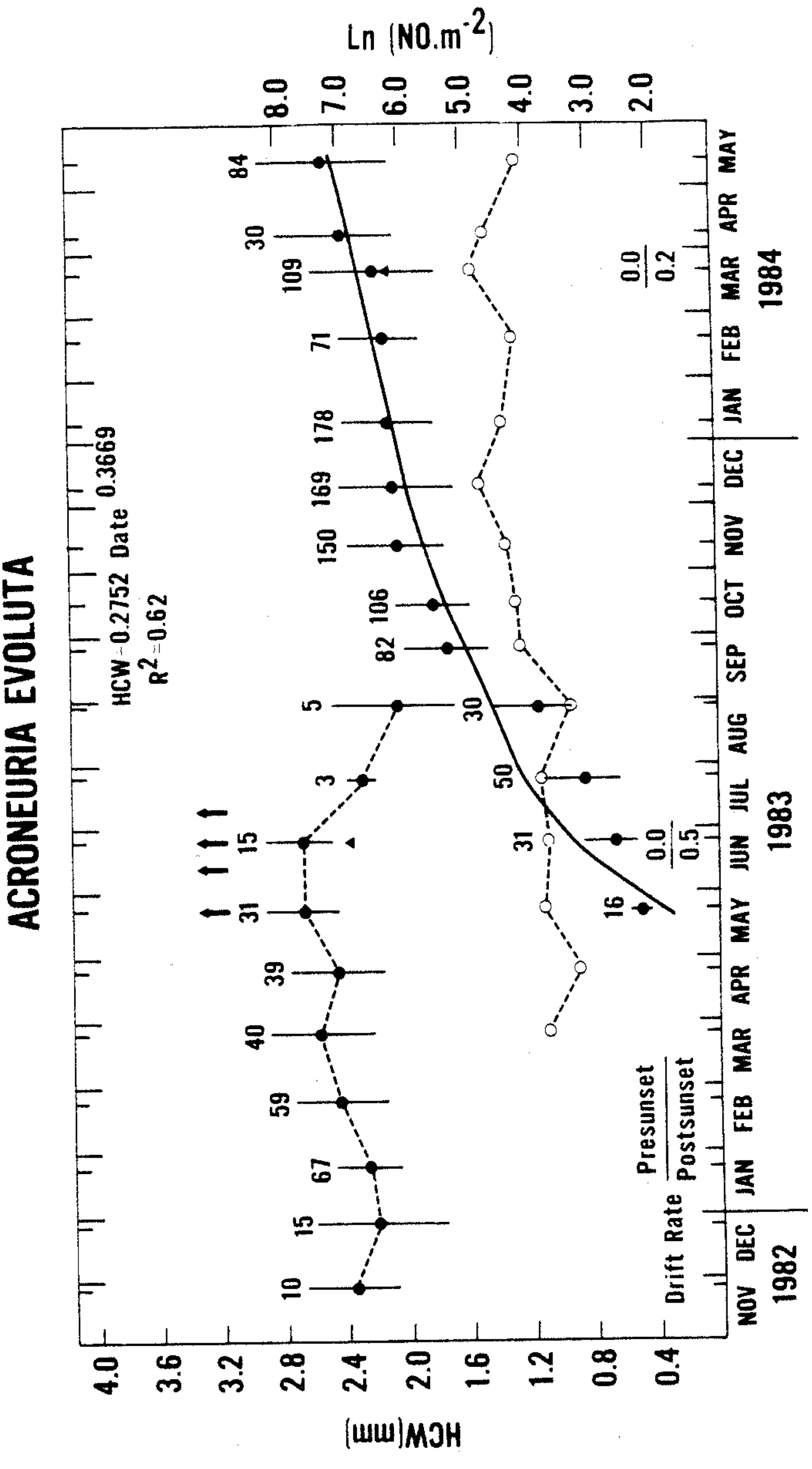
Fig. 11. Haploperla brevis growth and drift. ⧫ = $\overline{X}$ head capsule width ± 1 SD, with sample size above ▲ = $\overline{X}$ head capsule width of drifting nymphs, with drift density (No./10 m^3) along lower axis; o = benthic density, (No./0.1 m^2); = adults collected; solid line is predicted growth curve from respective model, indicated along upper axis.


HAPLOPERLA BREVIS
LNHCW=-1.4961+ 0.0063(Date)
R^2=0.41
LNHCW=-1.8730+0.0057(Date)
R^2=0.63
HCW(mm)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
Ln(No.m^{-2})
7
6
5
4
3
2
1
3
5
30
83
48
38
2
6
10
29
40
137
15
2
51
Drift Rate
Presunset / Postsunset
0.0 / 0.3
0.0 / 1.5
0.0 / 0.3
0.0 / 0.5
NOV
DEC
1982
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
1983
JAN
FEB
MAR
APR
MAY
1984

Acroneuria evoluta exhibited a univoltine, slow life cycle in Battle Branch, that was best modeled over its entirety by a power curve (Fig. 12, Table 1). Members of this genus have primarily been classified as semivoltine (Frison 1935, Hitchcock 1974). However, the accelerated nymphal development in Battle Branch relative to more northern populations of *A. delosa*, *P.completa*, *L. tenuis* (Harper 1973a), *H. brevis* (Harper and Magnin 1969) and *I. signata* (Jop and Szczytko 1984) may explain the univoltinism I found for *A. evoluta*. Emergence occurred in late May and Jun. when 311 adults were collected. Oviposition occurred during the evening and eggs apparently hatch within a month. Nymphs exhibit exponential growth through summer, with a marked reduction in growth rate during winter months. Sexual dimorphism probably accounted for the great variation in HCW, but sexing was not possible except for large female nymphs having a "V" notch on the posterior margin of the eight sternite. Only 3 mature nymphs were found in drift samples, all coming from post-sunset samples in Jun. 1983 and Mar. 1984 (Fig. 12). Benthic density was constant throughout the study period with a maximum of 124/m^2 in Mar. 1984.

Agnetina capitata was the only stonefly in Battle Branch to exhibit an apparent semivoltine life cycle. Modeling of growth was not attempted due to difficulty

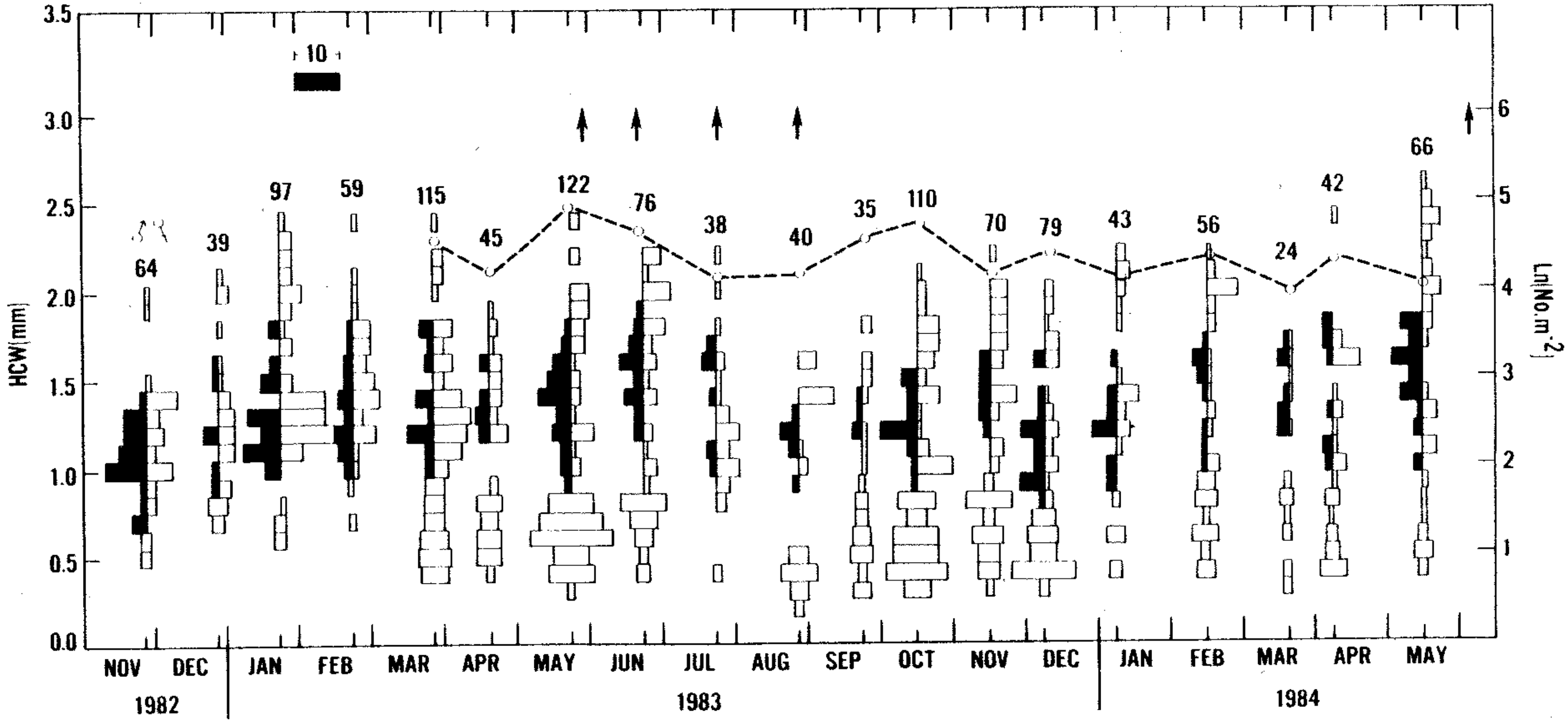
Fig. 12. *Acroneuria evoluta* growth and drift. ⧫ = $\bar{X}$ head capsule width $\pm$ 1 SD, with sample size above ▲ = $\bar{X}$ head capsule width of drifting nymphs, with drift density (No./10 m^3) along lower axis; o = benthic density, (No./0.1 m^2);   = adults collected; solid line is predicted growth curve from respective model, indicated along upper axis.


ACRONEURIA EVOLUTA
HCW=0.2752 Date 0.3669
R2=0.62
Ln (NO.m-2)
8.0
7.0
6.0
5.0
4.0
3.0
2.0
HCW(mm)
4.0
3.6
3.2
2.8
2.4
2.0
1.6
1.2
0.8
0.4
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
1982
1983
1984
Drift Rate Presunset/Postsunset
0.0/0.5
0.0/0.2
10
15
67
59
40
39
31
15
3
5
16
31
50
30
82
106
150
169
178
71
109
30
84

in separating the generations. This species has marked sexual dimorphism and a great deal of intrinsic variation in size (Fig. 13). Harper (1973b) found similar results in southern Ontario for *A. capitata* and concluded that size variability would be advantageous in niche partitioning for this relatively long lived predator. A similar hypothesis may explain the variation seen in *A. evoluta*, a morphologically and trophically similar species. However, the possibility also arises that some members of *A. capitata* exhibit different life cycles than others; possibly eggs that hatch immediately require one year for full development and those that are delayed require two years. Temperature acclimation suggests semivoltinism for Battle Branch *A. capitata* (Ernst et al. 1984); however laboratory rearing is needed to fully clarify the life cycle. Emergence was extended (May - Aug.), and monthly benthic densities were very uniform (Fig. 13), analogous to *A. evoluta*. Resource partitioning studies between *A. capitata* and *A. evoluta* are needed since both are in high densities throughout the year. No *A. capitata* were found in drift samples.

General Discussion: Although the applied models describe the observed data fairly well (Figs. 5 to 12), and are statistically significant, low R^2 values imply that much of the variation in HCW is not accounted for

Fig. 13. *Agnetina capitata* growth and drift. Size frequency histogram of monthly collections. ↑ = adults collected, o = $\bar{X}$ benthic density.


HCW(mm)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Ln(No.m^{-2})
6
5
4
3
2
1
10
64
39
97
59
115
45
122
76
38
40
35
110
70
79
43
56
24
42
66
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
1982
1983
1984

by date (time). This seems reasonable, given the influence on growth by temperature (Vannote and Sweeney 1980, Humpesch 1979, 1980, Brittain 1983, Markaria 1980, Heiman and Knight 1975, Sweeney 1978), food (Brittain 1973), and competition (Snellen and Stewart 1979). Concurrent measurements of these additional variables may provide better models of growth, but the intrinsic variation within stonefly populations may be best accounted for by its ecological importance in intraspecific resource partitioning. Utilizing only the mean HCW within these models, R^2 increases dramatically (compare to Table 1: I. namata, equation 2, 1984, $R^2 = 0.99$; L.tenuis, equation 2, 1983, $R^2 = 0.96$; A. delosa equation 2, 1983, $R^2 = 0.98$), indicating the adequacy of the models for mean data, and the variation in HCW on each sampling date responsible for the error within the models.

Humpesch (1979) found mayfly growth (body length) to be linear on semilog paper under laboratory conditions. In this and subsequent studies on mayflies and stoneflies (Humpesch 1980, Brittain 1983) growth was plotted on semilog paper, with linear sections modeled via equation 4. This equation has been extensively applied to fish growth data; however, it is generally applicable only to short time intervals (Everhart et al. 1975). I found equation 4 to conform to classic, exponential, "J" shaped growth curves (e.g. I. signata), but due to assignment of an initial constant HCW the model did not demonstrate flexibility to approximate growth deviating from the classic shape or growth during the entire nymphal developmental period. Utilization of body length rather than HCW should yield similar growth coefficients due to their linear relationship (Finne 1977, Brittain 1973, Jop and Szczytko 1984), although length is probably a less reliable measurement due to the telescopic nature of the abdomen (Vaught and Stewart 1974). Equation 5, in which the computer iteratively estimated initial HCW within the measured range, was generally more representative of entire observed nymphal growth periods (compare Error SS, Table 1). Also the difficulty in measuring, collecting and identifying early instars makes reliance on their measurement as a constant (equation 4) less appealing than estimating it in conjuction with later instar measurements (equation 5). Equation 2, yielded growth rates comparable to equation 5 (Table 1) and accounted for heteroscedasticity found in some populations (H. brevis, A. delosa).

For comparative purposes equation 2, the best model in 9 of 15 populations, was applied to all species (Table 1). The resulting regression coefficients corroborate the Hynes' descriptive scheme of categorizing time spent in the nymphal stage (Hynes 1961,1970), by quantifying the rate of growth during this period. The univoltine, slow cycle of *A. evoluta* exhibited the lowest growth rate (0.0017); *I. namata*, *H. brevis* and *L. tenuis* fast cycles had moderate growth rates (0.0045 to 0.0085), and *I. signata*, *A. delosa*, *P.completa* and *A. rickeri* fast cycles had the highest growth rates (0.0074 to 0.0173, Table 1). However, I emphasize that equation 2 is not the most appropriate model for some of these species; this approach was used for comparison rather than description or predictive purposes.

Knowledge of the limitations and applications of these models also provides a tool to quantify growth with reduced sampling intensity. A sampling regime designed to establish the shape of the growth curve, rather than typical monthly growth increments, would assist in the selection of an appropriate model to describe and compare nymphal growth.

Drift of Plecoptera was low in comparison to other insect orders in Battle Branch. Presunset samples revealed the following descending order for drift density: Diptera > Ephemeroptera > Tricoptera = Plecoptera, while post-sunset samples were structured differently with, Ephemeroptera > Diptera > Plecoptera

= Tricoptera (SNK, $p<0.05$). Although stonefly drift was low, there was a marked periodicity, with significantly more nymphs collected in post-sunset samples (Wilcoxon Rank Sum, $p=0.0018$). Organic matter, which can be thought of as passive drift control, showed no difference in amount (gms dry wt.) drifting before and after sunset (Wilcoxon Rank Sum, $p=0.8049$). It seems plausible that Plecoptera exhibit active drift, with post-sunset drift an adaptation to avoid predation by sight feeding fish (Griffith 1974, Cordes and Page 1980, Surat et al. 1980, Matthews et al. 1982). The nocturnal feeding habits and assumed increase in activity of less adept clingers may make them more susceptible to passive drift at this time (Chaston 1968, Elliot 1967b, Stewart and Szczytko 1983). I found the less adept clingers _A_. _delosa_ and _P_. _completa_ more commonly in the drift than strong clinging Perlidae, _A_. _evoluta_ and _A_. _capitata_.

Correlations of the number of Plecoptera in post-sunset drift and current velocity ($r=0.4385$, $p=0.0107$), organic matter ($r=0.4478$, $p=0.0090$) and benthic density ($r=0.0896$, $p=0.6199$) suggested a multivariate model might account for much of the variability in drift numbers. Collinearity between current velocity and organic matter ($r=0.9557$, $p=0.0001$) precludes their mutual use, thus retaining current velocity:

No. Plecoptera in drift= -4.4927 + 0.0061 (No./m)+
0.0391 (current velocity)

Where, No/m is species specific and current velocity equals (cm/sec)/0.4714. n=33, p=0.0107.

The resulting R^2 (0.25), suggests that a linear model incorporating benthic density and current velocity accounts for only 25% of the variability found in stonefly drift numbers. It seems reasonable to conclude that the remaining 75% of variability resides in life cycle stage, predator-prey interaction, density dependent relationships or other active mechanisms that do not necessarily conform to a linear model. In Battle Branch stonefly drift propensity was skewed toward relatively mature, pre-emergent nymphs and was associated with a decrease in mean benthic density (Figs. 2, 4, 5, 6, 8). These data support previous studies reporting stonefly drift as an active mechanism for dispersion (Elliot 1967a, stewart and Szczytko 1983).

CHAPTER IV

MICRODISTRIBUTION

Introduction

The benthic microdistribution of lotic insects has received much attention, since most species are not randomly distributed (Egglishaw 1969, Peterson and Cummins 1974, Elliot 1977, Minshall and Minshall 1977, Resh 1979). Several variables and their interactions have been studied in lotic ecosystems to determine their effect on insect distribution, such as: current (Malas and Wallace 1977, Minshall and Minshall 1977, Rabeni and Minshall 1977), mineral substratum size (Cummins and Lauff 1969, Brusven and Prather 1974, deMarch 1976, Minshall and Minshall 1977, Rabeni and Minshall 1977, Reice 1980), macrophytes (Barber and Kevern 1973), biotic interactions (Peckarsky and Dodson 1980a, b, Peckarsky 1983, 1984) and organic matter (Egglishaw 1964, 1968, 1969, Rabeni and Minshall 1977, Finni and Chandler 1979, Peckarsky 1980, Reice 1981). Minshall (1984) and Williams (1981) review much of the literature on insect microdistribution.

Minshall and Minshall (1977) found the distribution of various insects to be a result of an interaction between current, substratum, and detritus. In a subsequent study, Rabeni and Minshall (1977), found substratum size dictates the amount and kind of detritus retained, concluding that insect colonization was a response to the type of organic matter present. Egglishaw (1964, 1968) and Reice (1977) also demonstrated close associations of certain species with benthic organic matter. Peckarsky (1980) found only "shredder" distribution to be adequately described by the addition of leaf material to cages placed within the substratum.

Ozark streams have not been studied relative to the generally known importance of allochthonous material as food and habitat for insects in low order, woodland streams (Cummins 1974, Anderson and Sedell 1979, Bird and Kaushik 1981). Therefore, given that my second-order Ozark stream riffle, 1) receives a large autumnal pulse of allochthonous material, 2) has a long organic matter retention time and 3) has a relatively homogeneous current and substratum, I selected benthic organic matter as the major variable to test the microdistribution of 8 stonefly species. Hence, this study essentially follows the design of Egglishaw (1964, 1968, 1969), in an effort to examine if organic matter is correlated to either stonefly density or biomass distribution. My design differs from

Egglishaw's by using the dry weight of organic matter in two standardized size fractions, course particulate organic matter (CPOM, >1.18 mm) and fine particulate organic matter (FPOM, 153 um to 1.18 mm). This size fractionation is similar to those reported by Vannote et al. (1980), Bird and Kaushik (1981) and Minshall et al. (1983), and provides a more discriminate measure of specific associations of Plecoptera with organic matter.

Materials and Methods

Sampling was conducted monthly for one year (Mar. 1983 to Feb. 1984) in Battle Branch, a 3.9 Km springfed, unregulated, 2nd order stream in the Illinois River drainage of Delaware County, Oklahoma. Ten Surber samples (area 0.1 m^2, mesh 153 um) were taken monthly on a 20 X 3 m riffle. Riffle substratum was a homogeneous mixture of gravel and pebbles and a few cobbles (after Cummins 1962). A spectrum of organic matter was assured by biasing the 10 samples each month to a visual gradient of leaf pack surface area, roughly corresponding to 0, 25, 50, 75 and 100% of the area enclosed by the Surber. All organic matter and insects collected in the samples were preserved in 70% isopropanol and processed within 10 days.

Sample processing included: 1) Initial washing of large leaves or fragments with tap water over a 150 um (No.100) U.S.A. Standard testing sieve; 2) Microscopic sorting of all animals from remaining organic/inorganic matter under 6X; 3) Separating the organic fraction by decantations (ca. 5 times) over stacked 1.18 mm (No. 16) and 150 um sieves. All organic material retained by the 1.18 mm sieve minus sticks > 2 cm in length, was added to initial sorted organic material and considered CPOM. The fraction retained by the 150 um seive was considered FPOM; 4) CPOM was oven dried to a constant weight (24-48 hrs) at ca. 50°C in preweighted aluminum pans, 5) FPOM was washed from the sieve into a 200 mL beaker and water added for further decantations to separate out fine sand particles. It was filtered through pre-wetted, dried and weighed No.1 Whatman filter papers, allowed to vacuum drain and then dried for ca. 24 hrs. at 50°C before reweighing. Weights were taken to the nearest 0.1 mg on a Mettler electric balance. Possible weight loss due to the short preservation was not estimated. 6) Stoneflies from each sample were enumerated, and interocular width (HCW) measured with an ocular micrometer to the nearest 0.04 mm. Biomass as dry weight was calculated from dry weight vs. HCW regressions from a concurrent production study (K. Jop, personal communication) and summed for each Surber. Weights of Leuctra tenuis and Haploperla *brevis* were calculated from a regression established for *Allocapnia rickeri*, as these three species are of similar size and shape.

Distributions of nymphs were tested monthly and over their growth cycles for agreement with a Poisson series (random distribution) via the variance to mean ratio (Elliot 1977). Significant chi-square values for $n < 30$ were drawn from Table D.8 of Zar (1974). Sample sizes greater than 30 were checked for deviation from the Poisson series with the d statistic (Elliot 1977). Spearman Rank correlations (r_s) of density and biomass with CPOM or FPOM were preformed using a Statistical Analysis System (SAS) on an AS/8040 computer. Statistical significance constituted an alpha level $\leq$ 0.05, but consistency in signs of nonsignificant r_s were used to suggest trends, since relatively small sample sizes ($n=10$ monthly) can obscure biologically important results. Correlations of HCW and CPOM or FPOM were done on each species monthly and over their entire growth cycle. Diversity was measured as number of taxa (species level), except for inseparable congeners *Neoperla* spp. and *Zealeuctra* spp. Correlations were not done for individual species when nymphs were found in < 5 of the 10 monthly samples.

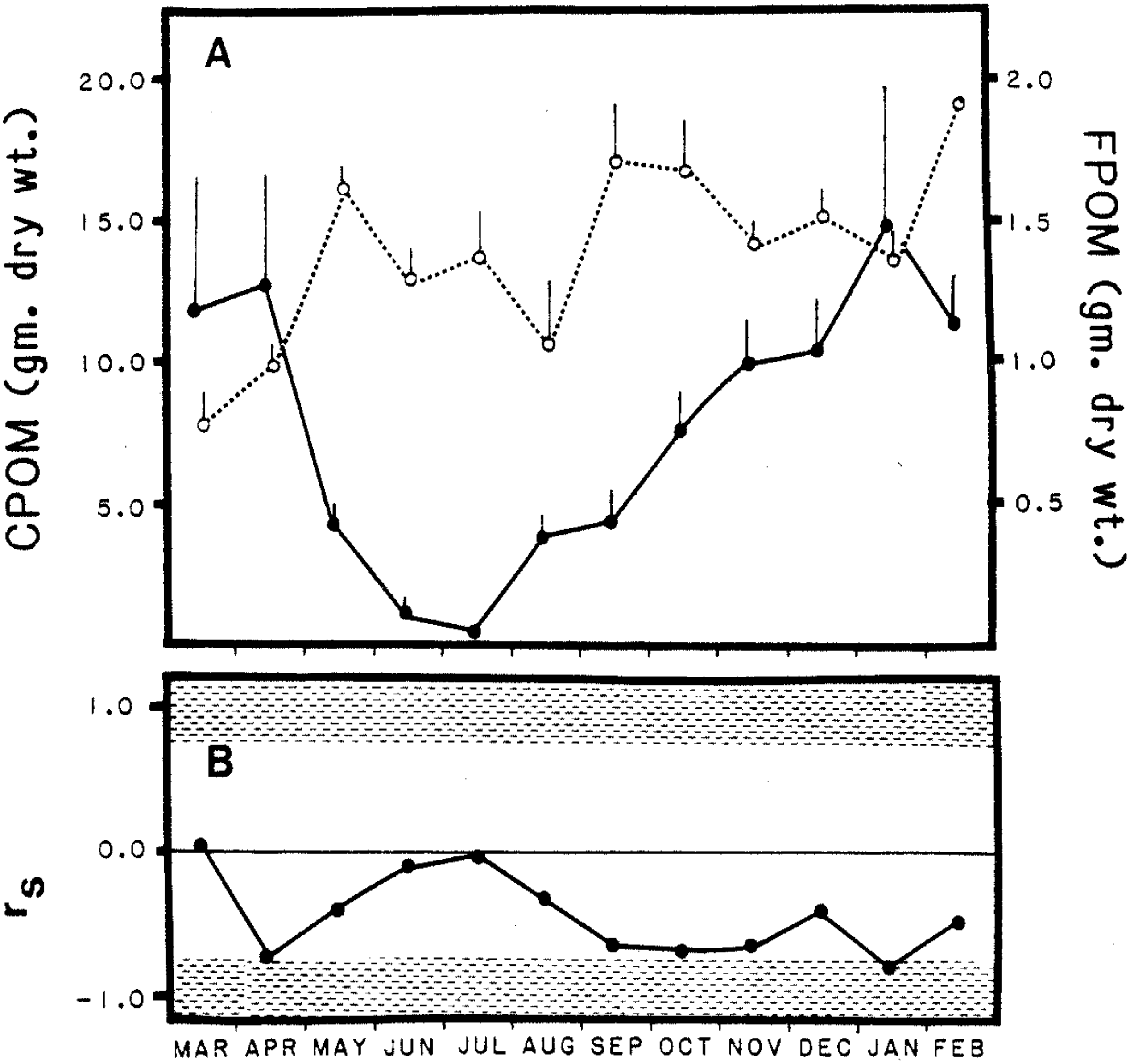
Results and Discussion

Organic Matter

Water and air temperature in Battle Branch ranged from 7.5 to 27.0°C and -11 to 40°C respectively. Discharge averaged (± 1 SD) 0.24 ± 0.23 m^3/ sec , with a maximum of 0.99 m^3/sec in spring. The watershed is heavily wooded, resulting in a large autumnal pulse of sycamore (*Platanus occidentalis*), oak (*Quercus* spp.), maple (*Acer* spp.) and dogwood (*Cornus* spp.) leaves being deposited in the stream.

Leaf input into Battle Branch began in late Aug. (Fig. 14), similar to that modeled by Boling et al. (1975). This continued throughout fall, winter and into early spring due to infrequent snow cover retaining leaves on the ground and rains or gusty winds that washed or blew leaves downslope or laterally into the stream. Observable CPOM was present during 10 months, excluding only Jun. and Jul. Relative composition of leaves in samples was not quantified, but sycamore appeared to be most abundant during fall, yielding to oak during winter and spring. Sampling an observable CPOM continuum resulted in deliberate contagious distributions ($p < 0.05$) among Surber samples for all months except Jun. and Jul., which were low in CPOM. FPOM was regularly distributed ($p < 0.05$) for all

Fig. 14. A. Mean monthly CPOM (solid dot and line) and FPOM ($\pm$ 1 SE) in Surber samples (n=10), Battle Branch, Oklahoma, Mar. 1983 - Feb 1984. B. Monthly Spearman rank coefficients (r_s) for CPOM vs. FPOM in Surber samples. Shaded area indicates $p<0.05$.


A
CPOM (gm. dry wt.)
20.0
15.0
10.0
5.0
FPOM (gm. dry wt.)
2.0
1.5
1.0
0.5
B
r_s
1.0
0.0
-1.0
MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB

months, except for a random distribution in Aug.

Rabeni and Minshall (1977) reported a relationship between the retention of detritus and the size of mineral substratum; large particle detritus (>3.95 mm) was associated with large substratum (4.5 x 7.0 cm), and small particle detritus (<3.95 mm) with small sized substratum (1.0 to 3.5 cm). The regular distribution of FPOM between Surber samples in Battle Branch reflected the uniformity of substratum size and associated interstitial retention space. However, CPOM, in the form of leaf packs, was usually entrained by a single cobble protuding from the bottom.

Table 2 shows monthly mean benthic densities and mean densities over the entire nymphal growth period for the 8 species and all species combined and indicates whether nymphal distributions are contagious (clumped) or random. Figs. 15 - 22 show correlations of stonefly density and biomass with CPOM and FPOM. Negative coefficients at given months indicate a trend toward inverse relationships of density or biomass with organic matter. Positive coefficients indicate a trend toward positive relationships of density or biomass with organic matter. Statistically significant relationships are indicated by coefficients in the shaded zones of the figures.

Table II. Monthly and Entire Nymph Growth Period $\overline{X}$ ($\pm$ 1 SD) Surber densities (No./0.1 m^2) for Battle Branch, Delaware Co., Oklahoma. 1983-1984. c = contagious distribution, ($p<0.05$); r = random distribution, ($p>0.05$) of nymphs among Surber samples. Monthly n=10.

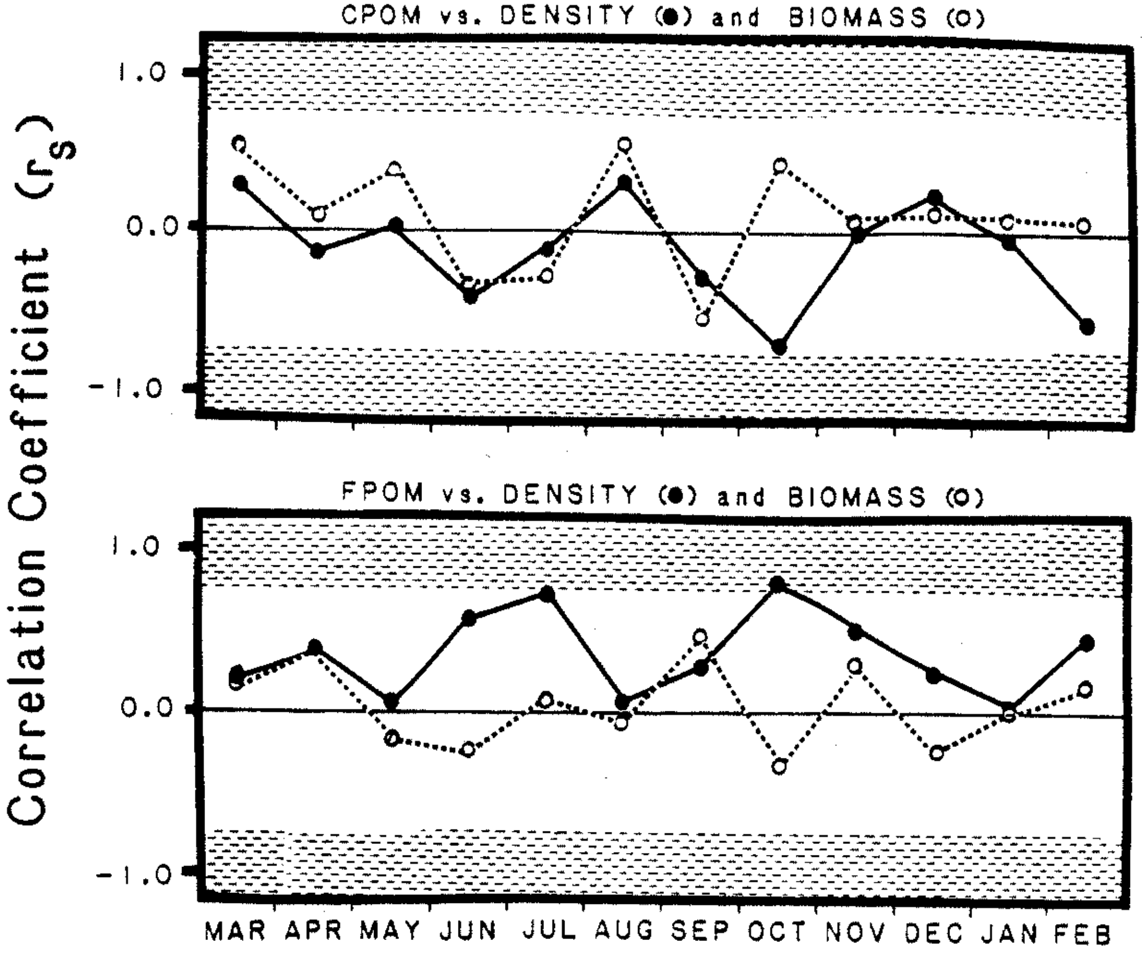
Period	*Agnetina capitata*	*Acroneuria evoluta*	*Neoperla* spp.	*Haploperla brevis*	*Isoperla namata*	*Amphinemura delosa*	*Prostoia completa*	*Leuctra tenuis*	All Species Combined
Entire Nymph Growth Cycle	9.8 ± 6.8^c	6.4 ± 4.9^c	8.5 ± 9.1^c	6.3 ± 7.0^c	61.4 ± 68.9^c	87.3 ± 200.3^c	54.13 ± 49.2^c	11.1 ± 11.1^c	112.8 ± 150.0^c
MAR	11.1 ± 6.0^c	4.1 ± 2.8^r	3.7 ± 5.6^c	8.5 ± 8.9^c	16.3 ± 15.0^c	236.8 ± 349.9^c		9.2 ± 8.1^c	290.0 ± 364.0^c
APR	7.7 ± 4.3^c	2.8 ± 1.5^r	4.2 ± 6.4^c	4.3 ± 5.1^c	8.7 ± 8.2^c	93.3 ± 113.7^c		13.3 ± 13.6^c	134.4 ± 109.7^c
MAY	18.5 ± 9.5^c	4.6 ± 3.3^c	5.9 ± 5.3^c	3.6 ± 2.6^r		11.6 ± 14.6^c		22.3 ± 11.0^c	68.5 ± 22.6^c
JUN	11.9 ± 7.7^c	4.6 ± 3.3^c	10.2 ± 11.8^c					14.0 ± 9.0^c	40.9 ± 20.8^c
JUL	6.4 ± 3.8^c	4.5 ± 2.8^r	11.2 ± 10.2^c					6.4 ± 7.6^c	28.5 ± 15.1^c
AUG	7.5 ± 3.7^r	3.3 ± 2.5^c	3.9 ± 3.7^c						15.7 ± 3.9^r
SEP	9.9 ± 7.6^c	6.5 ± 6.3^c	7.6 ± 8.8^c					0.8 ± 0.8^r	25.2 ± 14.2^c
OCT	13.9 ± 6.4^c	7.1 ± 4.6^c	12.1 ± 13.4^c		1.6 ± 1.7^r				37.4 ± 16.1^c
NOV	7.2 ± 3.2^r	10.6 ± 3.6^r	10.2 ± 9.8^c		61.7 ± 52.7^c				92.0 ± 49.7^c
DEC	9.2 ± 8.2^c	12.0 ± 6.3^c	7.6 ± 6.0^c	3.3 ± 3.9^c	75.6 ± 48.50^c		13.2 ± 12.0^c		122.6 ± 68.8^c
JAN	5.6 ± 4.9^c	9.3 ± 5.5^c	12.4 ± 8.6^c	4.3 ± 3.6^c	103.5 ± 65.18^c		43.3 ± 28.4^c		180.2 ± 85.5^c
FEB	8.5 ± 4.1^c	7.2 ± 4.8^c	13.2 ± 11.2^c	13.7 ± 9.3^c	162.2 ± 63.0^c	7.7 ± 7.0^c	105.9 ± 43.4^c		318.4 ± 87.5^c

Predators

Agnetina capitata (Pictet).- exhibited a probable semivoltine life cycle with an extended summer emergence in Battle Branch. Extended recruitment, strong sexual dimorphism and possibly differential growth rates resulted in great size overlap of nymphs in most months and consequently inseparable cohorts. Nymphs were present in 115 of 120 Surber samples in primarily contagious distributions (10 of 12 months, Table 2). Density, and therefore microdistribution, was positively related ($p<0.05$) to FPOM during Jul. and Oct., and the trend was similar but not significant over the remaining months (Fig. 15). A generally opposite association existed between this species and CPOM over the study. Therefore, *A. capitata* microdistribution is not strongly related to CPOM, but rather to open riffle substrate infiltrated with FPOM. There was a significant relationship between density and FPOM ($r_s=0.2516$, $p<0.05$) when all months were combined (n=120). Biomass was slightly more related to CPOM than FPOM based on 8 of 12 positive monthly coefficients (Fig. 15). HCW was generally positively related to CPOM and negatively related to FPOM.

Acroneuria evoluta Klapalek.- had a univoltine, slow life cycle in Battle Branch, with emergence in

Fig. 15. Monthly Spearman rank coefficients for *Agnetina capitata*. Shaded area indicates $p < 0.05$.


CPOM vs. DENSITY (●) and BIOMASS (○)
FPOM vs. DENSITY (●) and BIOMASS (○)
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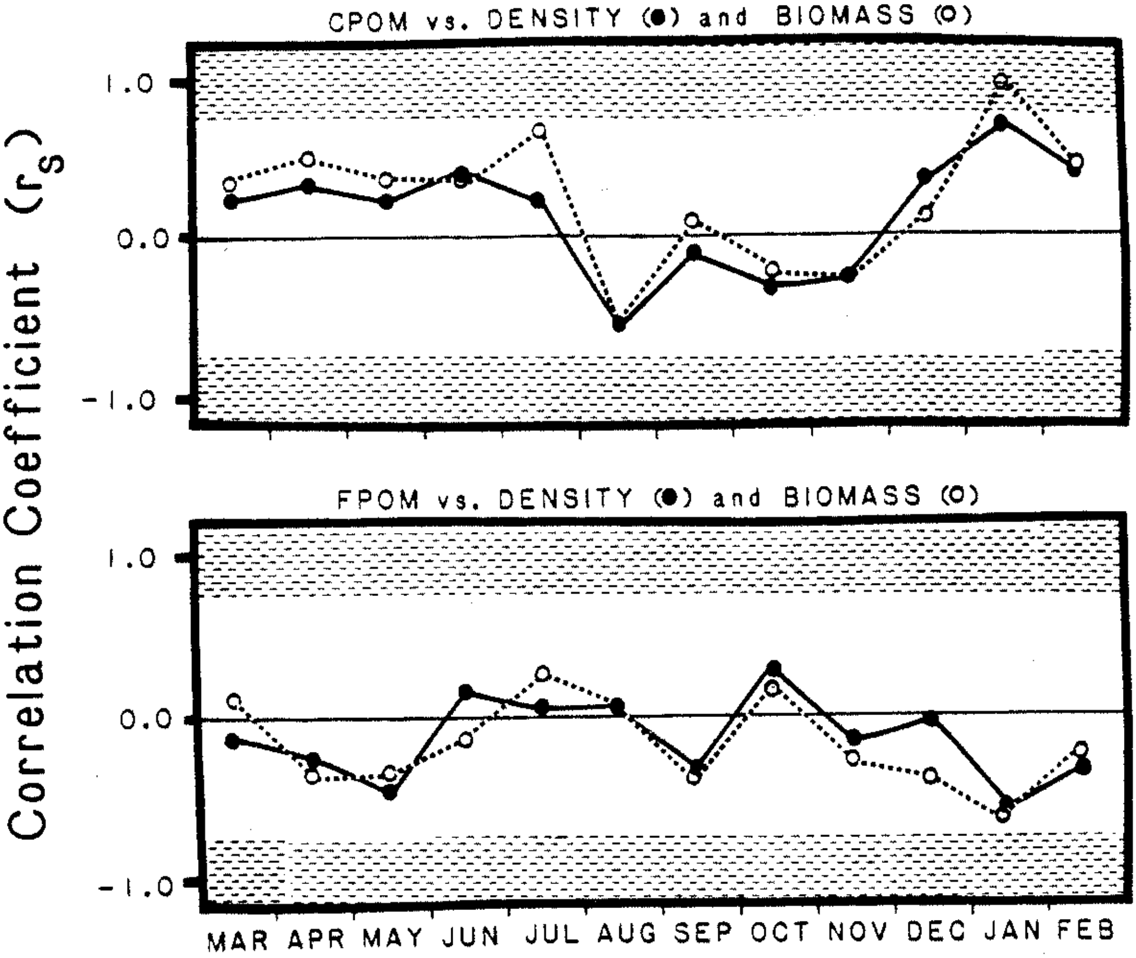
late spring. Like A. capitata, this species was common throughout the sampling period, being found in 115 of 120 samples. Nymphs generally demonstrated a contagious distribution ($P<0.05$) among monthly samples, but to a lesser degree than any other species studied (Table 2). Random distributions ($p>0.05$) in Mar., Apr., Jul. and Nov. suggest possible territoriality for this large predator. Peckarsky (1980a) found Acroneuria lycorias (Newman) presence to significantly reduce other invertebrate predator colonization of experimental cages. Density ($r_s=0.2807$, $p<0.05$) and biomass ($r_s=0.5631$, $p<0.05$) were correlated to CPOM annually. Monthly coefficients indicate a positive trend between density (8 of 12) and biomass (10 of 12) with CPOM (leaf packs), with nymphs showing greatest association during winter and spring (Fig. 16). Negative relationships during Sep., Oct. and Nov. may have resulted from insufficient CPOM conditioning time and prey colonization. Leaf conditioning has consistently been found to positively influence insect colonization (Cummins et al. 1973, Hynes et al. 1974, Iversen and Madsen 1977, Cowan et al. 1983). HCW of A. evoluta, as A. capitata, was positively correlated with CPOM annually ($r_s=0.4022$, $p<0.05$) and for 4 months, while negatively correlated with FPOM annually ($r_s=-0.0952$) and for 3 months.

Fig. 16. Monthly Spearman rank coefficients for *Acroneuria evoluta*. Shaded area indicates $p<0.05$.


CPOM vs. DENSITY (●) and BIOMASS (○)
FPOM vs. DENSITY (●) and BIOMASS (○)
Correlation Coefficient (r_s)
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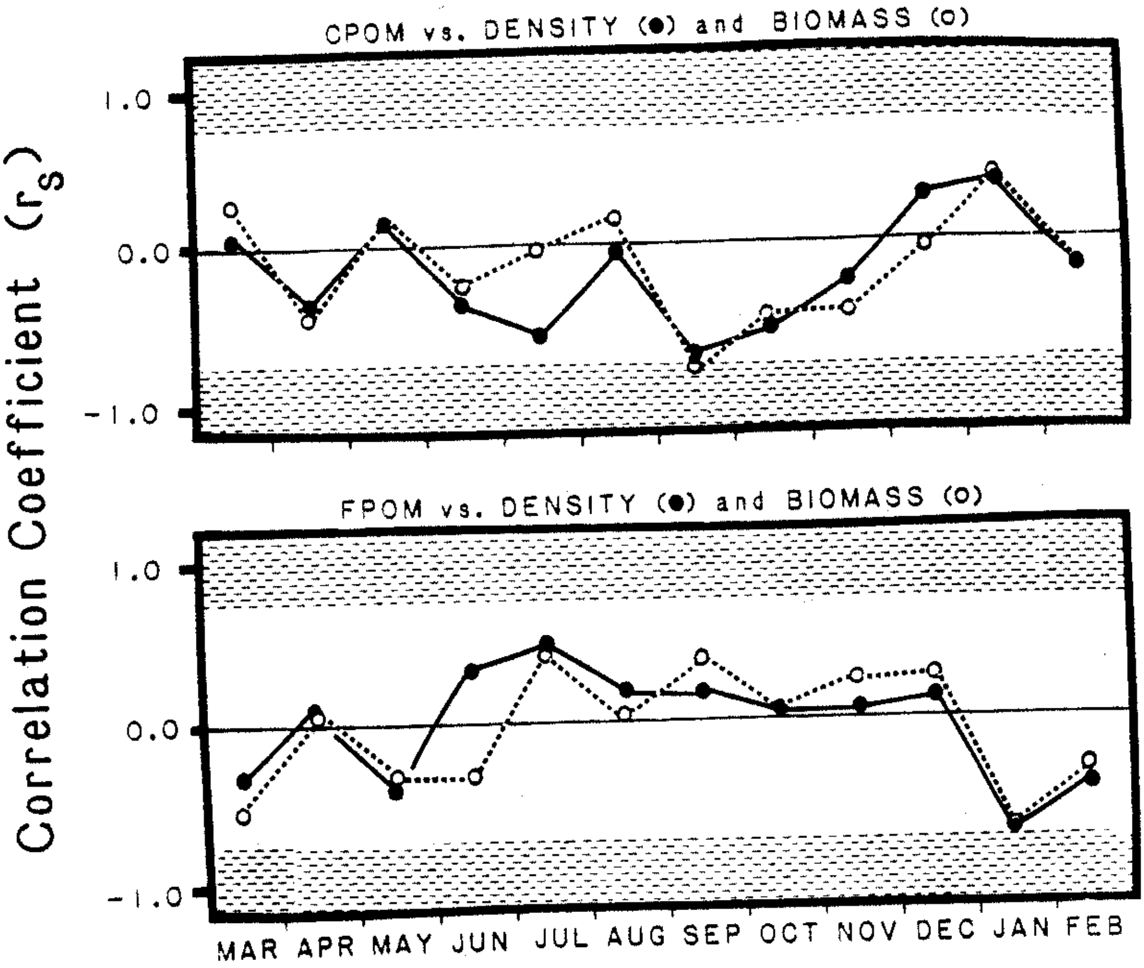
Neoperla spp. complex.- of Battle Branch was made up of 4 species based on adult collections (M. Ernst, B. Poulton and K. Stewart, unpublished data). Nymphs are presently inseparable, necessitating their association with organic matter as a group of congeners. I realize this could obscure possible species-specific associations or microdistributions in relation to organic matter. Nymphs were found in 108 of 120 samples in significantly contagious distributions ($P<0.05$) for all months (Table 2). Density displayed a negative trend with CPOM for 8 months (Fig. 17) and combined months for the entire sampling period. Density and FPOM neared significance ($r_s=0.1749$, $p<0.10$) annually and suggested a positive trend for 8 of 12 months indicating a probable distribution primarily in open gravel. Biomass closely tracked density (Fig. 17). HCW was related to CPOM annually ($r_s=0.2873$, $p<0.001$) and during Apr. and Jul.

Combined predators had an annual mean Surber density ($\pm$ 1 SD) of 24.68 + 13 in contagious ($p<0.05$) distributions for all months except Apr. and Aug. Density was significantly related to FPOM ($r_s=0.2740$, $p<0.05$) annually and during Jun ($r_s=0.6364$, $p<0.05$). Coefficients for density and FPOM were positive for 8 of the remaining 11 months. Density was negatively related to CPOM during Apr. ($r_s=-0.8842$, $p<0.001$) and

Fig. 17. Monthly Spearman rank coefficients for Neoperla spp. Shaded area indicates $p<0.05$.


CPOM vs. DENSITY (●) and BIOMASS (○)
FPOM vs. DENSITY (●) and BIOMASS (○)
Correlation Coefficient (r_s)
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Oct (r_s=-0.7679, $p<0.05$), and demonstrated a negative trend for 40% of the remaining months. Biomass was related to CPOM annually (r_s=0.5043, $p<0.001$) and during Jan (r_s=0.9030, $p<0.001$), with a positive trend for 9 of the remaining 11 months.

Since density is largely biased by numerous early instars and biomass by the relatively fewer larger instars, the positive relationships between density and FPOM and biomass and CPOM suggest possible ontogenetic shifts in habitat preference (Lehmkuhl and Anderson 1972, Jop and Szczytko 1984). Similarly and presumably associated ontogenetic shifts in food habits have also been observed (Sheldon 1979, Fuller and Stewart 1977, Feminella 1983). Feminella (1983) reported detritivorous feeding habits for *Acroneuria* spp., *Agnetina capitata* and *Neoperla* spp. among early instars, prior to carnivory. These early life history feeding habits may be responsible for the positive associations of density with FPOM in predominately open riffle, mineral substrates. Positive relations between HCW and biomass with CPOM suggest the larger nymphs may seek abundant prey associated with CPOM, particularly Chironomidae. Brusven and Prather (1974) demonstrated in laboratory experiments that a single cobble upon sand or pebble substrate enhanced substratum preference for *Pteronarcys californica* Newport and *Ephemerella* *grandis* Eaton. They concluded that unimpacted cobbles enhance colonization by large species incapable of occupying small interstices and/or having a behavior of hiding under cobbles. With respect to these findings and the observed association between CPOM and a retaining cobble in Battle Branch, *A*. *evoluta* and other large stonefly predators may prefer the heterogeneity of cobble-gravel-CPOM.

Peckarsky (1983,1984) suggested biological interactions influence distribution. In Battle Branch, densities of *A*. *capitata* and *Neoperla* spp. were generally associated with FPOM, while *A*. *evoluta* was more associated with CPOM. It is possible that this inverse association may have resulted from interactions representing an emergent property of this assemblage and/or possible microhabitat preference of these species. Qualitative sampling of other Ozark streams suggests that *A*. *evoluta* is not a common inhabitor of leaf packs unless *A*. *capitata* is abundant in the gravel. Active interspecific avoidance between perlodid predators *Magarcys* *signata* (Hagen) and *Kogotus* *modestus* (Banks) suggest a possible mechanism for observed habitat segregation (Peckarsky 1983). Sheldon (1979) found that two large predaceous stoneflies, *Calineuria* *californica* (Banks) and *Hesperoperla* *pacifica* (Banks), to partition their habitat in a

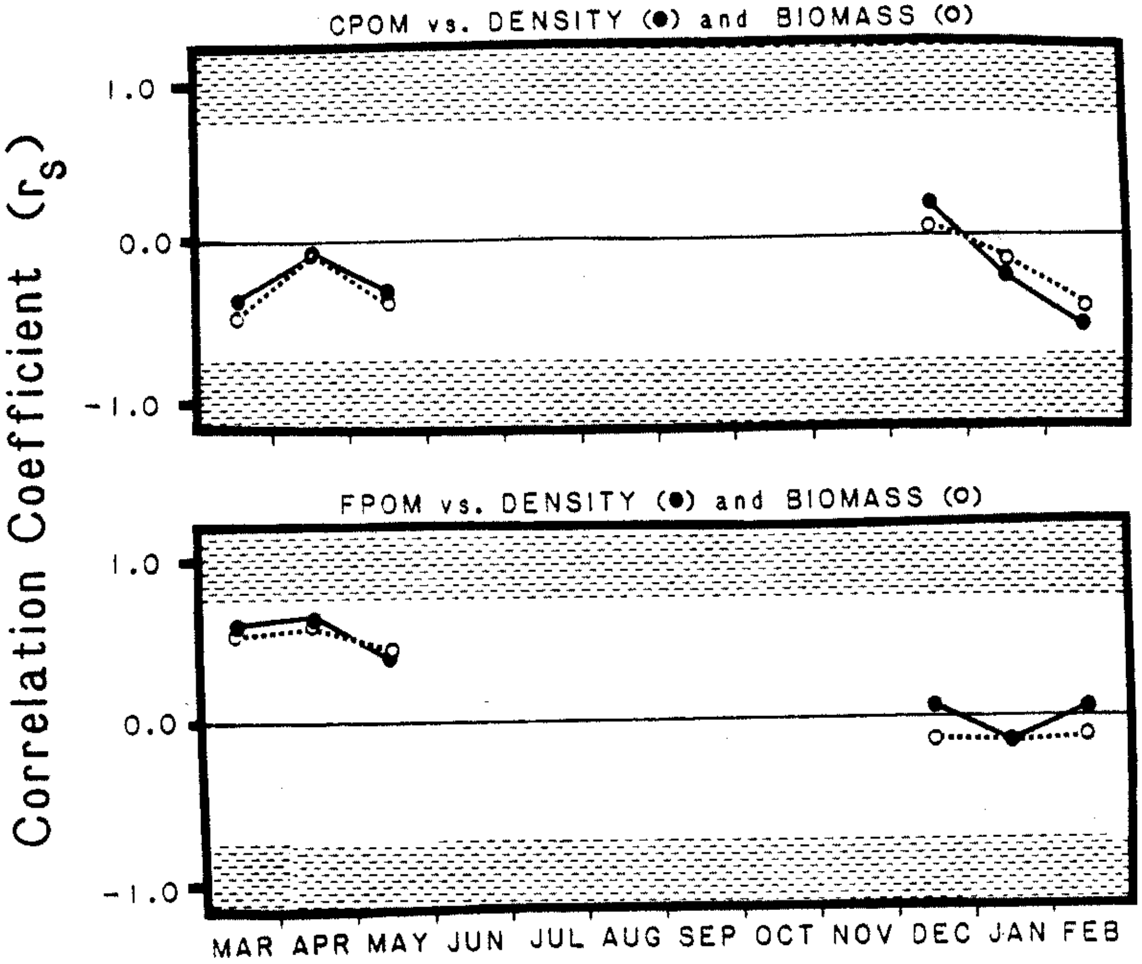
Montana stream, emphasizing the great degree of habitat overlap. The predator's significantly contagious distributions ($p<0.05$) for 10 of 12 months in Battle Branch also suggests habitat overlap, with correlation analyses providing some evidence for specific substratum associations.

Generalists

Haploperla brevis (Banks).- had a univoltine, fast cycle with emergence in late spring. Nymphs were in the stream for 8 months, Oct.-May. Their absence from more than 50% of samples in Oct. and Nov. precluded analysis of those months. Distribution was primarly contagious, except for May when pre-emergent nymphs were randomly distributed ($p>0.05$). Early instars revealed little association with either CPOM or FPOM, but later instars showed a positive trend of density and biomass with FPOM (Mar.-May, Fig. 18). HCW did not show a clear relationship with CPOM or FPOM. Additional qualitative sampling on adjacent riffles corroborated that later instar *H. brevis* were most abundant in gravel, and were rarely found in leaf packs.

Isoperla namata (Frison).- was univoltine, fast, with emergence in early spring. Mean Surber densities showed *I. namata* to be the 2nd most abundant species in

Fig. 18. Monthly Spearman rank coefficients for *Haploperla brevis*. Shaded area indicates $p<0.05$.



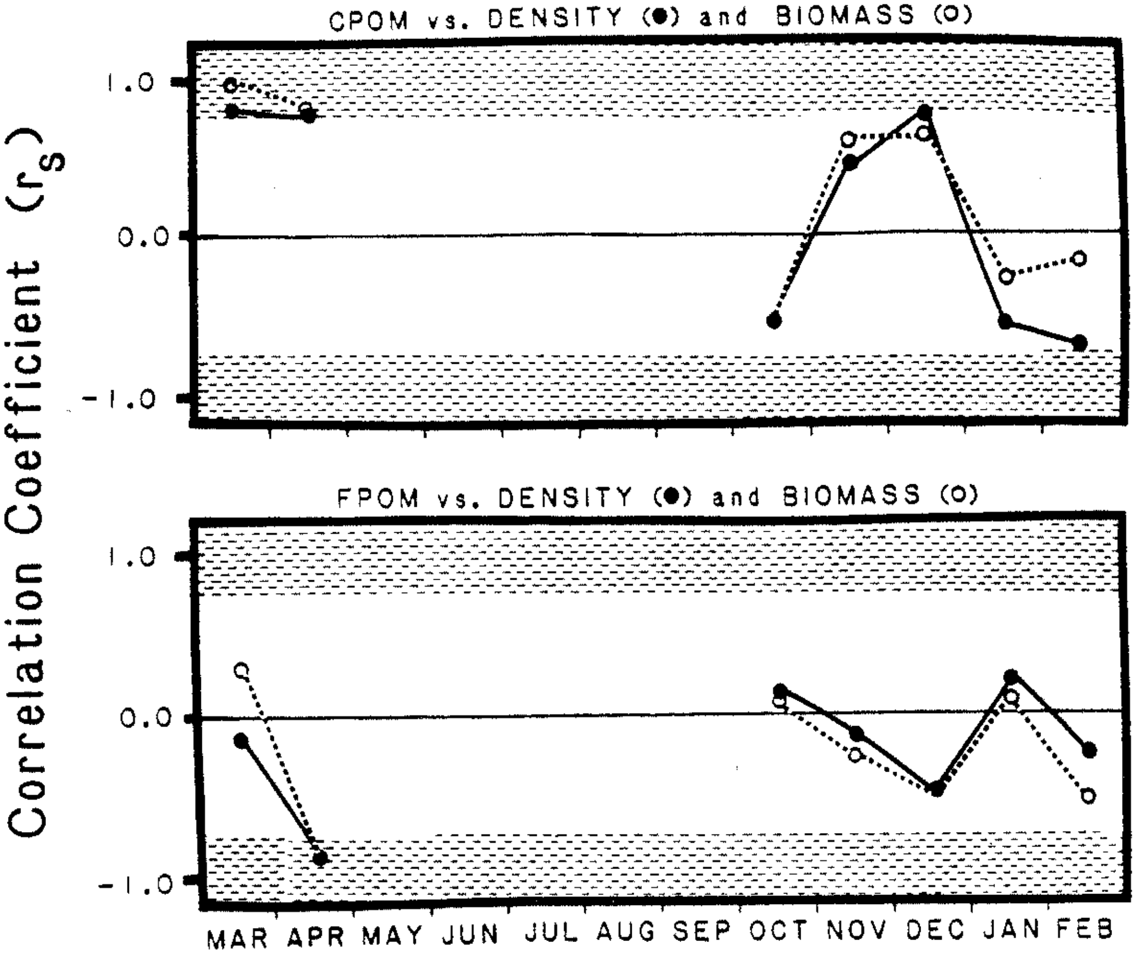
CPOM vs. DENSITY (●) and BIOMASS (○)

FPOM vs. DENSITY (●) and BIOMASS (○)

the stream (Table 2). Distributions were primarly contagious, except for Oct. ($p>0.05$), which initiates the time of recruitment for nymphs. Density was related to both CPOM and FPOM on an annual basis (r_s =0.2541 and 0.2444 respectively, $p<0.05$), reflecting monthly fluctuations in associations with organic matter. For example, a positive relationship with CPOM in Dec. ($p<0.05$) transposed to a negative trend in Jan. and a negative relationship in Feb. ($p<0.05$, Fig. 19). Feminella (1983) found I. namata to a be a common inhabitor of leaf packs in the Little Missouri River, Arkansas emphasizing their facultative omnivory or flexible feeding habits. In Battle Branch, I. namata also demonstrates habitat flexibility by variable associations with CPOM and FPOM, not related to ontogenetic shifts. It is possible that nymphs move between leaf packs and gravel substratum, maximizing their exploitation of available space and food and/or minimizing interspecific competition. Biomass associations were less variable than density, being related to CPOM annually ($r_s=0.3967$, $p<0.001$) and for 3 of the 7 months of nymphal presence (Fig. 19). HCW was more related to CPOM than FPOM with positive relationships ($p<0.05$) for 4 of 7 months.

Analysis of H. brevis and I.namata together as generalists, reveals primarly contagious distributions

Fig. 19. Monthly Spearman rank coefficients for *Isoperla namata*. Shaded area indicates $p<0.05$.


CPOM vs. DENSITY (●) and BIOMASS (○)
FPOM vs. DENSITY (●) and BIOMASS (○)
Correlation Coefficient (r_s)
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of nymphs, except for May and Oct. ($p>0.05$), corresponding to H. *brevis* emergence and I. *namata* recruitment, respectively. Density and biomass relationships are biased by the dominance of I. *namata*, and clearly demonstrate positive relationships between density and CPOM (all months combined, n=80, $r_s=0.2992$, $p<0.05$) and biomass and CPOM ($r_s=0.4109$, $p<0.001$). Monthly coefficients of the two species combined had directions and probabilities similar to I. *namata* (Fig. 19), except for May when H. *brevis* influenced a positive trend between density and FPOM (see Fig. 18). Although both species have life cycles in conjuction with major allochthonous (CPOM) input and retention, only I. *namata* appeared to utilize the resource as food and/or habitat.

Shredders

Amphinemura delosa (Ricker).- exhibited a univoltine, fast life cycle in conjuction with the major period of conditioned leaf material (Feb to Apr.). Recruitment began in Jan, but densities were too low (< 50% of samples contained nymphs) to include in analyses. Benthic densities were the highest among species studied and were in highly contagious distributions for all months considered ($p<0.001$, Table 2). Density and biomass were positively correlated to

CPOM for the growth period (r_s=0.5569 and 0.5116 respectively, $p<0.001$) and for all months analyzed except Feb. (Fig. 20). This association was fully expected, based on extensive collections of this species in Ozark streams, and therefore serves as a "control" against which correlations between other species and CPOM or FPOM have been interpreted. HCW reveals no apparent trend.

Prostoia completa (Walker).- also had a univoltine, fast life cycle in Battle Branch, in conjunction with abundant allochthonous retention. Nymphs were present in sufficient abundance to permit analysis only for a 3 month period, Dec.-Feb. Early instar (Nov.) and pre-emergent nymphs (Mar.) were not analyzed. Density and biomass showed a nearly significant, positive trend with CPOM over the considered nymphal growth period (r_s=0.3309 and 0.3143 respectively, $p<0.10$). Monthly, coefficients were all positive for density and biomass vs. CPOM, with biomass vs. CPOM correlations being significant in Dec. and Jan. (Fig. 21). Correlations were accordingly negative for relationships with FPOM. HCW revealed no consistent relationship with CPOM or FPOM.

Leuctra tenuis (Walker).- had a univoltine, fast cycle, with fall emergence in Battle Branch, encompassing the relatively depauperate CPOM summer

Fig. 20. Monthly Spearman rank coefficients for *Amphinemura delosa*. Shaded area indicates $p<0.05$.

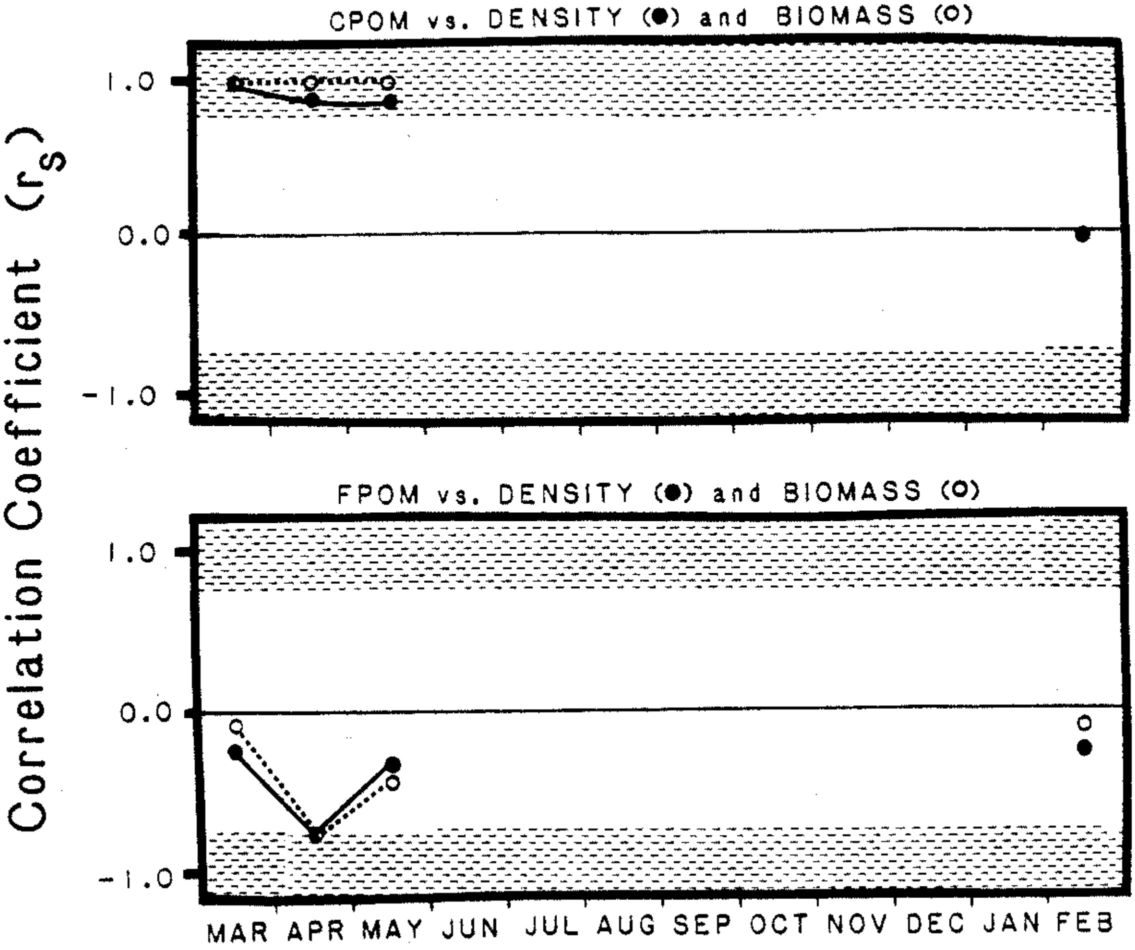
CPOM vs. DENSITY (●) and BIOMASS (○)
FPOM vs. DENSITY (●) and BIOMASS (○)
Correlation Coefficient (r_s)
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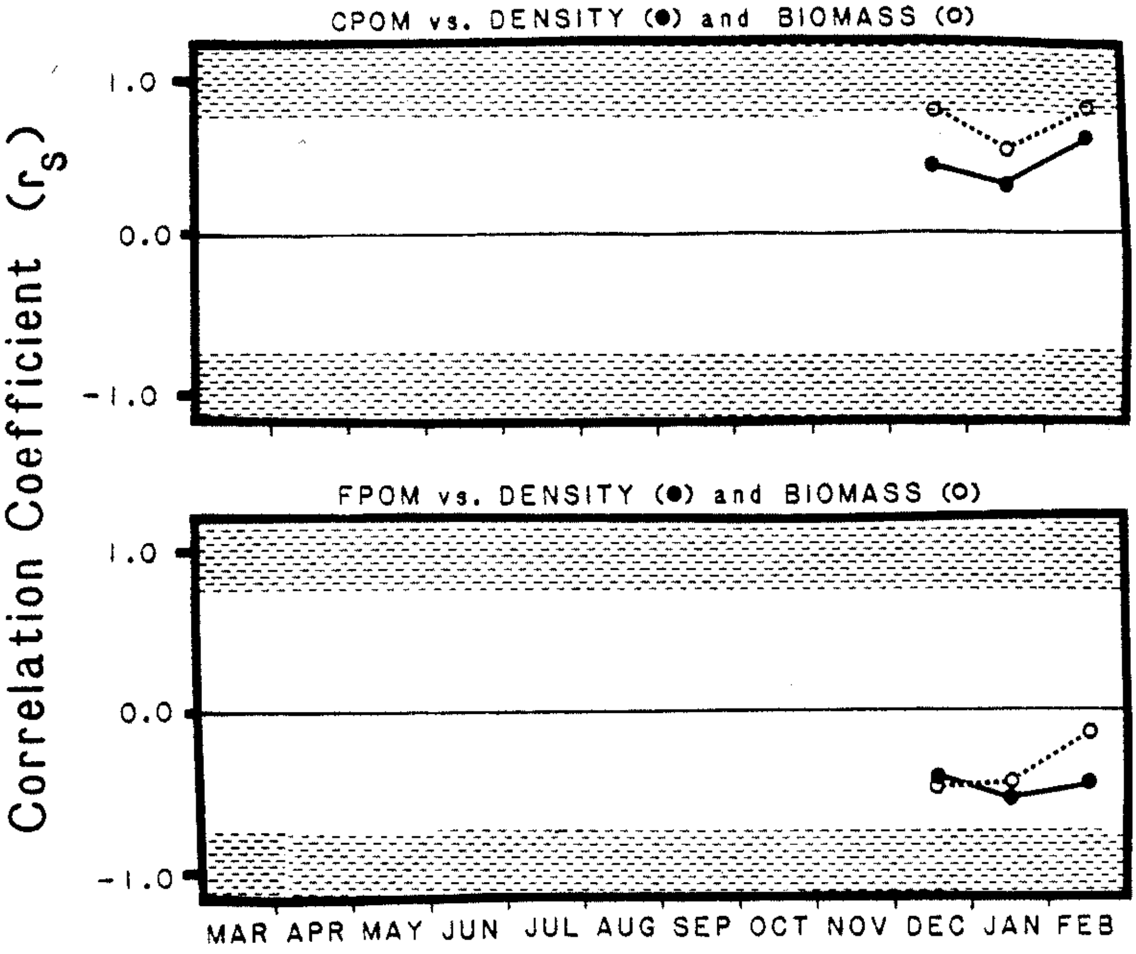
Fig. 21. Monthly Spearman rank coefficients for *Prostoia completa*. Shaded area indicates $p<0.05$.


CPOM vs. DENSITY (●) and BIOMASS (○)
FPOM vs. DENSITY (●) and BIOMASS (○)
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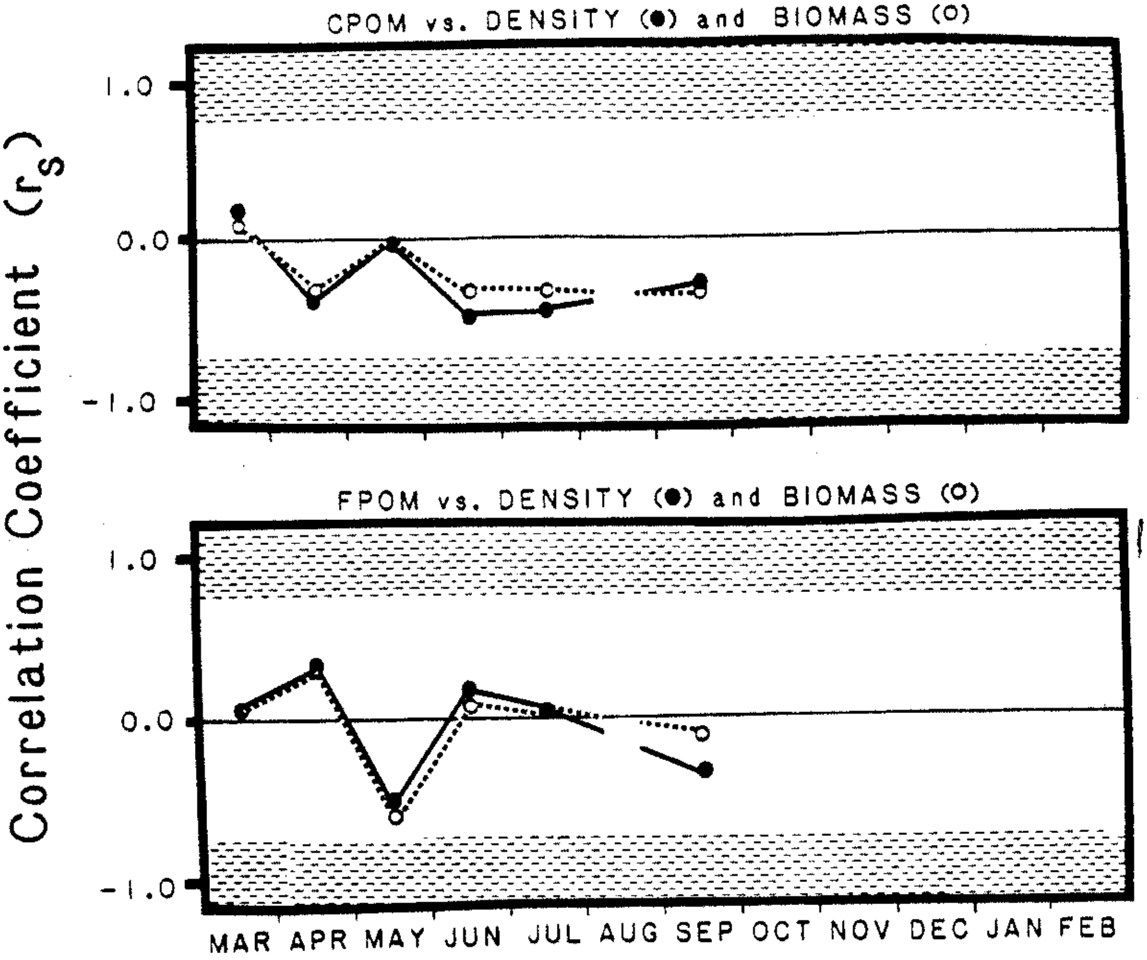
months. Low Surber densities in Aug. and Oct. precluded analysis of microdistribution in relation to CPOM/FPOM. During remaining months, nymphs demonstrated contagious distributions ($p<0.05$), except for Sep. when pre-emergent nymphs were randomly distributed (Table 2). Correlations show nymphs more associated with FPOM than CPOM, but the association is weak (Fig. 22). *Leuctra* are typically classed a shredders (Merritt and Cummins 1984), but based on no association with CPOM, the possibility of it being a collector should be investigated.

As a group these 3 shredders were present for 9 of the 12 months, excluding only Aug., Oct. and Nov. Mean benthic density during this period was 64.24 ± 139.98 with a maximum in Mar., solely attributable to *A. delosa* (Table 2). Overall, density was positively related to CPOM ($n=90$, $r_s=0.6058$, $p<0.001$) and monthly during Mar., Apr. ($p<0.001$) and May ($p<0.05$). Coefficients for density and FPOM were negative for 7 of 9 months, significant in Apr. and May. Biomass followed a similar pattern, emphasizing the significant results for *A. delosa* (Fig. 20) and *P. completa* (Fig. 21) during the period of high leaf retention in Battle Branch. Other studies have also suggested a strong relationship of shredders with organic matter in woodland streams with high leaf retention (Brink 1949,

Fig. 22. Monthly Spearman rank coefficients for *Leuctra tenuis*. Shaded area indicates $p<0.05$.


CPOM vs. DENSITY (●) and BIOMASS (○)
FPOM vs. DENSITY (●) and BIOMASS (○)
Correlation Coefficient (r_s)
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Peckarsky 1980, Short et al. 1980, Reice 1981, Short and Ward 1981, O'Hop et al. 1984). The life cycle and association with FPOM for L. tenuis demonstrate an exception, and therefore the functional food classification for this species may not be correct; this emphasizes the need for specific consideration of microdistribution (Minshall and Minshall 1977).

Overall Relationships.- Combining all 8 species showed a mean annual Surber density (n=120) of 112.81 ± 150.00 (Table 2). Distributions were significantly contagious for all months except Aug. (Table 2). Maximum density occurred in Feb. and minimum in Aug., resulting in a significant annual relationship to CPOM (r_s=0.5580, $p<0.001$). The syncrony of the life cycles and associations with CPOM of the numerically dominant species, A. delosa, I. namata and P. completa, are primarily responsible for this strong community relationship. Rabeni and Minshall's (1977) generalized model of insect microdistribution (their Fig. 6), emphasized small substratum and associated detritus retention as supportive of large populations of insects. The lack of leaf litter at their study site may have obscured the role I found CPOM to play in annual density enhancement. Stonefly life cycle syncrony with CPOM was also suggested by an annual relationship between diversity and CPOM (r_s=0.4739, p<0.001). Diversity was highest in Feb. ($\bar{X}$ ± 1 SD, 8.3 ± 0.48) and lowest in Aug. (3.3 ± 0.82). Species such as *Zealeucta warreni* Ricker and Ross, *Zealeuctra classeni* (Frison), *Allocapnia rickeri* Frison, *Paracapnia angulata* Hanson, *Strophopteryx fasciata* (Burmeister) *Clioperla clio* (Newman), *Isoperla signata* (Banks) and *Alloperla caudata* Frison were present as nymphs in Battle Branch only during the period of major allochthonous input and retention, but densities were too low for specific correlation analysis.

Benke (1984) inferred food quality, temperature, habitat complexity and biological interactions can influence insect production. Hynes (1963, 1970) addressed the syncrony of life cycles of many species with allochthonous input and implied the importance of this input to production. Other studies have also found allochthonous material to represent the primary source of energy in low order, woodland streams (Minshall 1967, Malmquist 1978).

Although density may be an appropriate measure for determining the microdistribution of a particular species, and diversity (no. of taxa) the structure of the community, biomass or production appears more applicable to assess the function of species in a community (O'Hop et al. 1984). The significant annual relationships between biomass and CPOM at the species level (*A. evoluta*, *I. namata*, *A. delosa*), functional group level (predators, generalists, shredders) and the community level ($r_s=0.5969$, $p<0.001$) indicate the importance of CPOM as both food and habitat. Annually, 72.5% of the total stonefly community biomass (13.39 gm. dry wt., n=120 Surber samples) is a result of the 4 most strongly associated species with CPOM (*A. evoluta* 7.44 gms, 55.6%; *I. namata* 1.34 gms, 10.0%; *A. delosa* 0.66 gms, 4.9%, and *P. completa* 0.27 gms, 2.0%).

Conclusion

The influence of allochthonous organic matter has been found to be of major importance in the structure and function of low order, woodland streams. In these types of streams the River Continuum Concept (Vannote et al. 1980) considers CPOM as an important food source for shredders. However, as this study reveals, CPOM associations are not limited to shredders (e.g. *A. delosa*, *P. completa*), but also include predators (eg. *A. evoluta*) and generalists (eg. *I.namata*). This suggests that CPOM provides an added niche dimension (habitat space) for these groups and is important in stream community structure and function. Iversen and Madsen (1977) and Malmquist et al. (1978) suggested that leaf litter was not only an important food, but also increased the heterogeneity and amount of substratum available for colonization.

From the standpoint of stream management (see Bird and Kaushik 1981, Cummins 1974), deforestation of watersheds or removal of most streamside brush may have detrimental effects on stoneflies, and their production.

LITERATURE CITED

Anderson, N.H. and D.M. Lehmkuhl. 1968. Catastrophic drift in insects in a woodland stream. Ecology 49:198-206.

Anderson, N.H. and J.R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Ann. Rev. Entomol. 24:351-377.

Barber, W.E. and N.R. Kevern. 1973. Ecological factors influencing macroinvertebrate standing crop distribution. Hydrobiologia 43:53-75.

Benke, A.C. 1984. Secondary production of aquatic insects. In: V.H. Resh and D.M. Rosenberg, eds. The ecology of aquatic insects. Praeger. New York, New York. U.S.A. pp. 289-322.

Bird, G.A. and N.K. Kaushik. 1981. Course particulate organic matter in streams. In: M.A. Lock and D.D. Williams, eds. Perspectives in running water ecology. Plenum. New York, New York. U.S.A. pp. 41-68.

Branham, J.M., A.R. Gaufin and R.L. Traver. 1975. Growth of Plecoptera (stonefly) nymphs at constant, abnormally high temperatures. Great Basin Natur. 35:51-61.

Brink, P. 1949. Studies on Swedish stoneflies. Opusc. Entomol. suppl. 11:1-250.

Brittain, J.E. 1973. The biology and life cycle of _Nemoura avicularis_ Morton (Plecoptera). Freshwater Biol. 3: 199-210.

Brittain, J.E. 1983. The influence of temperature on nymphal growth rates in mountain stoneflies (Plecoptera). Ecology 64:440-446.

Brown, A.V. and J.P. Ricker. 1982. Macroinvertebrate utilization of leaf detritus in a riffle of the Illinois River, Arkansas. Arkansas Acad. Sci. 36:10-13.

Brusven, M.A. 1979. Drift periodicity and upstream dispersion of stream insects. J. Entomol. Soc. Brit.

Colum. 64: 48-59.

Brusven, M.A. and K.V. Prather. 1974. Influence of stream sediments on distribution of macrobenthos. J. Entomol. Soc. Brit. Colum. 71:25-32.

Chaston, I. 1972. Non-catastrophic invertebrate drift in lotic systems. In J. Clarke, ed. Essays in Hydrobiolgy. Exetes Univ. Press. 33: 33-51.

Cloud, T.J. and K.W. Stewart. 1974a. The drift of mayflies (Ephemeroptera) in the Brazos River, Texas. Kan. Entomol. Soc. 47:379-396.

Cloud, T.J. and K.W. Stewart. 1974b. Seasonal fluctuations and periodicity in the drift of caddisfly larvae (Trichoptera) in the Brazos River, Texas. Ann. Entomol. Soc. Amer. 67: 805-810.

Coleman, M.J. and H.B.N. Hynes. 1970. The life histories of some Plecoptera and Ephemeroptera in a southern Ontario stream. Can. J. Zool. 48:1333-1339.

Cordes, L.E. and L.M. Page. 1980. Feeding chronology and diet compostion of two darters (Percidae) in the Iroquois River System, Illinois. Amer. Midl. Natur. 104:202-206.

Cowan, C.A., M.W. Oswood, C.A. Buttimore and P.W. Flanagan. 1983. Processing and macroinvertebrate colonization of detritus in and Alaskan subart. stream. Holarctic Ecol. 6:340-348.

Cummins, K.W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. Amer. Midl. Natur. 67:477-504.

Cummins, K.W. 1974. Structure and function of stream ecosystems. Bioscience 24:631-641.

Cummins, K.W. and G.H. Lauff. 1969. The influence of substrate particle size on the microdistribution of stream benthos. Hydrobiologia 34:145-181.

Cummins, K.W., R.C. Petersen, F.O. Howard, J.C. Wuycheck and V.I. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54:336-345.

deMarch, B.G.E. 1976. Spatial and temporal patterns in macrobenthic stream diversity. J. Fish. Res. Board

Can. 33:1261-1270.

Egglishaw, H.J. 1964. The distributional relationship between the bottom fauna and plant detritus in streams. J. Anim. Ecol. 33: 463-476.

Egglishaw, H.J. 1968. The quantitaive relationship between bottom fauna and plant detritus in streams of different calcium concentrations. J. Appl. Ecol. 5:731-740.

Egglishaw, H.J. 1969. The distribution of benthic invertebrates in fast-flowing streams. J. Anim. Ecol. 38;19-33.

Elliot, J.M. 1967a. The life histories and drifting of Plecoptera and Ephemeroptera in a Dartmoor stream. J. Anim. Ecol. 36: 343-362.

Elliot, J.M. 1967b. Invertebrate drift in a Dartmoor stream. Arch. Hydrobiol. 63:202-237.

Elliot, J.M. 1970. Methods of sampling invertebrate drift in running waters. Ann. Limnol. 6:133-159.

Elliot, J.M. 1979. Some methods for the statistical analysis of benthic invertebrates. 2nd ed. Freshwat. Biol. Assoc. No. 25. pp. 149.

Ernst, M.R., T.L. Beitinger and K.W. Stewart. 1984. Critical thermal maxima of nymphs of three Plecoptera species from an Ozark foothill stream. Freshwat. Invertebr. Biol. 3:80-85.

Everhart, W.H., A.W. Eipper and W.D. Youngs. 1975. Principles of fishery science. Comstock publishing Assoc., Cornell Univ. Ithaca, New York. U.S.A. pp. 288.

Feminella, J.W. 1983. Comparative feeding ecology of leaf pack-inhabiting Systellognathan stoneflies (Plecoptera) in the upper Little Missouri River, Arkansas. M.S. Thesis. North Texas State University. Denton, Texas. pp. 130.

Finni, G.R. 1977. Postdiapause instar discrimination and life history of the Capniid stonefly, Allocapnia granulata (Claassen) (Insecta: Plecoptera). Amer. Midl. Natur. 98:243-250.

Finni, G.R. and L. Chandler. 1979. The microdistribution of Allocapnia naiads (Plecoptera: Capniidae). J. Kan. Entomol. Soc. 52:93-102.

Frison, T.H. 1935. The stoneflies, or Plecoptera of Illinois. Bull. Ill. Natur. Hist. Surv. 20:281-471.

Fuller, R.L. and K.W. Stewart. 1977. The food habits of stoneflies (Plecoptera) on the upper Gunnison River, Colorado. Environ. Entomol. 6:293-302.

Gledhill, T. 1960. The Ephemeroptera, Plecoptera and Tricoptera caught by emergence traps in two streams during 1958. Hydrobiologia 15:179-188.

Griffith, J.S.Jr. 1974. Utilization of invertebrate drift by brook trout (Salvelinus fontinalis) and cutthroat trout (Salmo clarki) in small streams in Idaho. Trans. Amer. Fish. Soc. 103:440-447.

Hanushek, E.A. and J.E. Jackson. 1977. Statistical methods for social scientists. New York Academic Press. New York, New York. U.S.A. pp. 374.

Harper, P.P. 1973a. Life histories of Nemouridae and Leuctridae in southern Ontario (Plecoptera). Hydrobiologia 41:309-356.

Harper, P.P. 1973b. Emergence, reproduction and growth of setipalpian Plecoptera in southern Ontario. Oikos 24: 94-107.

Harper, P.P. 1976. Emergence patterns of Plecoptera. In: R.W. Baumann ed., A report on the fifth international symposium on Plecoptera. Proc. Biol. Soc. Wash. 88:399-428.

Harper, P.P. 1978. Variations in the production of emerging insects from a Quebec stream. Verh. Internat. Verein. Limnol. 20:1317-1323.

Harper, P.P. and E. Magnin. 1969. Cycles vitaux de quelques Plecoptera des Laurentides (insectes). Can. J. Zool. 47:483-494.

Harper, P.P. and H.B.N. Hynes. 1972. Life histories of Capniidae and Taeniopterygidae (Plecoptera) in southern Ontario. Arch. Hydrobiol., Suppl. 40:274-314.

Harper, P.P. and J.G. Pilon. 1970. Annual patterns of emergence of some Quebec stoneflies (Insecta: Plecoptera). Can. J. of Zool. 48:681-694.

Harris, T.L. and W.P. McCafferty. 1977. Assessing aquatic insect flight behavior with sticky traps. Great Lakes Entomol. 10:233-239.

Heiman, D.R. and A.W. Knight. 1975. The influence of temperature on the bioenergetics of the carnivorous stonefly nymph, *Acroneuria californica* Banks (Plecoptera: Perlidae). Ecology 32:105-116.

Hilsenhoff, W.L., J.L. Longridge, R.P. Narf, K.J. Tennessen and C.P. Walton. 1972. Aquatic insects of the Pine-Popple River Wisconsin. Wisc. Dept. Natur. Res. Tech. Bull. 54:1-44.

Hitchcock, S.W. 1974. Guide to the insects of Connecticut, Pt. VII. The plecoptera of stoneflies of Connecticut. St. Geol. Natur. Hist. Surv. Conn., Dept. Environ. Prot. Bull. 107:1-262.

Humpesch, U.H. 1979. Life cycles and growth rates of *Baetis* spp. (Ephemeroptera: Baetidae) in the laboratory and in two stony streams in Austria. Freshwat. Biol. 9:467-479.

Humpesch, U.H. 1981. Effects of temperature on larval growth of *Ecdyonurus dispir* (Ephemeroptera: Heptageniidae) from two English Lakes. Freshwat. Biol. 11:441-457.

Hynes, H.B.N. 1961. The invertebrate fauna of a Welsh mountain stream. Arch. Hydrobiol. 57:344-388.

Hynes, H.B.N. 1963. Imported organic matter and secondary productivity in streams. Int. Congr. Zool. 16:324-329.

Hynes, H.B.N. 1970. The ecology of running water. Univ. Toronto Press. Toronto, Canada. pp. 555.

Hynes, H.B.N., N.K. Kaushik. M.A. Lock, D.L. Lush, Z.S.J. Stocker, R.R. Wallace and D.D. Williams. 1974. Benthos and allochthonous organic matter in streams. J. Fish. Res. Board Can. 31:545-553.

Hynes, J.D. 1975. Downstream drift of invertebrates in a river in southern Ghana. Freshwat. Biol. 5:515-532.

Illies, J. 1952. Die Plecopteran und das Monardsche Prinzip. Ber. Limnol. Flusssta. Freudenthal 3:53-69.

Iversen, T.M. and B.L. Madsen. 1977. Allochthonous organic matter in streams. Danish Limnology: Reviews and Perspectives 17:17-20.

Jop, K. and S.W. Szczytko. 1984. Life cycle and production of Isoperla signata (Banks) in a central Wisconsin trout stream. Aquatic Insects 6:81-100.

Kerst, C.D. and N.H. Anderson. 1974. Emergence patterns of Plecoptera in a stream in Oregon. Freshwat. Biol. 4:205-212.

Knight, A.W., M.A. Simmons and C.S. Simmons. 1976. A phenomenological approach to the growth of the winter stonefly, Taeniopteryx nivalis (Fitch) (Plecoptera: Taeniopterygidae). Growth 40:343-367.

Krueger, C.C. and E.F. Cook. 1981. Life cycles, drift and standing stocks of some stoneflies (Insecta: Plecoptera) from streams in Minnesota, U.S.A. Hydrobiologia 83:85-92.

Lehmkuhl, D.M. and N.H. Anderson. 1972. Microdistribution and density as factors affecting the downstream drift of mayflies. Ecology 53:661-667.

Malas, D. and J.B. Wallace. 1977. Strategies for coexistence of three net-spinning caddisflies (Tricoptera) in second order Appalachian streams. Can. J. Zool. 55:1829-1840.

Malmquist, B., L.M. Nilsson and B.S. Svensson. 1978. Dynamics of detritus in a small stream in southern Sweden and its influence on the distribution of bottom animal communities. Oikos 31:3-16.

Markarian, R.K. 1980. A study of the relationship between aquatic insect growth and water temperature in a small stream. Hydrobiologia 75:81-95.

Matthews, W.J., J.R. Bek and E. Surat. 1982. Comparative ecology of the darters Etheostoma podotmone, E. flabellae and Percina roanoka in the upper Roanoke River drainage, Virginia. Copeia 4:805-814.

Merritt, R.W. and K.W. Cummins. 1984. An introduction to the aquatic insects of North America. 2nd ed. Kendall/Hunt. Debuque, Iowa. U.S.A. pp. 722.

Minshall, G.W. 1984. Aquatic insect-substratum relationships. In: V.H. Resh and D.M. Rosenberg, eds. The ecology of aquatic insects. Praeger. New York, New York. U.S.A. pp. 358-400.

Minshall, G.W. and J.N. Minshall. 1966. Notes on the life history and ecology of Isoperla clio (Newman) and Isogenus decisus Walker (Plecoptera: Perlodidae). Amer. Midl. Natur. 76:340-350.

Minshall, G.W. and J.N. Minshall. 1977. Microdistribution of benthic invertebrates in a Rocky Mountain (U.S.A.) stream. Hydrobiologia 55:231-249.

Minshall, G.W., R.C. Petersen. K.W. Cummins, T.L. Bott, J.R. Sedell, C.E. Cushing and R.L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. Ecol. Monog. 53:1-25.

Müller, K. 1973. Life cycles of stream insects. Aquilo. Ser. Zool. 14:105-112.

Narf, R.P. and W.L. Hilsenhoff. 1974. Emergence pattern of stoneflies (Plecoptera) in Otter Creek, Wisconsin. Great Lakes Entomol. 7:117-125.

Neves, R.J. 1978. Seasonal succession and diversity of stoneflies (Plecoptera) in Factory Brook, Massachusetts. New York Entomol. Soc. 86:144-152.

O'Hop, J., J.B. Wallace and J.D. Haefner. 1984. Production of a stream shredder, Peltoperla maria (Plecoptera: Peltoperlidae) in disturbed and undisturbed hardwood catchments. Freshwat. Biol. 14:13-21.

Peckarsky, B.L. 1980. Influence of detritus upon colonization of stream invertebrates. Can. J. Fish. Aquat. Sci. 37:957-963.

Peckarsky, B.L. 1984. Predator-prey interactions among aquatic insects. In: V.H. Resh and D.M. Rosenberg, eds. The ecology of aquatic insects. Praeger. New York, New York. U.S.A. pp. 196-254.

Peckarsky, B.L. and S.I. Dodson. 1980a. An experimental analysis of biological factors contributing to stream community structure. Ecology 61:1283-1290.

Peckarsky, B.L. and S.I. Dodson. 1980b. Do stonefly predators influence benthic distributions in streams? Ecology 61:1275-1282.

Petersen, R.C. and K.W. Cummins. 1974. Leaf processing in a woodland stream. Freshwat. Biol. 4:343-368.

Rabeni, C.F. and G.W. Minshall. 1977. Factors affecting microdistribution of stream insects. Oikos 29:33-34.

Radford, D.S. and R. Hartland-Rowe. 1971. Emergence patterns of some Plecoptera in two mountain streams in Alberta. Can. J. Zool. 49:657-662.

Reice, S.R. 1980. The role of substratum in benthic macroinvertebrate microdistribution and litter decomposition in a woodland stream. Ecology 61:580-590.

Reice, S.R. 1981. Interspecific associations in a woodland stream. Can. J. Fish. Aquat. Sci. 38:1271-1280.

Resh, V.H. 1979. Sampling variability and life history features: Basic considerations in the design of aquatic insect studies. J. Fish. Res. Board Can. 36:290-311.

Ross, H.H. and W.E. Ricker. 1971. The classification, evolution and dispersal of the winter stonefly genus Allocapnia. Ill. Biol. Mono. 45. Univ. Ill. Press, Chicago. 166pp.

SAS 1982. SAS user's guide: statistics. SAS Institute Inc. Cary, NC. 584 pp.

Sheldon, A.L. 1979. Resource division by perlid stoneflies (Plecoptera) in a lake outlet ecosystem. Hydrobiologia 71:155-161.

Sheldon, A.L. and S.G. Jewett. 1967. Stonefly emergence in a Sierra Nevada stream. Pan-Pac. Entomol. 43:1-8.

Short, R.A., S.P. Canton and J.V. Ward. 1980. Detrital processing and associated macroinvertebrates in a Colorado mountain stream. Ecology 61:727-732.

Short, R.A. and J.V. Ward. 1981. Trophic ecology of three winter stoneflies (Plecoptera). Amer. Midl. Natur. 105:341-347.

Snellen, R.K. and K.W. Stewart. 1979a. The life cycle and drumming behavior of Zealeuctra claasseni (Frison) and Zealeuctra hitei Ricker and Ross (Plecoptera: Leuctridae) in Texas, USA. Aquatic Insects. 1:65-89.

Snellen, R.K. and K.W. Stewart. 1979b. The life cycle of Perlesta placida (Plecoptera:Perlidae) in an intermittent stream in northern Texas. Ann. Entomol. Soc. Amer. 72:659-666.

Stanford, J.A. 1975. Ecological studies of Plecoptera in the upper Flathead and Tobacco Rivers, Montanna. Ph.D. Dissertation. University of Utah. 238pp.

Stark, B.P. and K.W. Stewart. 1973. Distribution of stoneflies (Plecoptera) in Oklahoma. J. Kan. Entomol. Soc. 46:563-577.

Stewart, K.W. and S.W. Szczytko. 1983. Drift of Ephemeroptera and Plecoptera in two Colorado Rivers. Freshwat. Invertebr. Biol. 2:117-131.

Surat, E.M., W.J. Matthews and J.R. Bek. 1980. Comparative ecology of Notropis albeolus, N.ardens and N. cerasinus in the upper Roanoke River drainage, Virginia. Amer. Midl. Natur. 107:13-24.

Vannote, R.L. and B.W. Sweeney. 1980. Geographical analysis of thermal equilibria: a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities. Amer. Natur. 115:667-695.

Vannote, R.L., G.W. Minshall, K.W. Cummins, J.R. Sedell and C.E. Cushing. 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.

Vaught, G.L. and K.W. Stewart. 1974. The life history and ecology of the stonefly Neoperla clymene (Newman) (Plecoptera: Perlidae). Ann. Entomol. Soc. Amer. 67:167-177.

Walton, O.E. Jr. 1980. Invertebrate drift from predator-prey associations. Ecology 61:1486-1497.

Walton, O.E. Jr., S.R. Reice and R.W. Andrews. 1977. The effects of density, sediment particle size and velocity on drift of Acroneuria abnormis (Plecoptera). Oikos 28:291-298.

White, T.R., P.H. Carlson and R.C. Fox. 1979. Emergence patterns of fall and winter stoneflies (Plecoptera:Filipalpia) in northwestern South Carolina. Proc. Entomol. Soc. Wash. 81:379-390.

Williams, D.D. 1981. Migrations and distributions of stream insects. In: M.A. Lock and D.D. Williams, eds. Perspectives of running water ecology. Plenum.. New York, New York. U.S.A. pp. 155-208.

Zar, J.H. 1974. Biostatistical analysis. Prentice-Hall. Englewood Cliffs, New Jersey. U.S.A. pp. 620.