COMPARATIVE FEEDING ECOLOGY OF LEAF PACK-INHABITING SYSTELLOGNATHAN STONEFLIES (PLECOPTERA) IN THE UPPER LITTLE MISSOURI RIVER, ARKANSAS

THESIS

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By

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The feeding ecologies of leaf pack-associated systellognathan stoneflies were examined from 6 June 1980 - 21 May 1981. Species composition, seasonal abundance, nymphal growth, feeding habits and mouthpart morphology were determined for the eight dominant stonefly species. Prey preferences and predator-prey size relationships were also examined for omnivorous and carnivorous species. Foregut analysis from 2860 individuals indicated opportunistic feeding on the most abundant prey insects, usually in proportion to prey frequency. Feeding preference studies generally indicated random feeding on major prey groups. Prey and predator sizes were usually highly correlated ($p<0.01$), with predators expanding their prey size thresholds with growth. The potential for competition between sympatric stoneflies for prey is discussed.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF ILLUSTRATIONS

LIST OF ILLUSTRATIONS (continued)

CHAPTER I

INTRODUCTION

The considerable body of information accumulated in recent years regarding invertebrate feeding ecology and predator-prey interactions in running waters has focused principally upon food habits of stoneflies (Plecoptera). They tend to be the most ubiquitous and important invertebrate predators in streams (Merritt and Cummins 1978). Many stonefly feeding studies have dealt exclusively with one predaceous species (Sheldon 1969; Siegfried and Knight 1976 a & b; Oberndorfer and Stewart 1977; Kovalak 1978; Malmquist and Sjostrom 1980) while others have centered on regional food habit surveys (Hynes 1941; Richardson and Gaufin 1971; Shapas and Hilsenhoff 1976). Still others have addressed comparative feeding ecology of two sympatric stoneflies or an entire predator community (Minshall and Minshall 1966; Sheldon 1972, 1980; Devonport and Winterbourn 1976; Fuller and Stewart 1977, 1979; Allan 1982). Research focus in these studies has included 1) ontogenetic shifts in the predators' diet, 2) prey preferences or electivity by predators for specific prey types and/or sizes, and 3) dietary similarity between sympatric predators (i.e. potential for interspecific competition).

Many studies have documented polyphagous feeding by stoneflies and dietary shifts from herbivory to almost complete carnivory with development (Fuller and Stewart 1977; Gray and Ward 1979; Allan 1982), while others noted qualitative changes in the diet irrespective of stonefly size (Siegfried and Knight 1976a). Though largely ignored in most trophic research, prey selection data are highly variable, with some workers reporting positive electivity for some taxa by stoneflies (Siegfried and Knight 1976a; Fuller and Stewart 1977), and others indicating the predominance of random feeding, with predators consuming prey roughly in proportion to their environmental frequencies (Hildrew and Townsend 1976). Extensive dietary overlap in prey types ingested by co-occurring predators has been widely observed (Devonport and Winterbourn 1976; Fuller and Stewart 1977, 1979; Sheldon 1980; Johnson 1981; Allan 1982), but those that assessed size relations between sympatric predators and prey usually found low similarity in prey sizes consumed (Fuller and Stewart 1979; Allan 1982).

Studies of feeding in predaceous stoneflies have generally been made in low to medium order streams, usually in stony riffles or in unspecified microhabitats. Since many aquatic insects exhibit some degree of microhabitat specialization (Cummins and Lauff 1969; Sheldon 1972; Finni 1979), feeding assessments that attempt to relate predator diet with the prey base in unspecified or mixed substrates may be subject to erroneus conclusions regarding true prey selection and actual coexistence of predators and prey. This is further compounded by a lack of information regarding use of multiple microhabitats as foraging areas by a single predator.

To date, no study has focused on feeding dynamics of stoneflies inhabiting natural leaf packs, despite their abundance in temperate-deciduous woodland streams (Minshall 1967; Fisher and Likens 1974; Winterbourn 1976), and the relatively high density and diversity of aquatic insects supported by these organic accumulations (Mackay and Kalff 1969; Anderson and Sedell 1979). By virtue of their dorso-ventrally flattened morphology, stonefly predators appear to have wide access to prey patches in natural leaf packs (unpbl. data) which may not be true in mixed mineral substrates, potentially providing greater prey refugia. Leaf pack habitats should therefore represent a substrate model that is more conducive for examining feeding habits and prey selection patterns in stoneflies; they should also facilitate testing of food resource partitioning by co-occurring predators.

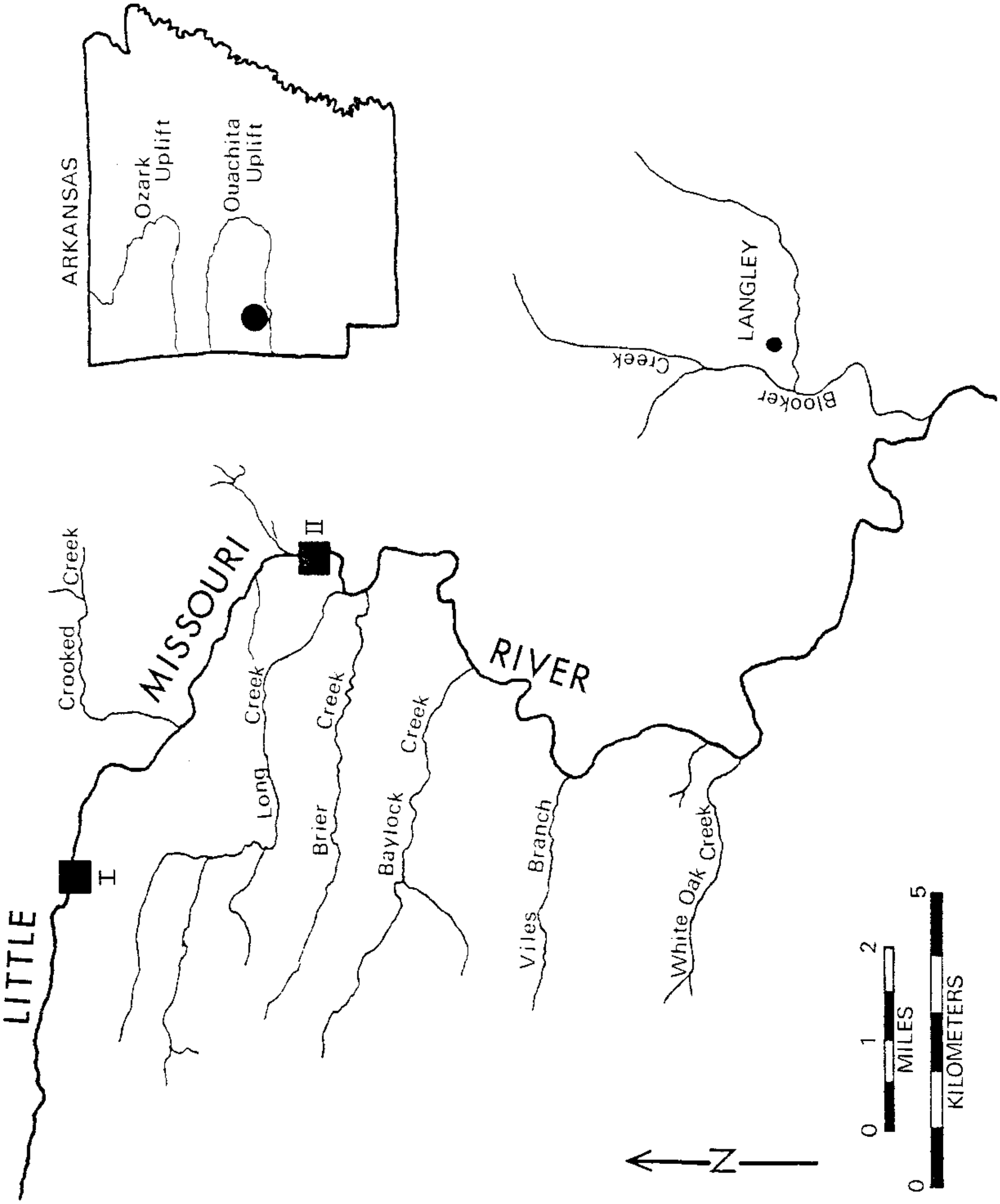
This paper specifically addresses the feeding ecology of leaf pack-associated predaceous stonefly nymphs in an Ouachita Mountain stream, and the degree to which food resources are shared by sympatric species.

CHAPTER II

DESCRIPTION OF THE STUDY AREA

The Upper Little Missouri River is a permanent first to second order stream located in the southern Ouachita Mountains of centralwestern Arkansas. The river flows southeastward through Montgomery County in the Ouachita National Forest, and empties into Lake Greeson which eventually merges with the Ouachita River in southcentral Arkansas. Two sampling sites were selected for study (Fig. 1). Site I was a first order stream located approximately 9 km (5.6 mi.) downstream from the spring source in western Polk County, and 100 m above the Little Missouri Falls Recreation Area. Approximate elevation and stream gradient were 372 m (1220 ft) and 10.6 m/km (34.8 ft/mi.) respectively. Site II was a second order stream located 9 km below Site I and 5 km (3.1 mi) below the confluence of Crooked Creek, a major tributary. Elevation and stream gradient at Site II approximated 293 m (961 ft) and 6.1 m/km (12.4 ft/mi) respectively. Both sites were situated in dense deciduous vegetation, dominated by oaks (*Quercus* spp.), sweetgum (*Liquidambar styraciflua*), American beech (*Fagus grandifolia*) hickories (*Carya* spp.) and maples (*Acer* spp.). At both sites, the substrate was

Figure 1. Map of the Upper Little Missouri River, Montgomery County, Arkansas, showing the location of the river within the state, the sampling sites, and all major tributaries in the area.


ARKANSAS
Ozark Uplift
Ouachita Uplift
LANGLEY
Blooker Creek
LITTLE MISSOURI RIVER
Crooked Creek
Long Creek
Brier Creek
Baylock Creek
Viles Branch
White Oak Creek
I
II
N
MILES
0
1
2
KILOMETERS
0
5

heterogeneous and was composed primarily of gravel and cobble (mostly < 30cm diameter), with some boulders. Standing crops of periphyton appeared low, although no direct estimates were made. Bacon (1983) provides a concise summary of the local geology, soil types, stream geomorphology, and climate for the Little Missouri River and the surrounding watershed.

CHAPTER III

MATERIALS AND METHODS

At each site five natural leaf packs that appeared visibly similar in degree of conditioning were collected from flowing water with a two-stage dip net (1000μm and 153μm mesh sizes). Leaf packs were approached from a downstream position, gently dislodged, and were swept by the current into the dip net. Care was taken not to disturb the underlying rock substrate. Samples were taken monthly from 6 Jun. 1980 to 21 May 1981. Since others have shown that invertebrate densities and leaf pack size are not linearly related (Benfield et al. 1979), similar-sized leaf packs were collected whenever possible to avoid sampling bias. At Site II, wooden stakes were embedded into the stream to enhance the retention of suitable amounts of proper-sized leaf packs.

Each sample consisted of loosely stacked leaves filling a gallon container, and was preserved with 80% isopropanol. Samples were rinsed in the laboratory over a 150μm mesh seive with tap water to separate the insects and fine detritus (< 10 mm diameter) from larger leaf particles. Leaves and large leaf fragments were then oven-dried to a constant mass at 50 C, and weighed to the nearest 0.01 gram. All aquatic invertebrates were microscopically sorted from the fine residual detritus, identified to the lowest possible taxon and enumerated. The residual detritus was also oven-dried and weighed, and added to the other leaf weights. Leaf species composition within leaf packs was surveyed quarterly and analyzed for differences in relative abundance by dry mass both between and within sites.

Prey availability, (i.e. the environmental complex of food organisms) was determined from the identifications and counts of invertebrates in the leaf packs. Densities were expressed as numbers of invertebrates per gram dry mass of leaf pack. Maximum head capsule width measurements (HCW) from individuals of each predaceous stonefly species were used to determine nymphal growth curves and to discern predator-prey size relationships. The nymphs of each stonefly species were apportioned into 2mm size classes and were graphed against mean prey size ingested. Predator food habits were assessed by examination of foregut contents as described by Hynes (1941). Each food item was identified and expressed as a percent by volume of the total gut contents. Prey items were identified to the lowest possible taxon, and all intact prey head capsules were measured to the nearest 0.001mm.

Mouthpart construction was examined for all stoneflies studied. Illustrations of the right maxilla (ventral view) and mandible (apical and ventral views) were made from intermediate sized middle-instar nymphs, to determine how closely these structures corresponded to individual diets. Prey preferences were estimated monthly for each major predator-prey complex, based on Jacobs' modified forage ratio and its natural log (Jacobs 1974).

Additional qualitative collections of leaf-inhabiting stoneflies were made during some months to supplement low numbers of nymphs in the quantitative samples. Adult stoneflies were collected to verify species identifications of nymphs. Methods included ultraviolet light trapping, random searching of stream banks, and rearing of mature nymphs collected from leaf packs.

At each site river discharge was measured monthly with a modified Kahl pigmy current meter, and temperature was continuously monitored with submersible Ryan temperature recorders. Site-specific chemical parameters were also measured and included pH, specific conductance, dissolved oxygen, total alkalinity, total hardness, turbidity, total solids, chlorides, orthophophate and nitrate nitrogen.

CHAPTER IV

RESULTS AND DISCUSSION

Physicochemical Parameters

The physical and chemical characteristics of each site are depicted in Figs. 2-4. During sampling, both sites were usually slightly acidic and possessed low total solids, chloride and nutrient levels. Each site generally responded alike in seasonal fluctuations of temperature (minima- 2.0 C, Jan.; maxima- 28-29 C, Jul.), dissolved oxygen (6 mg/l, Jun. to 10-12 mg/l, Nov.), specific conductance (20 µmhos/cm, Dec. to 35-50 µmhos/cm, Aug.), total alkalinity (4-6 mg/l, Dec. to 9-18 mg/l, Aug.), and total hardness (4-5 mg/l, Mar. to 14-22 mg/l, Sept., Oct.). River discharge fluctuated widely, but was generally lowest from summer through early autumn (low flows= 0.02 m^3/sec, Site I, Aug.; 0.09 m^3/sec, Site II, Sept.) and greatest from winter through spring (peak flows= 0.43 m^3/sec, Site I, Dec.; 1.14 m^3/sec, Site II, Dec.). Base flow conditions at each site were unusually low, due to the severe 1980 spring-summer drought. Specific conductance, total hardness, alkalinity and solids all responded inversely with discharge levels, since these parameters were either

Figure 2. Monthly variations in temperature (^{o}C), discharge (m^3/sec), dissolved oxygen (mg/l), and turbidity (NTU) at Sites I and II, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981.

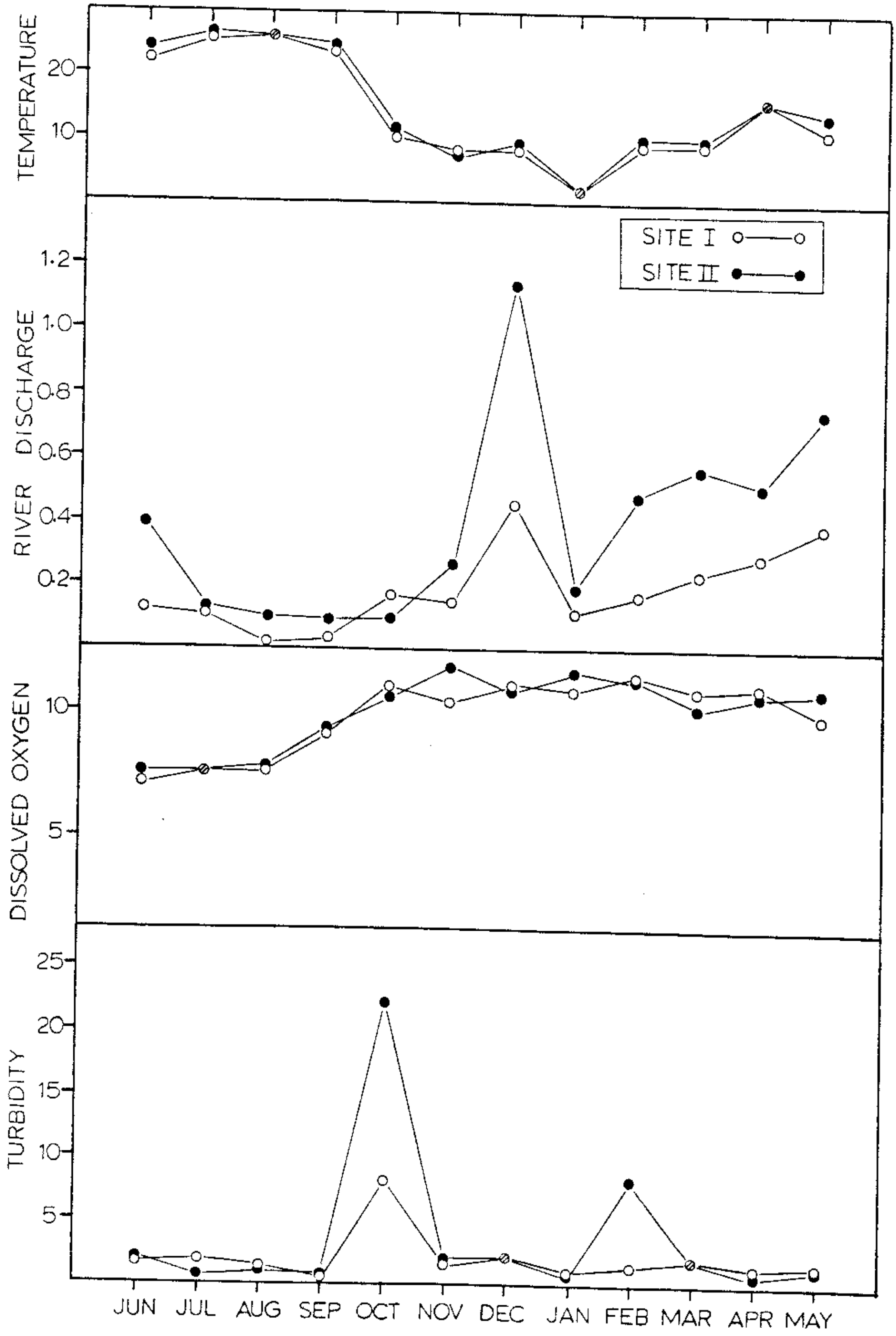

TEMPERATURE
20
10
SITE I
SITE II
RIVER DISCHARGE
1.2
1.0
0.8
0.6
0.4
0.2
DISSOLVED OXYGEN
10
5
TURBIDITY
25
20
15
10
5
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY

Figure 3. Monthly variations in chlorides (mg/l), total hardness and alkalinity (mg/l), and pH (units) at Sites I and II, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981.

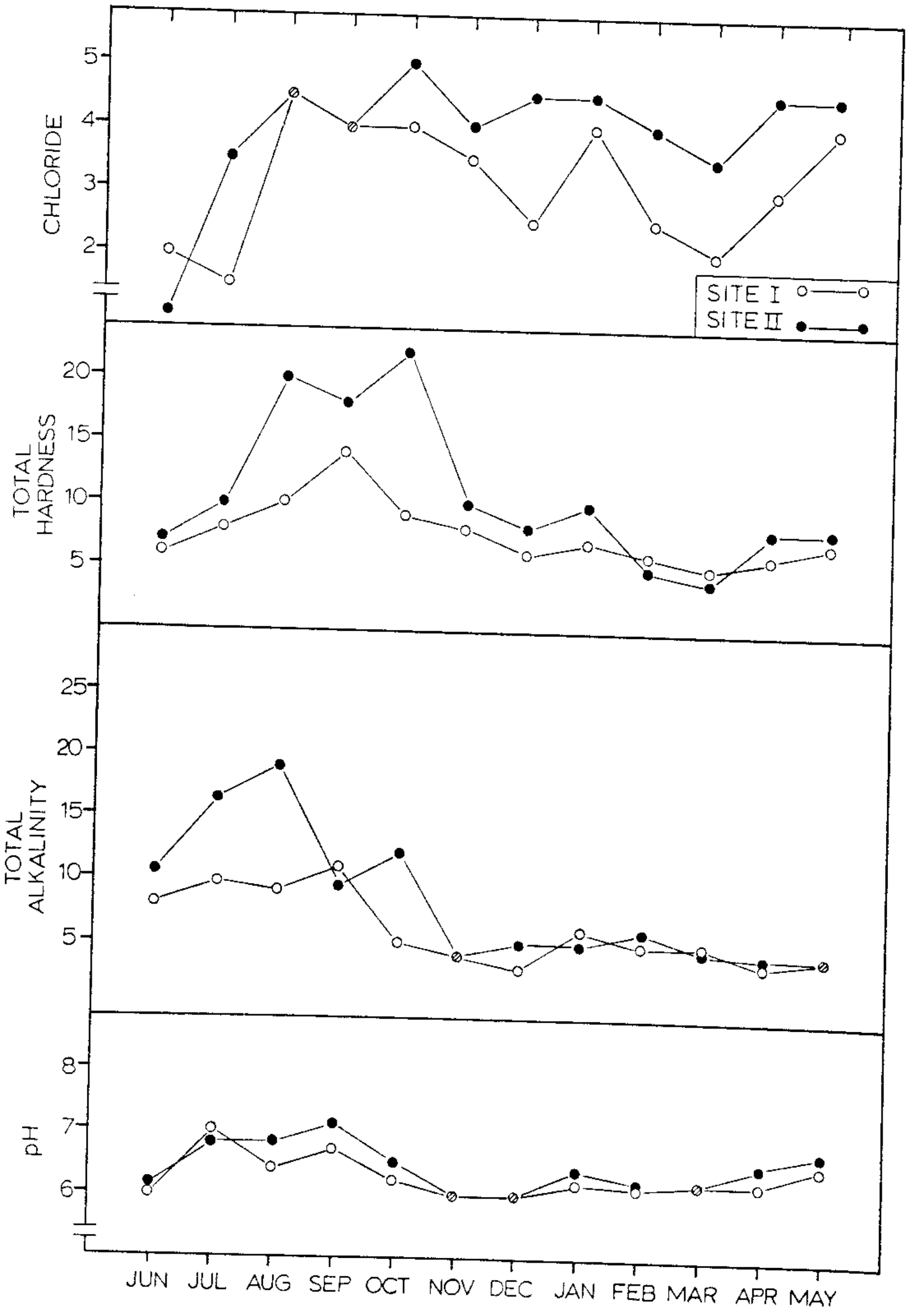
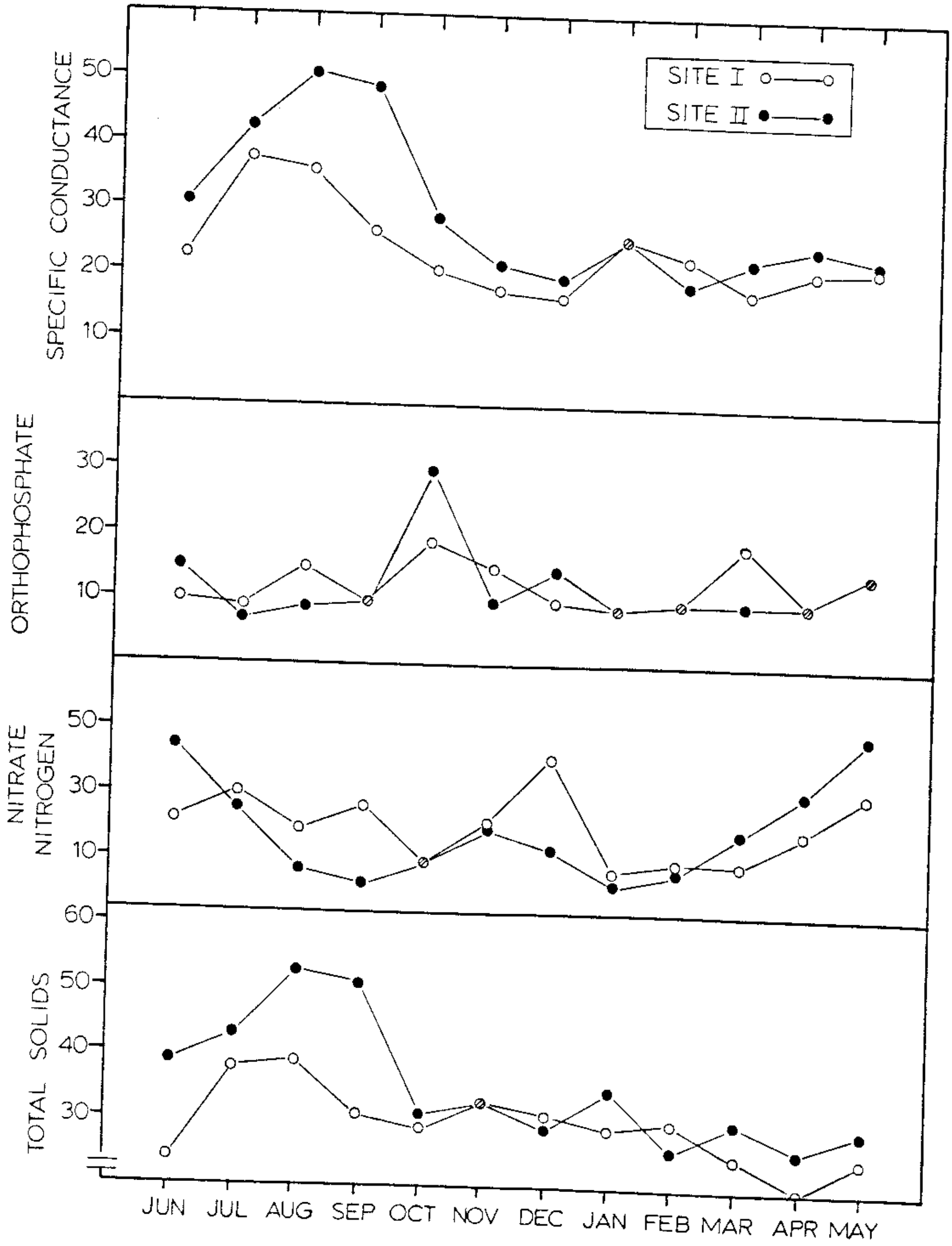

CHLORIDE
5
4
3
2
SITE I
SITE II
TOTAL HARDNESS
20
15
10
5
TOTAL ALKALINITY
25
20
15
10
5
pH
8
7
6
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY

Figure 4. Monthly variations in specific conductance (μmhos/cm), orthophosphate and nitrate nitrogen (μg/l), and total solids (mg/l) at Sites I and II, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981.


SITE I
SITE II
SPECIFIC CONDUCTANCE
50
40
30
20
10
ORTHOPHOSPHATE
30
20
10
NITRATE NITROGEN
50
30
10
TOTAL SOLIDS
60
50
40
30
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY

concentrated or diluted during periods of low and high flow, respectively. Turbidity was usually low (approximately 3 NTU) except in Oct. and Feb., when water samples, taken immediately following spates, contained large quantities of suspended matter. Despite very high discharge in Dec., turbidity levels were unaffected at the time of sampling, due to sustained high winter discharge and previous transport of suspended particles.

Leaf Pack Habitats

Like streams in most deciduous watersheds, the Little Missouri River received a large autumnal leaffall pulse from direct riparian input or blow-in from the adjacent valley slopes. Leaf packs, composed of numerous species, collected on submerged or emergent objects, and were usually available for sampling throughout the study period. Only in Jul. at Site I were leaf packs not present in ample quantities for collection. Site II consistently maintained relatively large amounts of well-conditioned leaves throughout the year, probably due to its lower gradient, greater amounts of organic import and a substrate that was more conducive to leaf entrapment (presence of wooden stakes and large cobble rocks). The sites did differ in stream distances between sampleable leaf packs. At Site II, leaf samples were in close proximity (< 15m apart) in all months. At Site I suitable leaf packs were more irregularly distributed along considerable stream distances (> 50-75m apart), particularly during seasons when leaf input was minimal. Well-conditioned leaves were rare during late summer at Site I (Aug., Sep.) due to low flow regimes. During these months fresh, relatively unconditioned leaf packs were collected almost exclusively.

At both sites, oak, sweetgum and American beech were the dominant species (Fig. 5). Between sites there were no clear trends in seasonal relative abundance of leaf species (Table 1). Leaf pack species composition tended to be most similar in winter ($p>0.05$, Mann-Whitney U test, Zar 1974) and least similar in spring ($p<0.05$). However, during autumn and summer, no consistent abundance patterns were observed for the majority of leaf species. In general, leaf packs at Site I contained greater percentages of sweetgum and beech leaves, while those at Site II contained greater percentages of oak leaves.

Within each site, consistent seasonal changes in leaf species abundances were observed and are summarized in Table 2. Percentages of sweetgum and maple were greatest in autumn ($p<0.05$, Student-Newman-Keuls MR test, Zar 1974), and subsequently decreased in later seasons, probably reflecting leaf abscission in autumn for both types, and rapid breakdown by microbial and invertebrate consumers.

Figure 5. Seasonal abundance by dry mass (g) of the major leaf species comprising natural leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981.

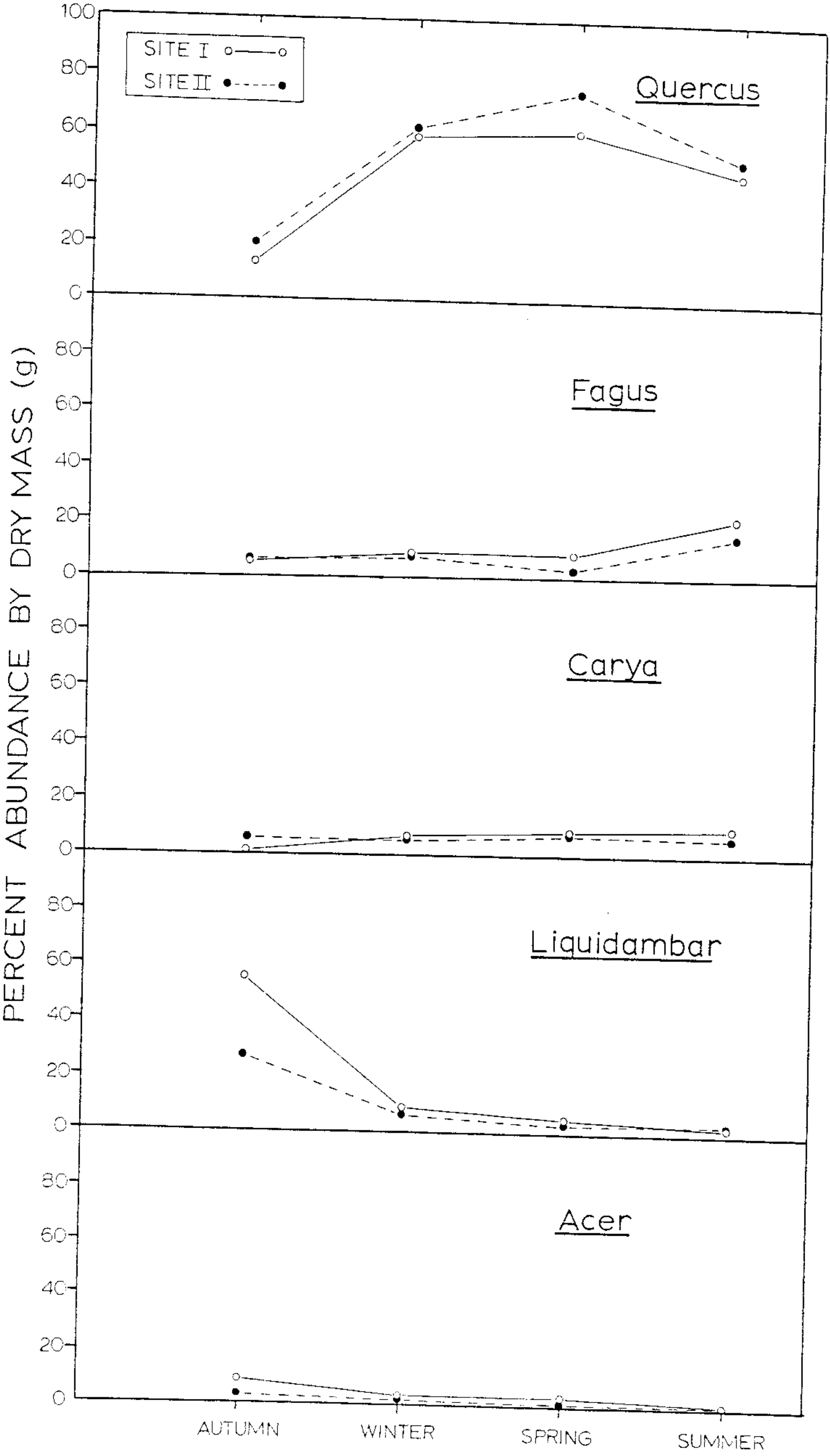

SITE I
SITE II
Quercus
Fagus
Carya
Liquidambar
Acer
PERCENT ABUNDANCE BY DRY MASS (g)
100
80
60
40
20
0
AUTUMN
WINTER
SPRING
SUMMER

Table 1. Mann-Whitney *U* results for between-site differences in abundance for the 5 major leaf types comprising natural leaf packs, Upper Little Missouri River, Arkansas, 1980-1981. Numbers represent mean % dry mass of total leaf pack. $\alpha=0.05$ (N=5).

SEASON	SITE I	SITE II	SIGNIFICANCE
	Acer spp.		
Fall	8.38	2.94	N.S.
Winter	3.24	1.51	N.S.
Spring	3.13	0.75	**$p<0.05$
Summer	0.75	0.67	N.S.
	Fagus grandifolia		
Fall	5.78	5.92	N.S.
Winter	8.36	6.17	N.S.
Spring	8.34	2.31	**$p<0.05$
Summer	21.59	15.22	**$p<0.05$
	Carya spp.		
Fall	1.50	6.28	**$p<0.05$
Winter	6.96	8.21	N.S.
Spring	8.45	7.41	N.S.
Summer	9.91	6.12	N.S.
	Liquidambar styraciflua		
Fall	55.95	27.78	**$p<0.05$
Winter	8.54	8.02	N.S.
Spring	5.29	3.70	**$p<0.05$
Summer	2.26	3.68	**$p<0.05$
	Quercus spp.		
Fall	12.37	19.93	**$p<0.05$
Winter	59.12	62.21	N.S.
Spring	61.86	74.86	**$p<0.05$
Summer	46.22	51.49	N.S.

Table 2. Student-Newman-Keuls multiple range test results for seasonal differences in abundance for the 5 major leaf types comprising natural leaf packs, Upper Little Missouri River, Arkansas, 1980-1981. Numbers represent mean percentage dry mass of total leaf pack. Means joined by horizontal lines are not significantly different at $\alpha=0.05$.[a]

		Quercus spp.		
SITE I	12.37 AUTUMN	46.22 SUMMER	59.12 WINTER	61.64 SPRING
SITE II	19.93 AUTUMN	51.49 SUMMER	62.20 WINTER	74.86 SPRING
		Fagus grandifolia		
SITE I	5.78 AUTUMN	8.34 SPRING	8.36 WINTER	21.59 SUMMER
SITE II	2.31 SPRING	5.92 AUTUMN	6.17 WINTER	15.22 SUMMER
		Carya spp.		
SITE I	1.50 AUTUMN	6.96 WINTER	8.45 SPRING	9.91 SUMMER
SITE II	6.02 SUMMER	6.28 AUTUMN	7.41 SPRING	8.21 WINTER
		Liquidambar styraciflua		
SITE I	2.23 SUMMER	5.29 SPRING	8.54 WINTER	55.95 AUTUMN
SITE II	3.58 SPRING	3.68 SUMMER	8.02 WINTER	27.78 AUTUMN
		Acer spp.		
SITE I	0.75 SUMMER	3.13 SPRING	3.24 WINTER	8.38 AUTUMN
SITE II	0.67 SUMMER	0.75 SPRING	1.51 WINTER	2.94 AUTUMN

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[a] (N=5).

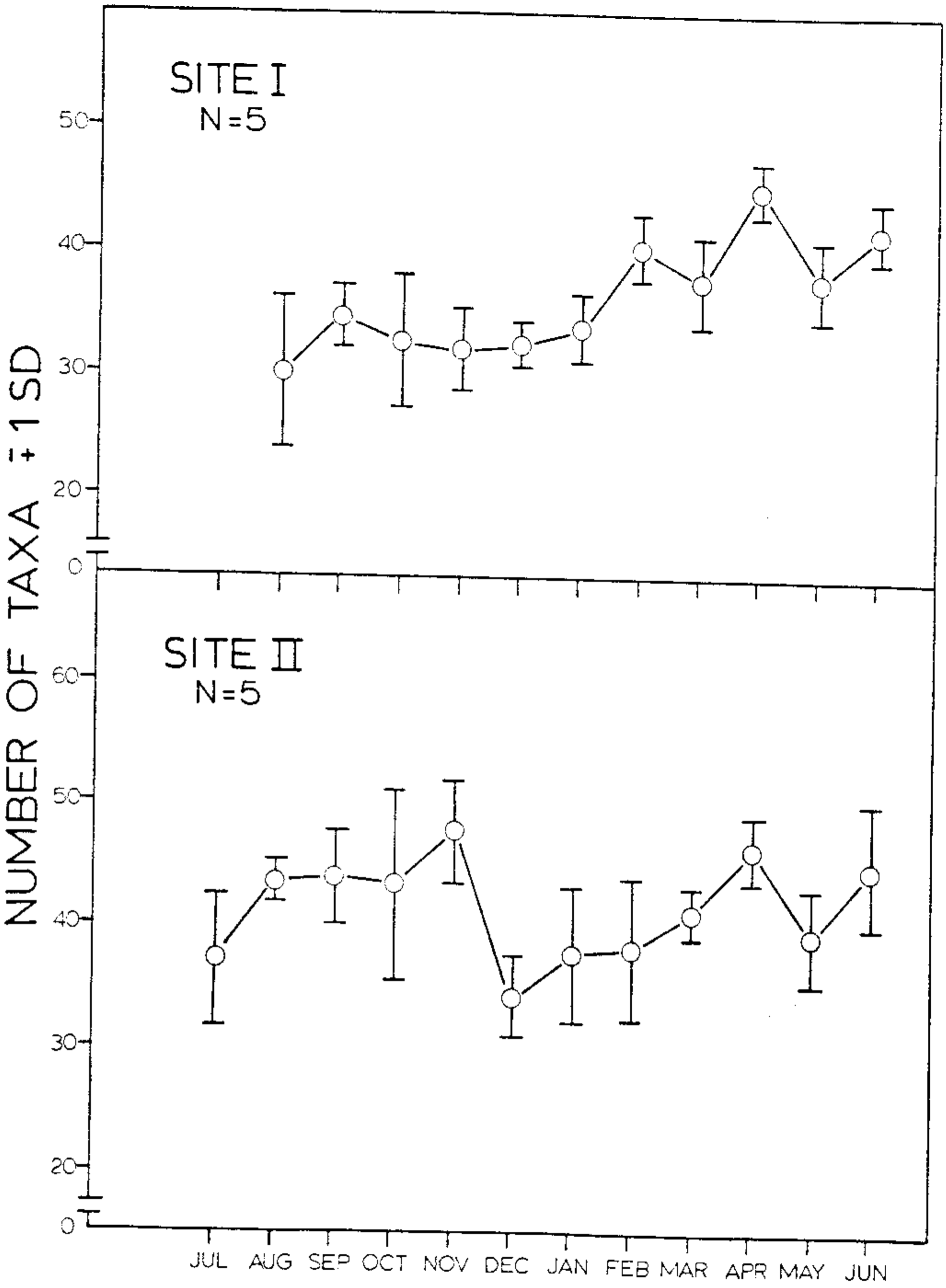
Maple is a rapidly decomposing or "fast" leaf type, with a relatively high percentage of labile compounds that readily dissociate from the leaf matrix after immersion (Peterson and Cummins 1974). No data concerning breakdown rates are available for sweetgum, and its rapid disappearance from leaf packs may also be attributable to processing. Qualitative differences in sweetgum leaf condition were observed each month after abscission (Oct.), with most leaves becoming discolored and at least partially skeletonized by Dec.

By contrast, percent abundance of oak and beech leaves in leaf packs was relatively low in autumn ($p<0.05$) and increased in subsequent seasons. Oak leaves were most abundant in winter and spring at both sites ($p<0.05$), and beech leaves were most common in summer leaf packs ($p<0.05$). The persistence of oak and beech, in contrast to maple and sweetgum, was probably due to their more refractory nature and lower acceptability as potential food for processing groups, which is consistent with their classification as "slow" leaves (Peterson and Cummins 1974; Suberkropp et al. 1975). Despite a major presence in leaf packs, hickory showed no significant seasonal differences at either site ($p>0.05$), and its incorporation into leaf packs may have been more related to random assortment, rather than to processing-related changes in seasonal abundance.

Leaf Pack Insects

Submerged leaves were an important substrate for many aquatic insects in all seasons, though they varied somewhat in monthly relative abundance. Species richness was roughly equivalent each month between sites, as is shown in Appendix A. Leaf packs at Site II contained slightly higher monthly numbers of taxa ($\bar{x}=41$) than Site I ($\bar{x}=36$) (Fig. 6). Site-specific coefficients of variation (CV) for species richness within each month were low, usually approximating 10 and rarely exceeding 20 percent sample variation. The relatively constant monthly numbers of insect species in leaf packs indicate that they were stable substrates, or were colonized quickly. Seasonal richness patterns were generally similar between sites except during summer-early autumn, when conditioned leaves and associated invertebrates were scarce at Site I. During other times, numbers of taxa tended to be lowest in winter and highest in spring and also in autumn for Site II. Most insect taxa underwent annual population cycling, but only the phenologies of baetid nymphs (*Baetis* spp., *Centroptilum rufostrigatum*), and dryopoid larvae and adults (*Microcylloepus pusillus*, *Stenelmis* spp., and *Helichus* spp.) accounted for the major fluctuations in total

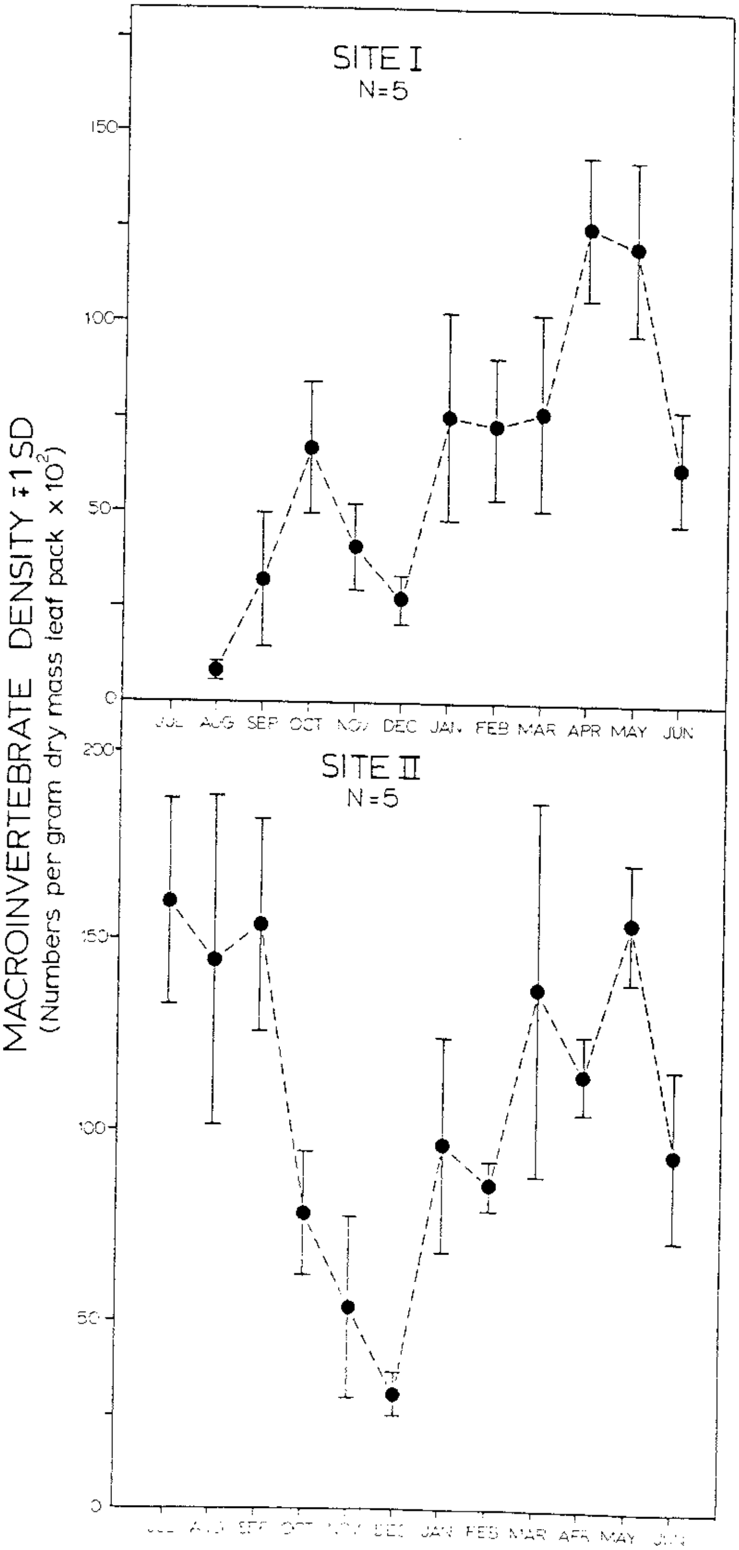
Figure 6. Seasonal variations in numbers of leaf-inhabiting invertebrate species, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Plotted values represent means ± one standard deviation.


SITE I
N=5
SITE II
N=5
NUMBER OF TAXA ±1 SD
50
40
30
20
0
60
50
40
30
20
0
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN

species numbers. Although caddisfly, stonefly and dipteran populations varied greatly throughout the year, their relative contributions to faunal richness remained constant, due to a uniform seasonal replacement of species.

Site-specific patterns in insect total density were also strongly tied to season (Fig. 7). Extremely low densities in Aug. and Sept. at Site I differed markedly from Site II, and probably were related to low availability of suitably conditioned leaf packs. During these months fresh or otherwise unconditioned leaves predominated at Site I, and were probably avoided by most colonizing insects (Benfield et al. 1977; Short et al. 1980). With this one exception, general seasonal trends in total density were similar between sites, with low numbers in winter months and high densities in spring and summer. Density decreases from late autumn through winter were largely due to mayfly and caddisfly emergence, and to increased availability of conditioned leaf packs for chironomids and other sympatric insects. Suitable leaf packs were noticeably more prevalent in both sites during this period than in summer or early autumn, owing to the large autumnal leaf input pulse. This superabundance of well conditioned leaves may have reduced rates of insect colonization and consequently diluted average densities per leaf pack. I speculate that high Dec. discharge regimes

Figure 7. Seasonal variations in total densities of leaf-inhabiting invertebrates, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Plotted values represent means ± one standard deviation.


SITE I
N=5
SITE II
N=5
MACROINVERTEBRATE DENSITY ±1 SD
(Numbers per gram dry mass leaf pack × 10²)
0
50
100
150
200
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN

may have also been a factor contributing to density reductions at both sites in that month (Fig. 2), when flow levels were at least twice as great as in any other month. High flows could have physically dislodged many insects from leaf packs, or possibly induced insect emigration into more stable stony, hyporheic substrates. Relatively high late-winter and spring densities were attributed to positive recruitment of chironomid larvae, baetid and heptageniid mayflies, and caddisflies, particularly Hydropsychidae and *Chimarra* spp. In addition, high densities may have resulted from a decrease in leaf pack biomass, which may have had a concentrating effect on insect numbers.

Systellognathan Stonefly Fauna

Sixteen systellognathan stonefly species (sensu Zwick 1973), representing three familes, occurred in leaf packs during the study (Table 3). Of these, *Phasganophora capitata* (Pictet), *Neoperla* spp.(2), *Perlesta* spp.(2), *Acroneuria* spp.(2), *Clioperla clio* (Newman) (formerly *Isoperla clio* (Newman), see Szczytko and Stewart 1981), *Helopicus nalatus* Frison, *Isoperla namata* Frison and *I. mohri* Frison were commonly collected. Only these dominant stoneflies are considered in the following discussion of life cycles and feeding ecology.

Table 3. Species list of systellognathan stoneflies collected from leaf packs, Upper Little Missouri River, Arkansas, 6 June 1980 to 21 May 1981.

Perlidae	*Phasganophora capitata* (Pictet)
	Neoperla catherae Stark and Baumann
	Neoperla sp. A[1]
	Perlesta spp.[2]
	Acroneuria perplexa Frison
	Acroneuria evoluta Klapalek
	Perlinella ephyre (Newman)
Perlodidae	*Clioperla clio* (Newman)
	Isoperla namata Frison
	Isoperla mohri Frison
	Helopicus nalatus (Frison)
	Hydroperla crosbyi (Needham and Claassen)
Chloroperlidae	*Alloperla hamata* Surdick
	Alloperla ouachita Stark and Stewart
	Hastaperla sp.

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[1] Undescribed species (B. P. Stark, personnal communication).

[2] Two undescribed species, currently recognized as *Perlesta placida* (B. P. Stark, personnal communication).

Two undescribed *Perlesta* species and two *Neoperla* species (one undescribed) were identified from adults. However, since these and *Acroneuria* nymphs are presently indistinguishable to species, assessment of life cycles and feeding differences within congeneric groups was precluded. Emergence data documented the presence of both *Perlesta* species during most dates light traps were used (Jun.-Jul.), although one species was usually numerically dominant over the other (approximately 9:1). *Acroneuria* emergence records showed considerable temporal overlap between *A. perplexa* Frison and *A. evoluta* Klapalek though *A. perplexa* was always more numerous and comprised approximately 80 percent of the adults collected (Table 4). Examination of *Neoperla* egg and adult characters revealed that the undescribed *Neoperla* species and *N. catherae* were temporally isolated, with the undescribed species reaching peak emergence in early summer (Jun.) and *N. catherae* during late summer-early autumn (Sept.).

Stonefly Density

Fig. 8 shows the seasonal abundance of the major systellognathan stoneflies that inhabited leaf packs. Due to large seasonal variance, densities were log-transformed. Perlid stoneflies reached greatest densities during late summer, early autumn and spring, with *Phasganophora*,

Table 4. Emergence records of adult Perlidae, Upper Little Missouri River, Arkansas, 4 June to 21 September 1980.

Phasganophora capitata

Date	Site	No. ♂	No. ♀	Total No.
4 June	II	0	4	4
6 June	II	7	1	8
12 June	II	15	8	23
12 June	I	4	0	4
13 June	II	6	0	6
30 June	II	1	15	16

Perlinella ephyre

Date	Site	No. ♂	No. ♀	Total No.
4 June	II	0	12	12
6 June	II	2	0	2
12 June	II	1	4	5
12 June	I	1	0	1
30 June	II	2	4	6
1 July	I	0	1	1

Perlesta spp.[a]

Date	Site	No. ♂	No. ♀	Total No.
4 June	II	4	25	29
6 June	II	13	3	16
12 June	II	14	19	33
12 June	I	7	6	13
13 June	II	14	11	25
30 June	II	33	203	236
1 July	I	0	5	5

Neoperla spp.

Date	Site	species A		*N. catherae*		Total no.
		no. ♂	no. ♀	no. ♂	no. ♀	
4 June	II	20	100	-	-	120
6 June	II	32	4	-	-	34
12 June	II	20	3	-	-	23
12 June	I	6	3	-	-	9
13 June	II	69	32	-	-	101
30 June	II	41	188	-	-	229
1 July	I	2	6	-	-	8
21 Sept	II	-	-	7	78	85

Table 4 continued.

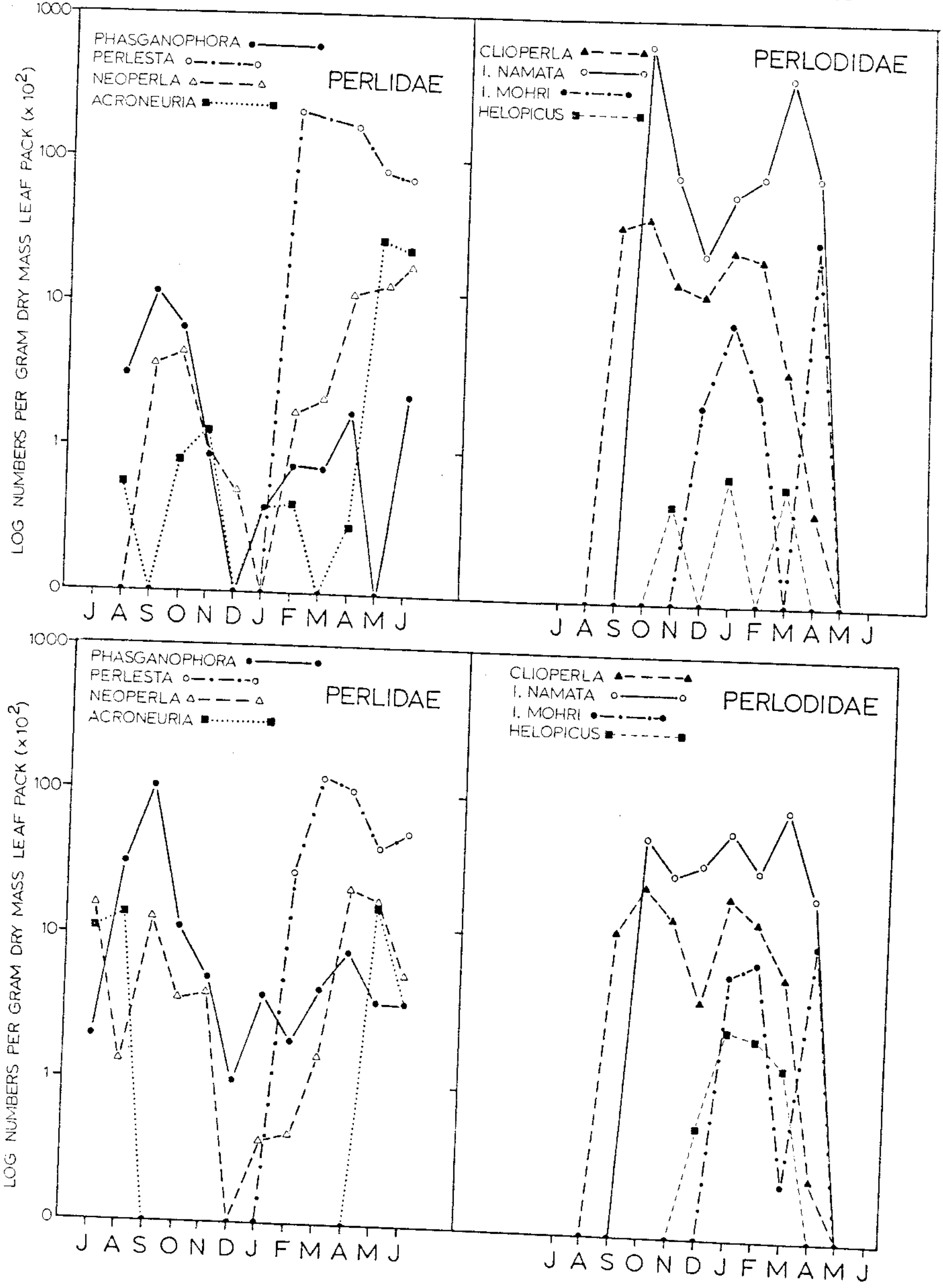
Acroneuria spp.

Date	Site	No. ♀		No. ♂[b]	Total no.
		A. perplexa	*A. evoluta*		
4 June	II	30	4	3	37
6 June	II	-	-	5	5
12 June	II	4	3	6	13
12 June	I	22	1	1	24
13 June	II	0	1	5	6
30 June	II	60	16	9	85

---

a- species not determined for entire emergence sample.
b- males not identified to species.

Figure 8. Seasonal density variations of systellognathan stoneflies inhabiting natural leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Plotted values represent means. Top panel: Site I; bottom panel: Site II.


PERLIDAE
PHASGANOPHORA
PERLESTA
NEOPERLA
ACRONEURIA
LOG NUMBERS PER GRAM DRY MASS LEAF PACK ($\times 10^2$)
1000
100
10
1
0
J A S O N D J F M A M J
PERLODIDAE
CLIOPERLA
I. NAMATA
I. MOHRI
HELOPICUS
J A S O N D J F M A M J
PERLIDAE
PHASGANOPHORA
PERLESTA
NEOPERLA
ACRONEURIA
LOG NUMBERS PER GRAM DRY MASS LEAF PACK ($\times 10^2$)
1000
100
10
1
0
J A S O N D J F M A M J
PERLODIDAE
CLIOPERLA
I. NAMATA
I. MOHRI
HELOPICUS
J A S O N D J F M A M J

Neoperla and Perlesta being the most dominant. Phasganophora densities were high in Sept. at both sites, following recruitment, and numbers steadily decreased, reaching their lowest levels in winter. Nymphs began to reappear in greater densities during the following spring prior to emergence of the earlier age class. Neoperla nymphs also exhibited sharp density decreases in winter and a subsequent increase in number the following spring and early summer. This suggests a habitat shift involving substantial nymphal emigration from leaves into other mineral substrates during quiescent stages of development.

Perlesta was the only perlid group to occur in large numbers in leaf packs throughout its nymphal life cycle. Their monthly densities and seasonal abundance patterns were equivalent at both sites. Acroneuria densities were sporadic, though in general, nymphs were more common at Site I and reached their highest abundance during summer (May to Aug.), just after recruitment of early instars. This cohort almost entirely disappeared from leaf samples by Oct. and was not collected in sizeable numbers again until May. Large Acroneuria specimens from earlier cohorts were rarely present at either site.

Perlodid stoneflies occurred in leaf packs only in autumn and spring; at these times they were numerically dominant over all other predaceous stoneflies (Fig. 8).

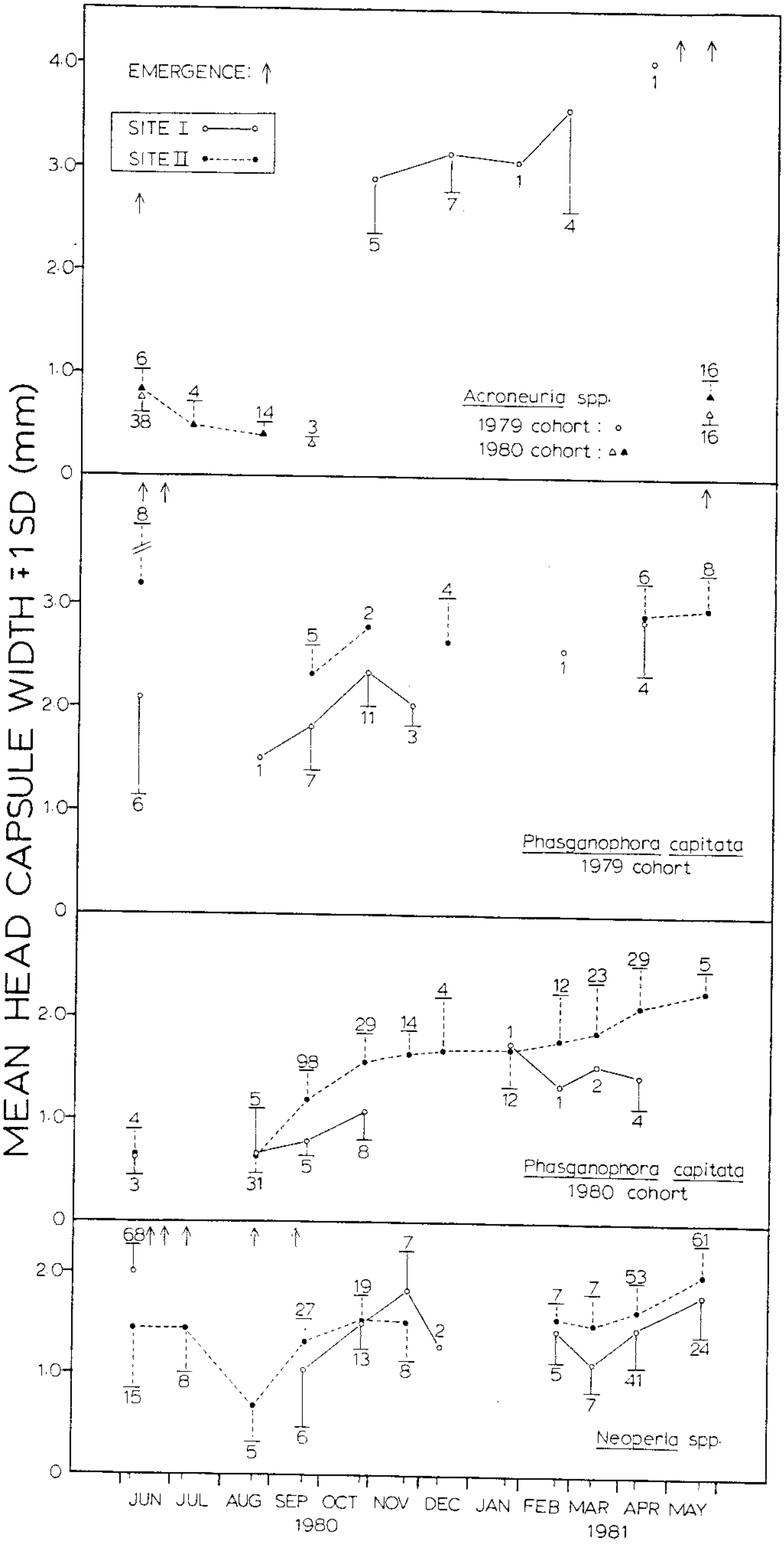
Clioperla clio and *Isoperla namata* were the most numerous species, and were regular components of the insect fauna throughout their nymphal development. Although they had overlapping life cycles, *I. namata* densities always greatly exceeded those of *Clioperla* during times when both were present. Abundances of both species in leaf packs tended to sag in Nov. and Dec., but recovered to more typical levels by Jan. As in the perlids *Phasganophora* and *Neoperla*, I feel that although natural mortality may have been partially responsible for this decline, density recovery in Jan. suggested a shift from leaf packs in Nov., Dec. perhaps related to variable monthly stream discharges, particularly in Dec. when flow levels were considerably greater than in adjacent months. A similar observation was made by Minshall and Minshall (1966) in a Kentucky stream; they felt that increased discharge was an important seasonal factor that reduced numbers of *Clioperla.* *Helopicus nalatus* was collected at Site II through most of winter and early spring, but densities never approached those of *Isoperla namata* and *Clioperla*. Monthly numbers of *Isoperla mohri* varied greatly, at times being fairly abundant (Jan., Feb., Apr.) or virtually absent from leaf packs (Mar.).

Life Cycles

Seasonal distribution and nymphal growth for Sites I and II (Figs. 9 and 10), indicate that all three basic insect life cycle patterns described by Hynes (1961) were exhibited by stoneflies in the Little Missouri River. *Neoperla* spp. displayed a slow seasonal cycle (S) (Fig. 9), with a short interval between oviposition and eclosion, followed by steady recruitment and nymphal growth through autumn. These stoneflies largely disappeared from winter leaf packs, but the relatively small increase in size of nymphs by early spring indicated a slowing or perhaps complete cessation of growth during winter months. Vaught and Stewart (1974) reported a similar life cycle for *Neoperla clymene* in the Brazos River, Texas and suggested that differential growth rates were caused by seasonal changes in stream temperature.

Phasganophora capitata and *Acroneuria* spp. (Fig. 9) were the only semivoltine stoneflies, and possessed two or three-year life cycles. The life histories of these large perlids generally fit the non-seasonal or "N" pattern (Hynes 1961), although small sample sizes of *Acroneuria* through most months prevented an adequate assessment of growth. Maximum nymphal growth of *Phasganophora* during the first year (1980 cohort) took place in Sept. and Oct., which was followed by a sharp decline in growth rates

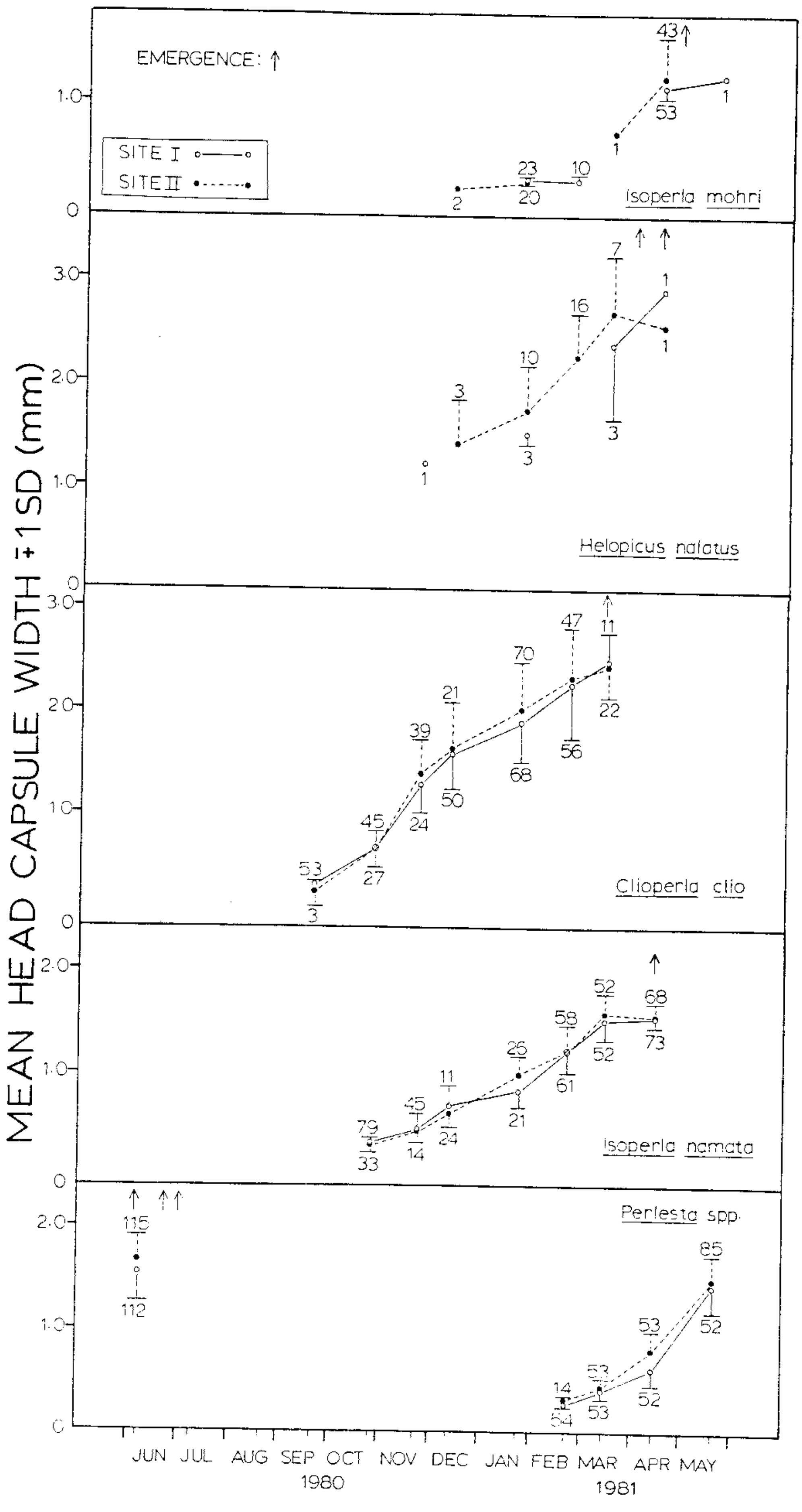
Figure 9. Seasonal distribution and growth of Acroneuria spp., Phasganophora capitata, and Neoperla spp., collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Solid lines represent those individuals from Site I; dashed lines for those from Site II. Plotted values indicate means ± one standard deviation. Numbers represent sample size of stoneflies measured at each interval.


MEAN HEAD CAPSULE WIDTH ∓1 SD (mm)
EMERGENCE: ↑
SITE I
SITE II
Acroneuria spp.
1979 cohort : ○
1980 cohort : △▲
Phasganophora capitata
1979 cohort
Phasganophora capitata
1980 cohort
Neoperla spp.
0
1.0
2.0
3.0
4.0
JUN
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
1980
1981

during winter, and a subsequent recovery phase in late spring. Though large *Phasganophora* nymphs were scarce, two distinct size classes were usually present in the samples. This suggests a two-year life cycle, and concurs with Harper's conclusions (1973) concerning voltinism in southern Ontario *Phasganophora* populations.

Five univoltine stoneflies exhibited fast seasonal cycles (F), with an extended egg or nymphal diapause, rapid growth, and emergence in spring or early summer (Fig. 10). The three most abundant taxa, *Clioperla clio*, *Isoperla namata*, and *Perlesta* spp. were sympatric over most of their life cycles. However, there was a marked dissimilarity in nymphal sizes between species through all months, probably due to differential eclosion or growth rates. Early instar *Clioperla* appeared approximately one month before *I. namata*, which were collected four months earlier than recruited *Perlesta* nymphs. For *Clioperla*, fastest growth rates occurred from Oct. to Nov., though in general, nymphs steadily increased in size unitl Mar. emergence. The length of *Clioperla*'s life cycle in the Little Missouri River was approximately two months less and emergence two months earlier than in populations reported from more northern latitudes (Southern Ontario: Harper 1973; Kentucky: Minshall and Minshall 1966), but agrees with the peak emergence time reported from a North Alabama stream of

Figure 10. Seasonal distribution and growth of *Isoperla mohri*, *Helopicus nalatus*, *Clioperla clio*, *Isoperla namata*, and *Perlesta* spp., collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Solid lines represent those individuals from Site I; dashed lines for those from Site II. Plotted values indicate means ± one standard deviation. Numbers represent sample size of stoneflies measured at each interval.


EMERGENCE: ↑
SITE I ○——○
SITE II ●- - - -●
Isoperla mohri
Helopicus nalatus
Clioperla clio
Isoperla namata
Perlesta spp.
MEAN HEAD CAPSULE WIDTH ∓1 SD (mm)
0
1.0
2.0
3.0
JUN JUL AUG SEP OCT NOV DEC JAN FEB MAR APR MAY
1980
1981
2
23
20
10
1
43
53
3
16
7
70
47
11
22
56
68
21
39
50
24
45
27
53
79
33
14
26
58
52
61
73
115
112
85
54

similar latitude (Jayne 1978). This suggests that temperature and perhaps photoperiod differences in lower latitudes may act to accelerate growth and reduce time to emergence, thus shortening the total nymphal development period for *Clioperla*.

Growth of *I. namata* (Fig. 10) proceeded at similar rates in both sites, with uniform growth through the first five months (Oct.-Mar.) followed by a Mar.-Apr. leveling-off period. A sustained emergence during this latter interval was documented by laboratory rearing studies of pre-emergent nymphs, and field observations which showed no growth and a decline in density (Fig. 8). *Perlesta* exhibited the longest diapause period (approximately seven months) and, consequently, were the fastest to complete their nymphal development (Fig. 10). Maximum growth during the Apr.-May interval and mid-June emergence resembled observations made by Snellen and Stewart (1979) of *Perlesta placida* in northern Texas. However, hatching times (Oct.-Nov.) and length of the growth cycle (8 months) for Texas populations were considerably earlier and longer respectively, than *Perlesta* spp. from the Little Missouri River. I did not perform egg incubation experiments to precisely determine eclosion, which may account for the discrepancy in hatching time. However, nymphal sizes of *P. placida* collected in Nov.

(Snellen and Stewart 1979) were similar to Feb. Perlesta spp. from the Little Missouri River, which would indicate a three-month nymphal diapause if hatching times were equivalent.

Helopicus nalatus was the largest perlodid stonefly to possess a fast seasonal cycle (maximum HCW =3.31mm), and was first collected in Nov.-Dec. leaf packs. Intermediate-sized nymphs appeared at this time (approximately 1.2mm HCW), and exhibited rapid, continual growth until emergence in mid-March (Fig. 10). This growth cycle resembled that of Hydroperla crosbyi from northern Texas (Oberndorfer and Stewart 1977), a perlodid that is morphologically very similar and closely related to Helopicus. Despite its sporadic occurrence in leaves, the growth of Isoperla mohri showed an extended initial phase of little growth (Dec.-Feb.) and a subsequent acute growth increase (Feb.-Apr.) leading up to emergence (Fig. 10).

Common Prey Groups

A wide variety of stream organisms were subject to stonefly predation (see Appendix B). However, most taxa were only periodically ingested, and thus did not represent prominent dietary components of predators. Table 5 lists the dominant items in stonefly guts, and the log-transformed seasonal abundances of the major prey

Table 5. List of commonly ingested insect prey categories and taxa included in food habit analysis of stoneflies, Upper Little Missouri River, Arkansas, June 1980 - May 1981.

MAJOR PREY CATEGORY	TAXA INCLUDED
Ephemeroptera	*Baetis* spp.
	Centroptilum sp.
	Pseudocloeon spp.
	Misc. Baetidae
	Paraleptophlebia sp.
	Stenonema spp.
	Heptagenia sp.
	Misc. Heptageniidae
Plecoptera	*Allocapnia* spp.
	Amphinemura delosa
	Taeniopteryx burksi
	Misc. Leuctridae
	Misc. Euholognatha
Trichoptera	*Cheumatopsyche* sp.
	Hydropsyche sp.
	Misc. Hydropsychidae
	Chimarra sp.
	Agapetus sp.
	Misc. Trichoptera
Simuliidae	*Simulium* sp.
	Prosimulium sp.
	Misc. Simuliidae
Corynoneurini	*Corynoneura* sp.
	Misc. Corynoneurini
Orthocladiinae	Misc. Orthocladiine
Misc. Chironomidae	Misc. Tanypodinae
	Misc. Tanytarsini
	Misc. Chironomini

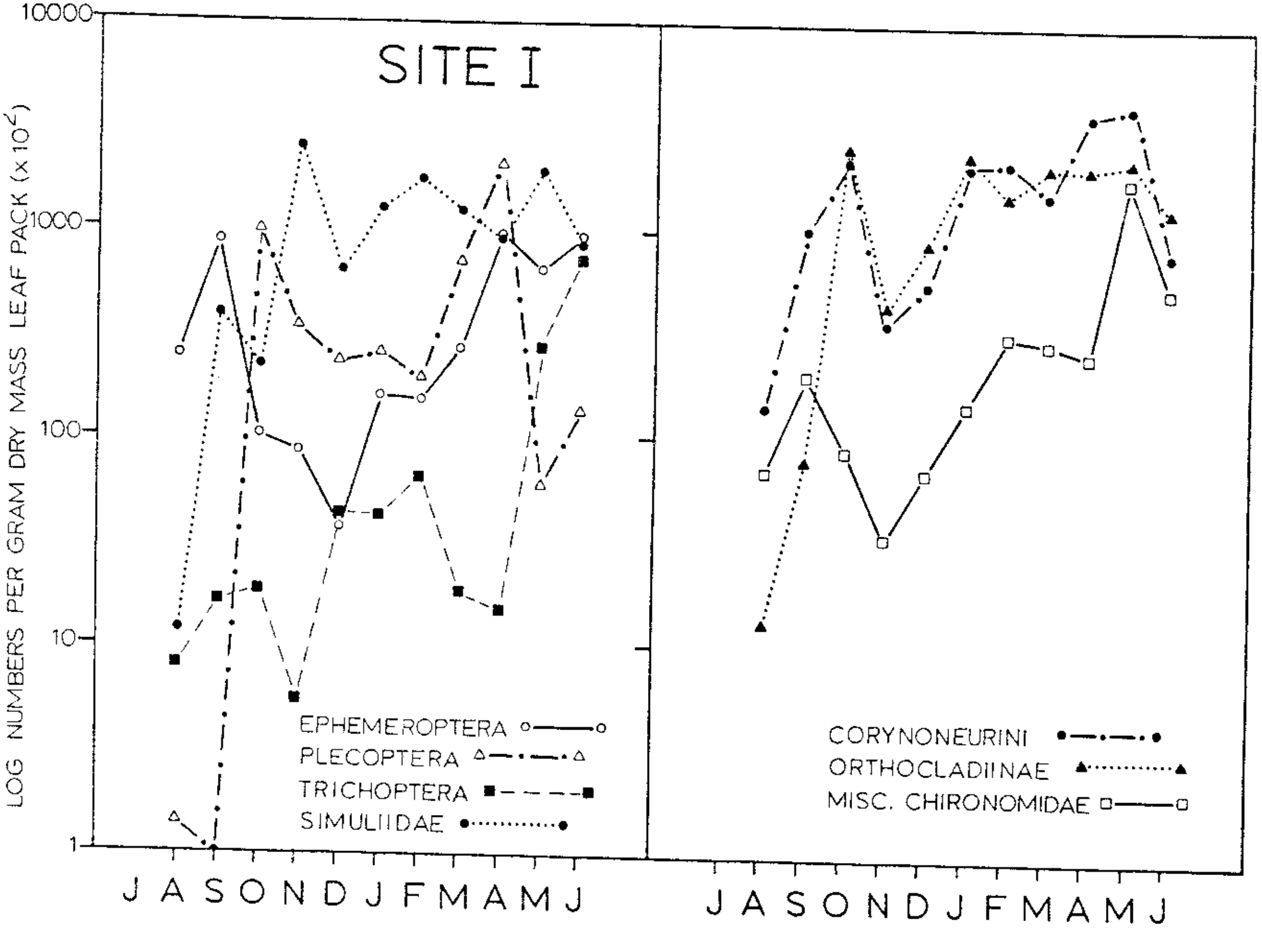
categories for each taxon are given in Fig. 11. The orthoclad Chironomidae usually outnumbered all other insect taxa in the leaf packs at both sites. The Corynoneurini, a tribe of small midges, were the most abundant insects, and comprised as much as 50-60% of the total benthic fauna (Oct., Feb.-Apr., Site II). Simuliidae were also numerically dominant during some months, especially during the recruitment stages of *Prosimulium* sp. in late autumn (20-60%) and *Simulium* sp. in spring and summer (11-23%).

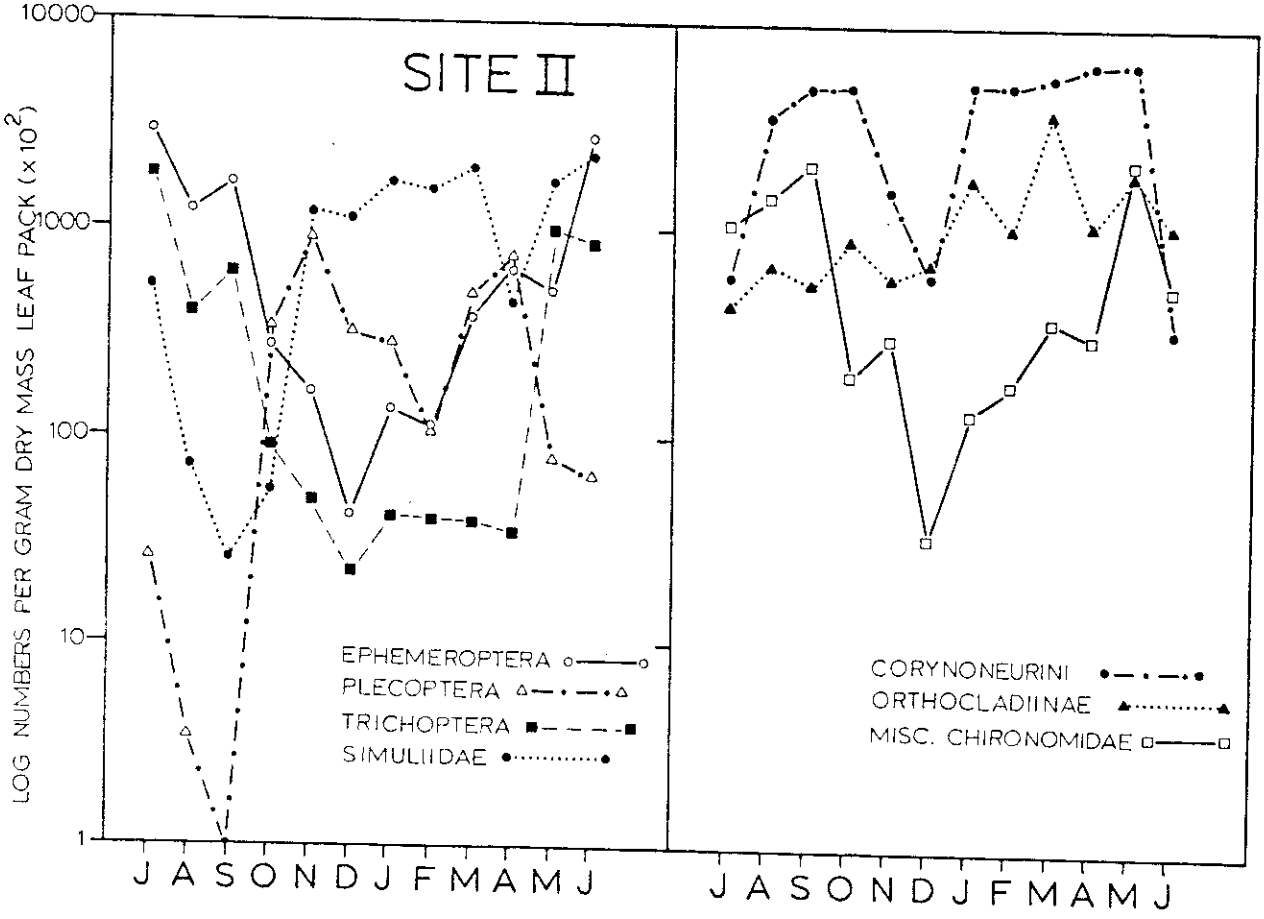
Euholognathan stoneflies usually made only minor contributions to insect densities, although recruited *Allocapnia* spp., *Taeniopteryx burksi* and other non-predaceous stoneflies occasionally comprised 15-20% of the total insect standing crop (Oct., Nov., Apr.). The importance of Ephemeroptera and Trichoptera as prey varied seasonally, with both groups exhibiting peak densities in spring and summer, and subsequent reductions in numbers during autumn and winter. Taxa most responsible for high spring/summer densities were the mayflies *Baetis* spp., *Centroptilum rufostrigatum* and *Stenonema* spp. (15-27%), and the caddisflies *Cheumatopsyche* spp. and *Chimarra* spp. (7-11%).

Stonefly Food Habits

Foregut analysis was performed on 2860 systellognathan

Figure 11. Seasonal density variations of major prey groups in leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Plotted values represent means.


SITE I
LOG NUMBERS PER GRAM DRY MASS LEAF PACK (x 10²)
10000
1000
100
10
1
EPHEMEROPTERA ○——○
PLECOPTERA △—·—·—△
TRICHOPTERA ■— — —■
SIMULIIDAE ●··········●
CORYNONEURINI ●—·—·—●
ORTHOCLADIINAE ▲··········▲
MISC. CHIRONOMIDAE □——□
J A S O N D J F M A M J
J A S O N D J F M A M J


SITE II
LOG NUMBERS PER GRAM DRY MASS LEAF PACK (x 10²)
10000
1000
100
10
1
EPHEMEROPTERA ○——○
PLECOPTERA △—·—·—△
TRICHOPTERA ■— — —■
SIMULIIDAE ●··········●
CORYNONEURINI ●—·—·—●
ORTHOCLADIINAE ▲··········▲
MISC. CHIRONOMIDAE □——□
J A S O N D J F M A M J
J A S O N D J F M A M J

stoneflies, specifically noting diet composition, relative fullness and prey sizes ingested. Twenty to 25% of the foreguts were empty, mostly from freshly molted teneral individuals, or possibly from those that were beginning to molt.

Sampling was not designed to allow a definitive analysis of diel feeding periodicity. However, the fresh prey seen in most guts and the low percentage of totally empty foreguts, from predators collected in early to mid-morning, probably indicates that stonefly predators were nocturnally active. Many others have made similar observations (Brinck 1949; Vaught and Stewart 1974; Kovalak 1978; Johnson 1981), though Allan (1982) cautioned that large foregut volumes in morning samples does not necessarily provide evidence for nocturnal foraging, but rather may represent a slowing of digestion, and thus a greater food retention time during the cooler night temperatures. This contention needs further analysis, with intensive diel sampling and laboratory feeding study.

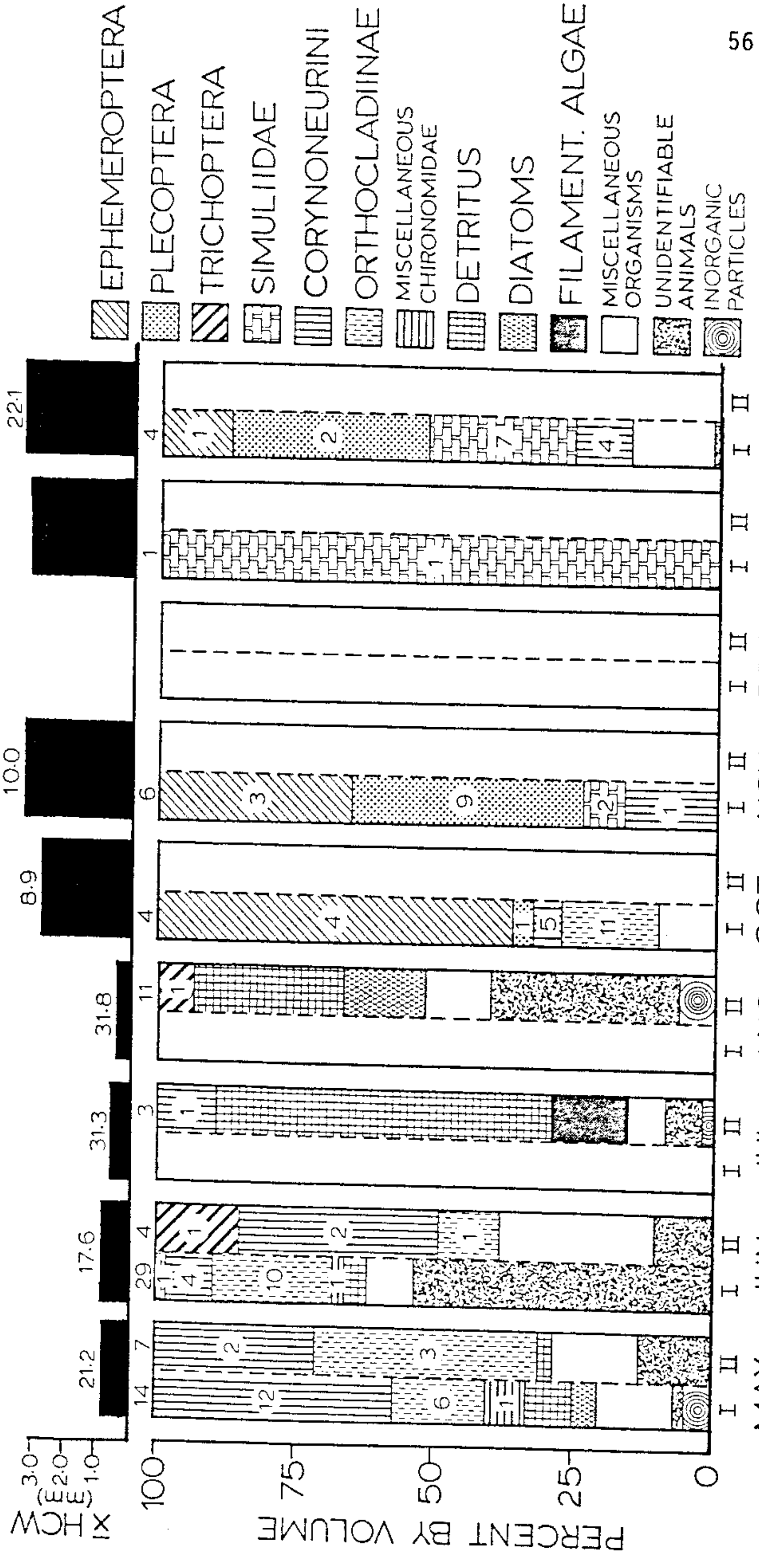
As noted by other investigators (Cather and Gaufin 1975; Oberndorfer and Stewart 1977; Swapp 1972), foreguts from pre-emergent nymphs in the Little Missouri River contained little to no food. In many instances the gut walls of these nymphs appeared unusually membranous and completely lacked the typical anteriorly-directed sclerotized hooks in the proventriculus (Hynes 1941). This suggests either an alteration or resorption of the foregut wall prior to transformation.

Figs. 12-20 depict seasonal sizes (top graph) and site-specific food habits (bottom graph) for the principal systellognathan stoneflies through their nymphal development and/or occurrence in leaf packs. The monthly mean of each major dietary fraction was expressed as a percent by volume and coded to show a particular food item (see legend). Those months with bars entirely lacking food categories represent periods when no nymphs were collected, or occasionally when all examined foreguts were empty. Mean sizes of fed stonefly predators, pooled from both sites, are illustrated above monthly food habits.

Acroneuria spp.

Nymphs were carnivorous through virtually all but the first few instars. Recruited nymphs (1980 cohort) were common in May and Jun. leaf packs and fed mostly on Corynoneurini, miscellaneous orthoclads (Fig. 12), and also other small invertebrates (e.g. Cladocera, Hydracarina and Rhizopodea). By Jul. the $\bar{x}$ stonefly size declined with the appearance of a second cohort, and overall numbers also dropped, possibly due to an emigration of the older nymphs to more favorable microhabitats. Food habits of the

Figure 12. Seasonal variations in stonefly head capsule width (top graph) and food habits (bottom graph) for 83 *Acroneuria* spp. nymphs collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Dietary fractions are expressed as a percent by volume to the total gut composition. Numbers within each specific prey category represent the total number of prey eaten. Numbers at the top of each food habit bar indicate number of foreguts examined that contained food. Roman numerals along the horizontal axis indicate site. Those months with bars entirely lacking food categories represent periods when no nymphs were collected. Numbers at the top of each HCW bar are percent coefficient of variation. Food habits from May through August are for the 1980 cohort; those October through February are for the pre-1980 cohort.



Acroneuria spp.

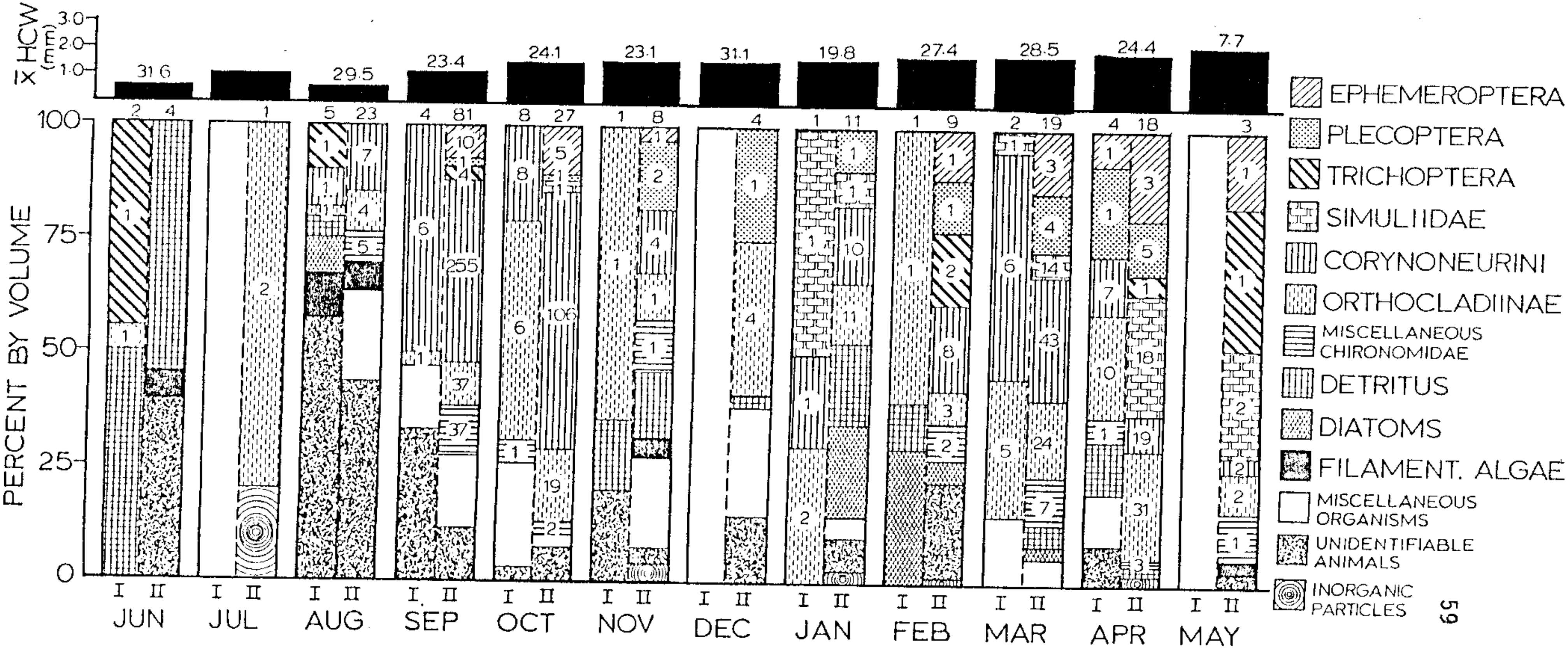
younger instars included larger non-animal fractions composed of fine particulate detritus, diatoms and filamentous algae. Neither cohort was collected in leaf packs after Aug. Large Acroneuria (HCW > 2.7mm) were present only in Site I and were strict carnivores. In each month the nymphs fed predominantly on larger-bodied prey (e.g. mayflies, stoneflies and simuliids), and proportionately less on the abundant but relatively small-sized chironomids. However, small sample size in each instance may have overemphasized the role these larger insects play as important prey groups.

Phasganophora capitata

The diet of this semivoltine species is illustrated on two separate graphs, one showing the 1980 cohort (Fig.13), and the second showing the larger nymphs from the previous generation (Fig. 14). The nymphs were carnivorous in all but the earliest instars (Jun.) (Fig. 13), though these data may have been biased by low sample size. Small to intermediate-sized nymphs (HCW= 0.5-2.1mm) were usually more abundant at Site II, though diets overall between sites were similar. Corynoneurini and miscellaneous orthoclads were the predominant prey taken by these nymphs in volume (40-70%) and numbers ingested (80%). Simuliid prey increased in importance for intermediate-sized

Figure 13. Seasonal variations in stonefly head capsule width (top graph) and food habits (bottom graph) for 237 Phasganophora capitata nymphs (1980 cohort) collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Dietary fractions are expressed as a percent by volume to the total gut composition. Numbers within each specific prey category represent the total number of prey eaten. Numbers at the top of each food habit bar indicate number of foreguts examined that contained food. Roman numerals along the horizontal axis indicate site. Those months with bars entirely lacking food categories represent periods when no nymphs were collected. Numbers at the top of each HCW bar are percent coefficient of variation.

Phasganophora capitata



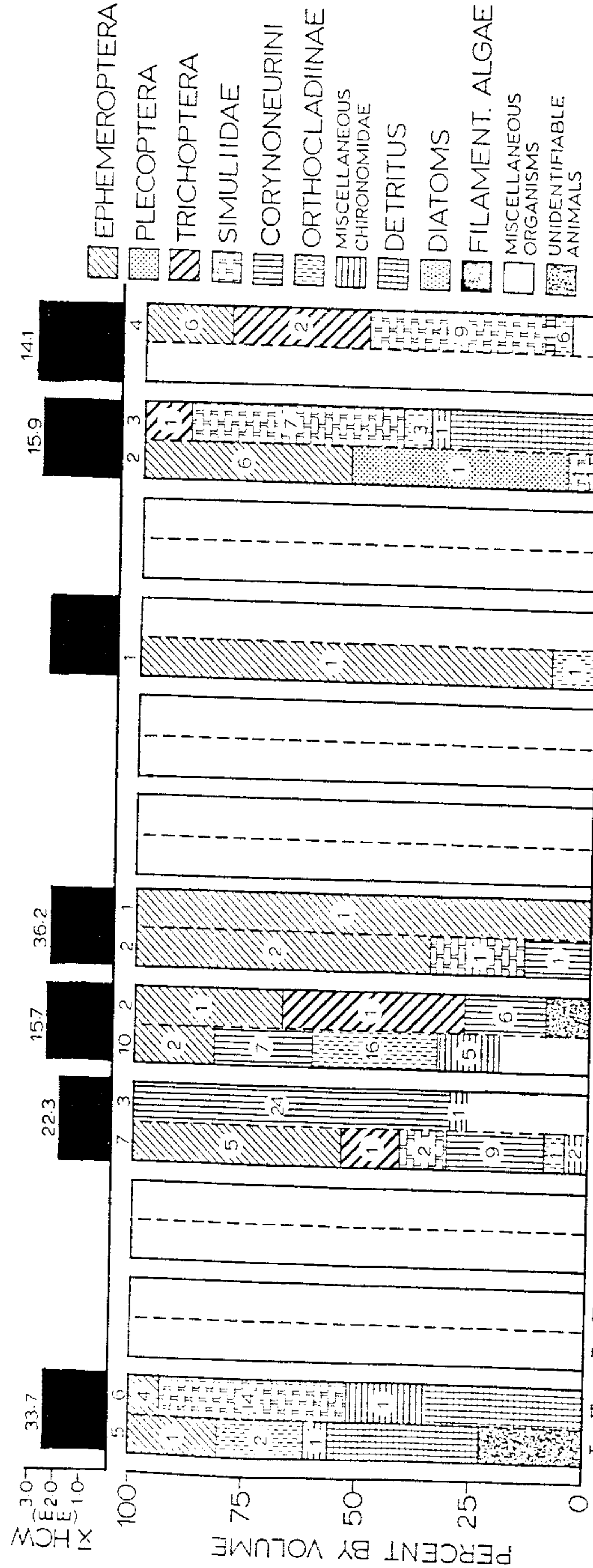
Phasganophora during Apr. and May (Site II) when recruited Simulium sp. appeared in the leaf packs. Young mayflies (Baetidae) and stoneflies (Allocapnia) were more frequently eaten during these months as well, although neither group exceeded 20% by volume of Phasganophora's diet.

Variable numbers of larger Phasganophora (HCW= 2.0-3.2mm) (Fig. 14) precluded a thorough analysis of seasonal food habits. Large volumes of detritus in foreguts during Jun. and Apr. (Site II) in all likelihood had been accidentally ingested by foraging nymphs, or possibly came from prey guts. A preponderance of large prey insects, such as Baetis spp., Pseudocloeon sp. and Simulium sp. occurred in the spring diet of these larger Phasganophora at Site II, when chironomids were only occasionally consumed, despite high leaf pack densities. Chironomids were important dietary fractions only in Sept., Site I and Oct., Site II.

These observations generally support results cited in other Phasganophora capitata feeding studies. Chironomids were predominant prey items, followed in importance by mayflies (Johnson 1981, and Shapas and Hilsenhoff 1976), although neither study addressed seasonal shifts in prey with increasing predator size. Kovalak (1978) found that chironomids were of minor importance relative to larger-bodied caddisflies, mayflies and simuliids in the

Figure 14. Seasonal variations in stonefly head capsule width (top graph) and food habits (bottom graph) for 46 Phasganophora capitata nymphs (1979 cohort) collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Dietary fractions are expressed as a percent by volume to the total gut composition. Numbers within each specific prey category represent the total number of prey eaten. Numbers at the top of each food habit bar indicate number of foreguts examined that contained food. Roman numerals along the horizontal axis indicate site. Those months with bars entirely lacking food categories represent periods when no nymphs were collected. Numbers at the top of each HCW bar are percent coefficient of variation.

Phasganophora capitata



diets of small and large *Phasganophora* size classes. Despite the limited number of larger nymphs I encountered and studied (N= 46), there was a decided shift from a chironomid-based diet in smaller instars to larger mayflies and simuliids in later instars. Allan (1982) also observed similar size-related feeding shifts toward larger prey by *Claassenia sabulosa* and *Megarcys signata* from a Colorado river.

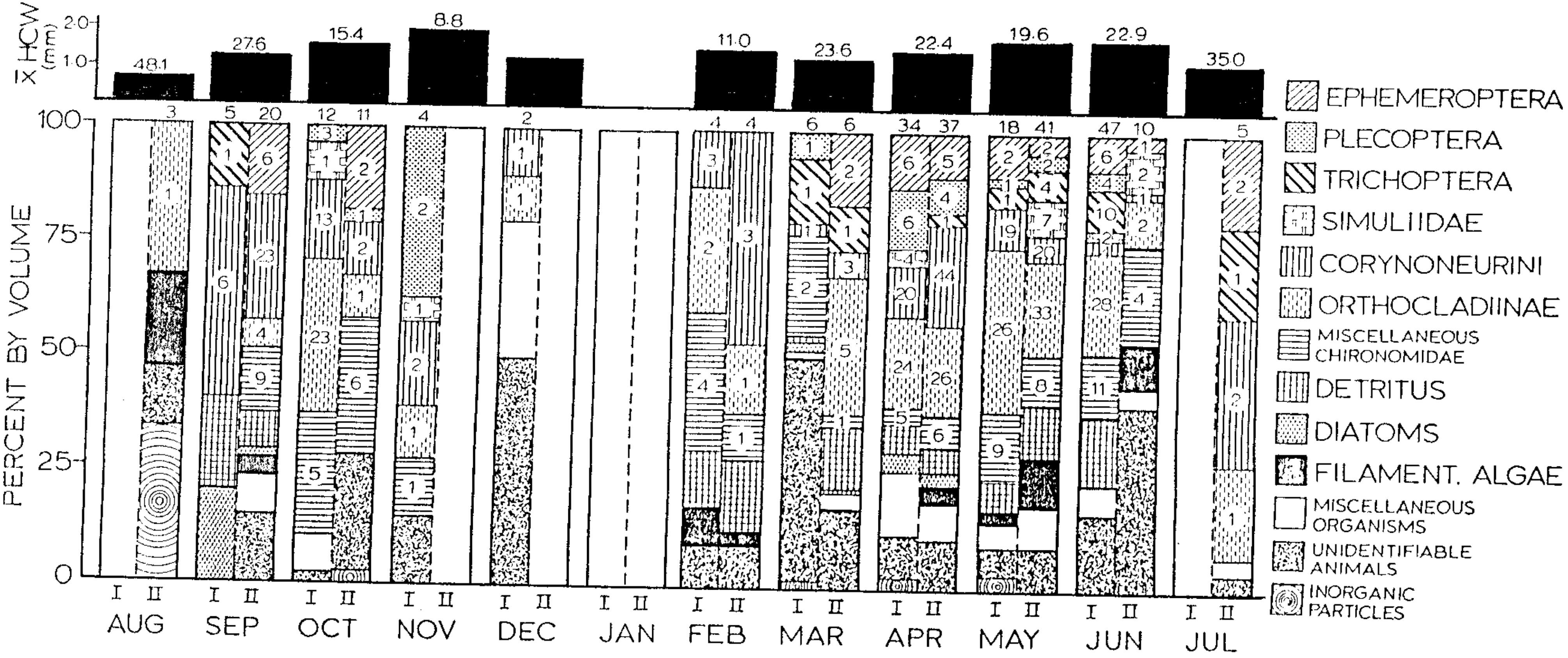
Neoperla spp.

During most months *Neoperla* spp. nymphs were carnivorous and relied heavily on chironomid prey, especially Corynoneurini, miscellaneous orthoclads and Tanypodinae (Fig. 15) (overall 47% by vol. and 73% by number). Baetid and heptageniid mayflies, hydropsychid caddisflies and stoneflies (*Taeniopteryx* and early instar *Acroneuria*) increased in importance from late winter through early summer, when their early instars appeared in the leaf packs. At this interval, *Neoperla* were apparently of suitable size to harvest them. Detritus, filamentous green algae and diatoms were consistently present in foreguts from Feb.-Jun. These relatively small volumes probably came from prey guts and by accidental ingestion during feeding.

Vaught and Stewart (1974) reported markedly different

Figure 15. Seasonal variations in stonefly head capsule width (top graph) and food habits (bottom graph) for 269 Neoperla spp. nymphs collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Dietary fractions are expressed as a percent by volume to the total gut composition. Numbers within each specific prey category represent the total number of prey eaten. Numbers at the top of each food habit bar indicate numbers of foreguts examined that contained food. Roman numerals along the horizontal axis indicate site. Those months with bars entirely lacking food categories represent periods when no nymphs were collected. Numbers at the top of each HCW bar are percent coefficient of variation.

Neoperla spp.



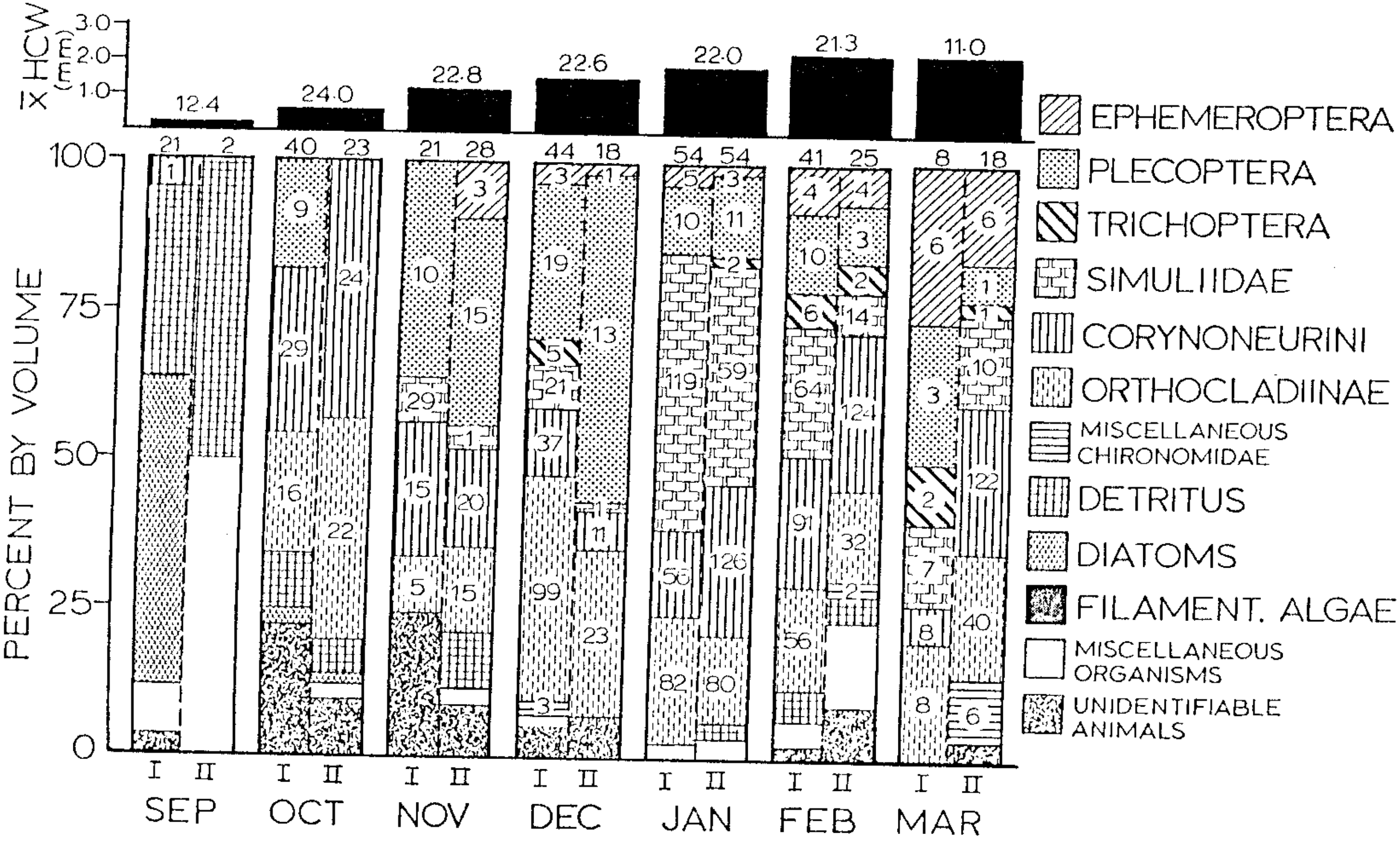
proportions of prey eaten by *Neoperla clymene* in the Brazos River, Texas. Their study showed that in riffles dominated by caddisflies (*Cheumatopsyche* spp.), with relatively low numbers of chironomids, *N. clymene* ingested 58% by number of caddisfly eggs and larvae, and 10% chironomids. These differences probably reflect the different prey complexes in the two rivers, and suggest that the abundance of suitable prey within a predator's microhabitat is probably a significant factor affecting prey choice.

Clioperla clio

The feeding patterns of *Clioperla clio* (Fig. 16) showed distinct seasonal transitions in general food and prey types consumed at each site, that were apparently linked to growth and development. Early instar nymphs in Sept. were herbivore-detritivores, ingesting substantial quantities of diatoms and detritus. A conspicuous shift to carnivory was noted in Oct. (65-80% animal matter by volume), which persisted through the rest of nymphal life. Chironomid larvae (misc. orthoclads and Corynoneurini), that were most abundant in leaf packs, contributed most sigificantly to the overall diet (37% by vol.; 70% by number). *Allocapnia* spp. were also important prey during early nymphal stages, through Dec. These small stoneflies were never numerically abundant in predator foreguts, but

Figure 16. Seasonal variations in stonefly head capsule width (top graph) and food habits (bottom graph) for 397 *Clioperla clio* nymphs collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Dietary fractions are expressed as a percent by volume to the total gut composition. Numbers within each specific prey category represent the total number of prey eaten. Numbers at the top of each food habit bar indicate number of foreguts examined that contained food. Roman numerals along the horizontal axis indicate site. Those months with bars entirely lacking food categories represent periods when no nymphs were collected. Numbers at the top of each HCW bar are percent coefficient of variation.

Clioperla clio

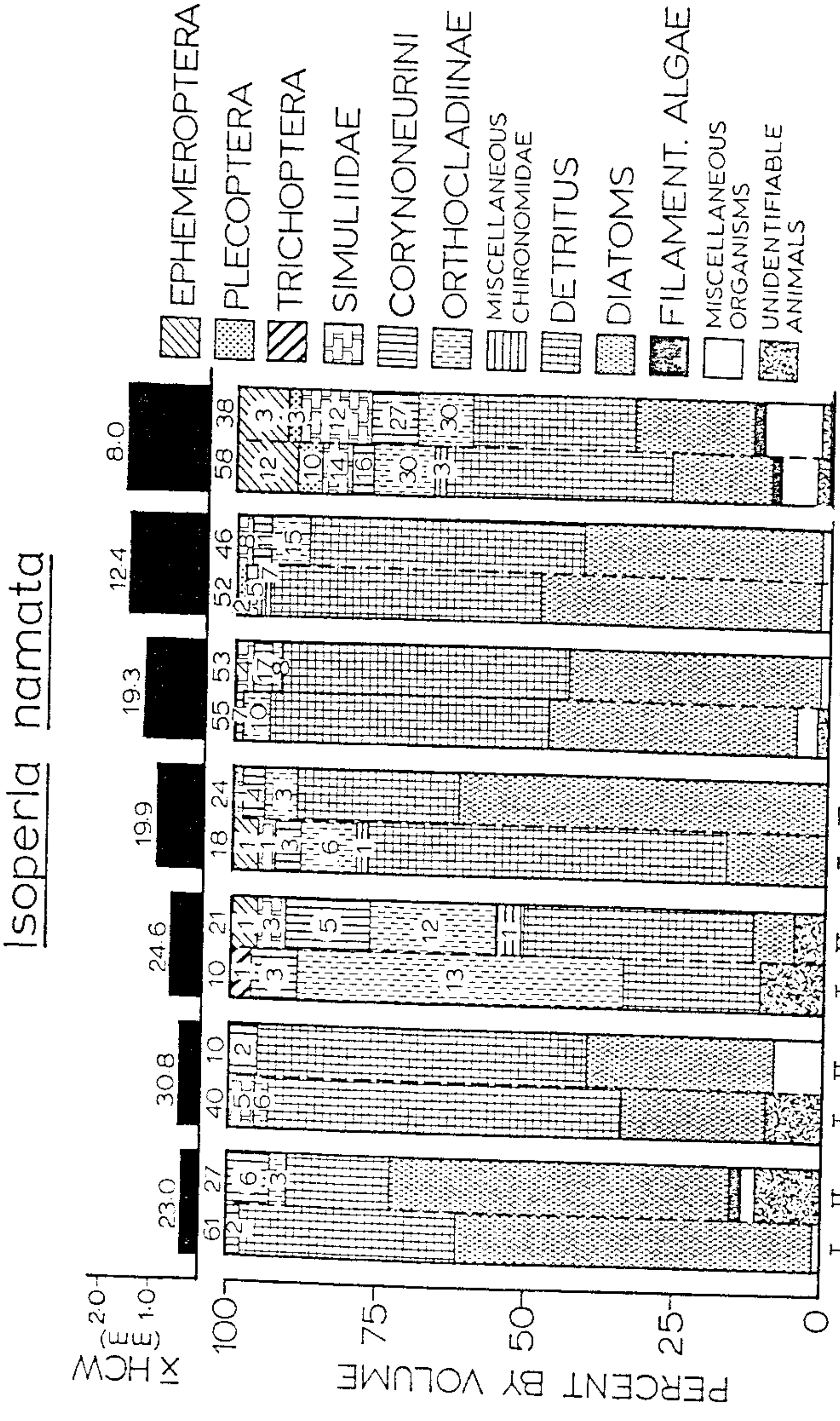


in several instances accounted for 25-51% by volume of the total animals eaten in Nov.-Dec. As _Clioperla_ grew, newly recruited _Prosimulium_ sp. were more heavily consumed, and during Jan. became equally important in the diet with chironomids. Mayflies and caddisflies in general were minor dietary components, though in Mar. mayflies (_Pseudocloeon_ sp., _Baetis_ spp., _Paraleptophlebia_ sp. and _Stenonema_ sp.) constituted 15-25% by volume of the diet, presumably due to an increase in _Clioperla_ size and a concomitant greater predation ability on these larger insects. These results compare favorably with Minshall's (1967) study of moderate to large size _Clioperla_ feeding in Morgan's Creek, Kentucky, on chironomids, heptageniid and baetid mayflies, caddisflies, isopods and _Allocapnia_ sp.(75-100% of diet). He presented no dietary information for earlier instar nymphs, which might have corroborated my observance of a detritus/diatom food habit in newly recruited nymphs.

Isoperla namata

Detritus and diatoms constituted a major portion of this species' diet over the entire nymphal growth period at both sites (Fig. 17). Early instars exhibited feeding patterns very much like young _Clioperla clio_ in Oct. A shift to omnivory was observed in Dec., when nymphs

Figure 17. Seasonal variations in stonefly head capsule width (top graph) and food habits (bottom graph) for 513 *Isoperla namata* nymphs collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Dietary fractions are expressed as a percent by volume to the total gut composition. Numbers within each specific prey category represent the total number of prey eaten. Numbers at the top of each food habit bar indicate number of foreguts examined that contained food. Roman numerals along the horizontal axis indicate site. Those months with bars entirely lacking food categories represent periods when no nymphs were collected. Numbers at the top of each HCW bar are percent coefficient of variation.

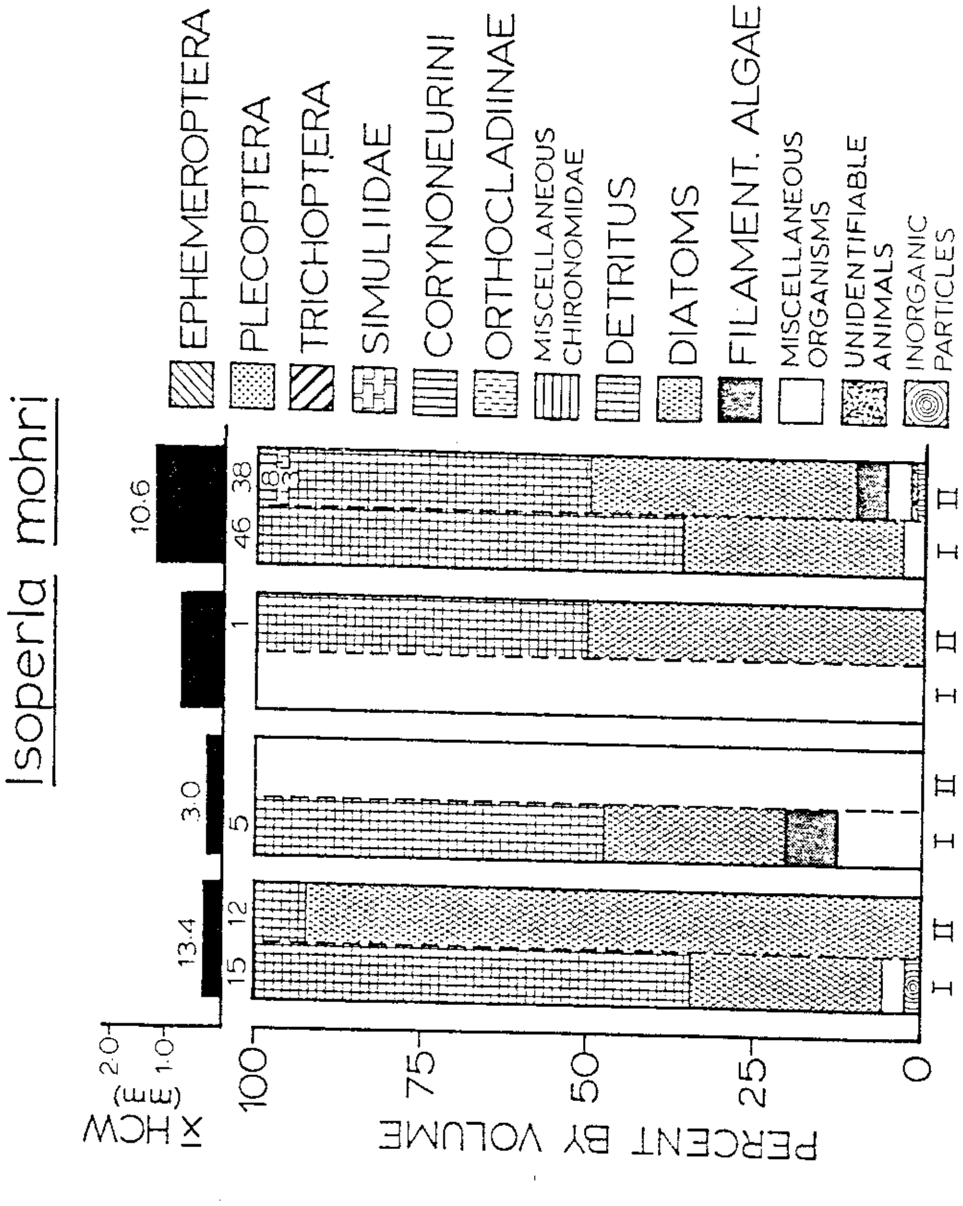

Isoperla namata
x̄ HCW (mm)
2.0
1.0
23.0
30.8
24.6
19.9
19.3
12.4
8.0
PERCENT BY VOLUME
100
75
50
25
0
61
27
40
10
10
21
18
24
55
53
52
46
58
38
I
II
OCT
NOV
DEC
JAN
FEB
MAR
APR
EPHEMEROPTERA
PLECOPTERA
TRICHOPTERA
SIMULIIDAE
CORYNONEURINI
ORTHOCLADIINAE
MISCELLANEOUS CHIRONOMIDAE
DETRITUS
DIATOMS
FILAMENT. ALGAE
MISCELLANEOUS ORGANISMS
UNIDENTIFIABLE ANIMALS

ingested approximately 50% animal food by volume at Site I, and 70% at Site II. Orthoclad chironomids, the most abundant insects in the leaf packs, were the predominant prey taken, comprising 40-50% by volume of the diet. In Jan. intermediate-sized nymphs shifted back to a detritus-diatom food habit and this continued until Apr., when mature nymphs began consuming a greater proportion and diversity of animal prey. Greatly distended foreguts (75-95% full), containing large volumes of detritus and diatoms, were observed Jan.-Mar. when nymphs exhibited fastest growth rates. _I. namata_ prey items included mostly chironomid larvae and pupae; _Baetis_ spp., _Centroptilum rufostrigatum_, _Paraleptophlebia_ sp., _Simulium_ spp. and _Taeniopteryx burksi_ were also present in small proportions.

Isoperla mohri

This species was the smallest systellognathan stonefly in the leaf packs. Intermediate sizes were rare, and early and late instar nymphs collected (N=117) were almost exclusively herbivore-detritivores (Fig. 18). The few chironomids and small Hydracarina, Rhizopodea, Rotifera, and Collembola present in the diet in Jan., Feb., and Apr., were usually mixed in the foreguts with detritus, diatoms or filamentous algae, and probably represented incidental ingestion by some nymphs while foraging for non-animal

Figure 18. Seasonal variations in stonefly head capsule width (top graph) and food habits (bottom graph) for 117 *Isoperla mohri* nymphs collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Dietary fractions are expressed as a percent by volume to the total gut composition. Numbers within each specific prey category represent the total number of prey eaten. Numbers at the top of each food habit bar indicate number of foreguts examined that contained food. Roman numerals along the horizontal axis indicate site. Those months with bars entirely lacking food categories represent periods when no nymphs were collected. Numbers at the top of each HCW bar are percent coefficient of variation.

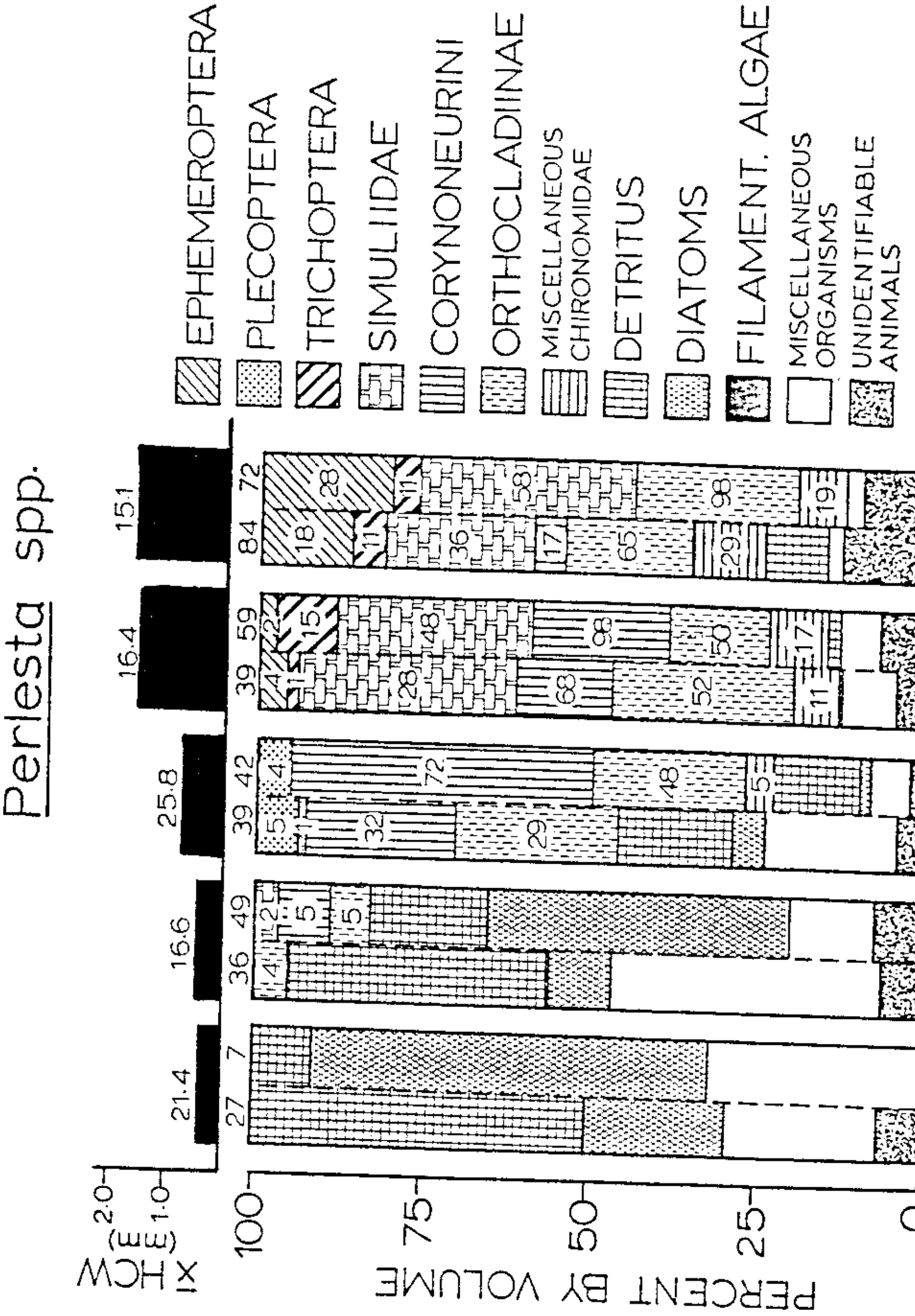

Isoperla mohri
x̄ HCW (mm)
2.0
1.0
PERCENT BY VOLUME
100
75
50
25
0
13.4
3.0
10.6
15
12
5
1
46
38
18
13
I II
JAN
I II
FEB
I II
MAR
I II
APR
EPHEMEROPTERA
PLECOPTERA
TRICHOPTERA
SIMULIIDAE
CORYNONEURINI
ORTHOCLADIINAE
MISCELLANEOUS CHIRONOMIDAE
DETRITUS
DIATOMS
FILAMENT. ALGAE
MISCELLANEOUS ORGANISMS
UNIDENTIFIABLE ANIMALS
INORGANIC PARTICLES

foods. In sharp contrast to my findings, Frison (1935) reported a carnivorous feeding habit for *I. mohri* in Illinois. Reports of exclusively herbivorous perlodids are rare, including *Isoperla signata* and *I. slossonae*, from Wisconsin streams (Shapas and Hilsenhoff 1976). *Isoperla* is a large and morphologically diverse genus (approx. 50 North American species) and further studies of other species will undoubtedly reveal a wide diversity of food habits.

Perlesta spp.

This predator taxon actually included two undescribed species (B. P. Stark, personal communication) based on adults, and were indistinguishable as nymphs. Both species would currently be included in *Perlesta placida*. These stoneflies exhibited regular changes in seasonal diet that were similar between sites, probably related to seasonal shifts in prey abundance and predator size (Fig. 19). Early instars fed omnivorously in Feb.-Mar. on detritus, diatoms (60-80% by volume) and small volumes of the microinvertebrate Rotifera, Harpactacoidea, Hydracarina and Rhizopodea. Rotifers constituted 18% by volume of young nymphs diet during this period. By Apr. they had shifted to a carnivorous diet, consuming Corynoneurini and other orthoclads (47-68% by volume) and rotifers, chironomid

Figure 19. Seasonal variations in stonefly head capsule width (top graph) and food habits (bottom graph) for 454 Perlesta spp. nymphs collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Dietary fractions are expressed as a percent to the total gut composition. Numbers within each specific prey category represent the total number of prey eaten. Numbers at the top of each food habit bar indicate number of foreguts examined that contained food. Roman numerals along the horizontal axis indicate site. Those months with bars entirely lacking food categories represent periods when no nymphs were collected. Numbers at the top of each HCW bar are percent coefficient of variation.

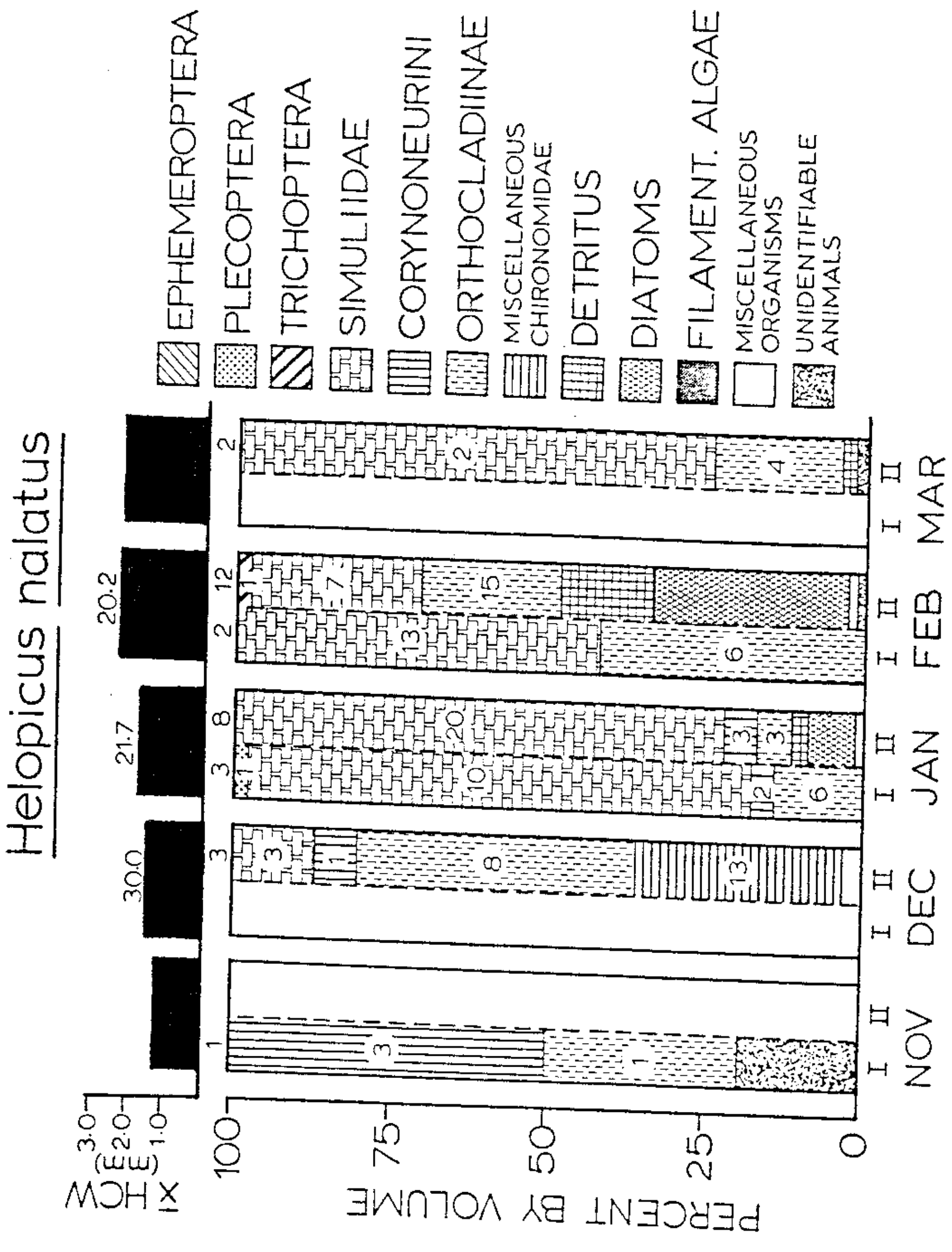

Perlesta spp.
EPHEMEROPTERA
PLECOPTERA
TRICHOPTERA
SIMULIIDAE
CORYNONEURINI
ORTHOCLADIINAE
MISCELLANEOUS CHIRONOMIDAE
DETRITUS
DIATOMS
FILAMENT. ALGAE
MISCELLANEOUS ORGANISMS
UNIDENTIFIABLE ANIMALS
x̄ HCW (mm)
2.0
1.0
PERCENT BY VOLUME
100
75
50
25
0
21.4
16.6
25.8
16.4
15.1
27
7
36
49
39
42
39
59
84
72
I II
FEB
MAR
APR
MAY
JUN
4
2
5
5
5
1
32
29
4
72
48
5
4
15
28
68
52
11
2
15
48
98
50
17
18
11
36
17
65
29
28
11
58
98
19

pupae and *Taeniopteryx burksi*. Mature nymphs continued to prey heavily on chironomids in May-Jun., while consuming greater volumes of abundant *Simulium* sp.(23-32%), the mayflies (*Baetis* spp. and *Centroptilum rufostrigatum* (4-13%), and hydropsychid caddisflies (3-7%). Increased predator size, and potentially greater capture success, by *Perlesta* was probably partially responsible for the shift to larger-bodied prey in May-Jun. Major prey taxa were usually consumed in proportion to their environmental densities, leading to their greater predominance in predator diets during recruitment phases. Snellen and Stewart (1979) found that *Perlesta placida* in an intermittent Texas stream fed principally on chironomids throughout development, which they attributed to preference or greater availability.

Helopicus nalatus

Helopicus nymphs consumed dipteran prey almost exclusively, in all stages examined (Fig. 20). However, food habits of earlier instars could not be determined since they did not occur in leaf packs. Medium-sized *Helopicus* preyed mostly on miscellaneous chironomids (Nov.-Dec.) and shifted to *Prosimulium* sp. as they became available in Jan.-Mar., which comprised 50% by vol. and 46% by number of the diet. Chironomids then became the second

Figure 20. Seasonal variations in stonefly head capsule width (top graph) and food habits (bottom graph) for 31 Helopicus nalatus nymphs collected from leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Dietary fractions are expressed as a percent by volume to the total gut composition. Numbers within each specific prey category represent the total number of prey eaten. Numbers at the top of each food habit bar indicate the number of foreguts examined that contained food. Roman numerals along the horizontal axis indicate site. Those months with bars entirely lacking food categories represent periods when no nymphs were collected. Numbers at the top of each HCW bar are percent coefficient of variation.


Helopicus nalatus
x̄ HCW (mm)
3.0
2.0
1.0
30.0
21.7
20.2
PERCENT BY VOLUME
100
75
50
25
0
1
3
1
3
3
1
8
13
3
8
1
10
20
2
3
3
6
2
13
6
12
7
15
2
2
4
I II
NOV
I II
DEC
I II
JAN
I II
FEB
I II
MAR
EPHEMEROPTERA
PLECOPTERA
TRICHOPTERA
SIMULIIDAE
CORYNONEURINI
ORTHOCLADIINAE
MISCELLANEOUS CHIRONOMIDAE
DETRITUS
DIATOMS
FILAMENT. ALGAE
MISCELLANEOUS ORGANISMS
UNIDENTIFIABLE ANIMALS

largest fraction. Low Helopicus densities in leaf packs, despite their relatively large size and feeding on the abundant insect prey, made it unlikely that they significantly influenced prey numbers or other predaceous stoneflies during any month.

Mouthpart Morphology

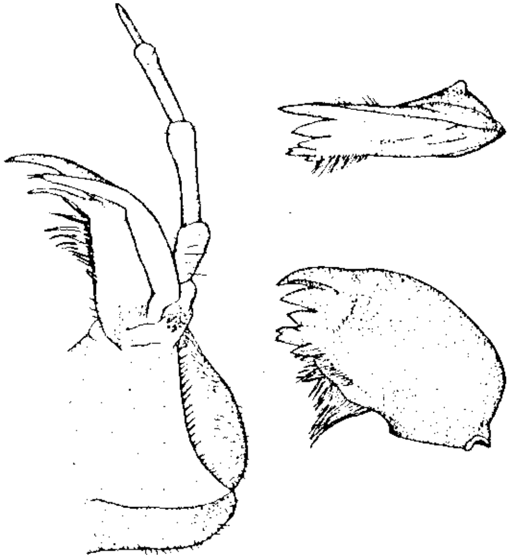
The morphology of feeding structures, such as insect mouthparts, is often an indicator of food resource use. Brinck (1949) stated that for stoneflies, diet is intimately associated with mouthpart structure. He contrasted the general mouthpart morphologies in the carnivorous suborder Setipalpia and the phytophagous suborder Filipalpia, but did not address specific variations in mouthpart types which may have related to dietary differences between species. Schoener (1974) also felt that for consumers in general, the relative size of feeding structures often relate directly to the specific food sizes and types ingested.

More recent feeding studies of Systellognatha, which have reported polyphagous food habits by "supposed" carnivorous species (Siegfried and Knight 1976a; Fuller and Stewart 1977; Gray and Ward 1979; Allan 1982), have not related development of mouthpart structure with dietary shifts.

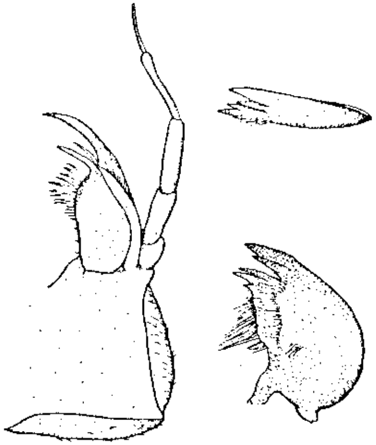
Two general morphological mouthpart types were apparent in the Little Missouri River, which were strongly associated with the diet of the stoneflies possessing them. *Acroneuria* spp., *Perlesta* spp., *Phasganophora capitata*, *Neoperla* spp., *Clioperla clio*, and *Helopicus nalatus* all possess maxillae and mandibles typically associated with carnivorous stoneflies (Fig. 21). The lacinia bear elongate, sharply pointed, apical and subapical teeth, used for impaling invertebrate prey (Brinck 1949), or for corralling struggling prey while they are being engulfed (Claassen 1931). The well developed mandibles are multi-cusped, with at least four sharp, heavily chitinized teeth for grasping small-bodied prey or for shearing off pieces of larger prey prior to ingestion (Brinck 1949). Predaceous mouthparts of this type were observed in all instars of these species, including those that consumed large volumes of detritus and diatoms as young nymphs (e.g. *Clioperla clio*, *Perlesta* spp.). Thus, in concert with analyses of diet, mouthpart structures provided morphological evidence that moderate to large sized nymphs of these stoneflies are specialized to harvest living, mobile organisms.

The mouthparts of *Isoperla namata* and *I. mohri* nymphs, which fed mostly on fine detritus and vegetative matter, were markedly different and more general in structure than

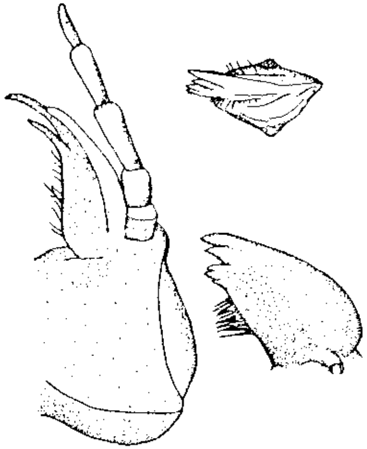
Figure 21. Nymphal mouthparts of carnivorous systellognatha, Upper Little Missouri River, Montgomery County, Arkansas, 6 June - 21 May 1981. Illustrated structures include the right maxilla (ventral view) and mandible (apical and ventral views).



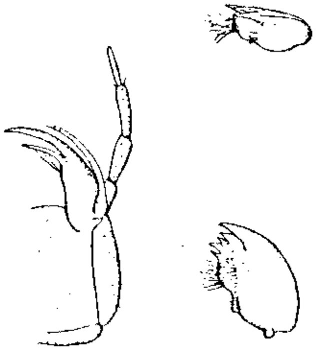
Acroneuria spp.



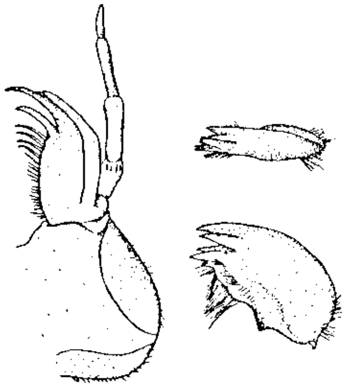
Clioperla clio



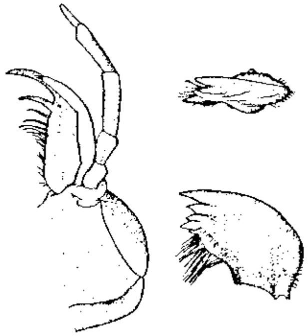
Helopicus nalatus



Perlesta spp.



Phasganophora capitata



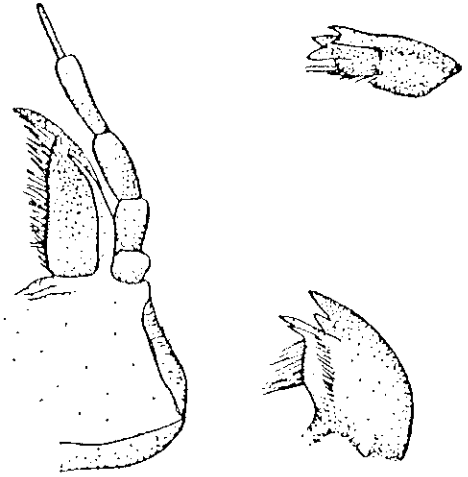
Neoperla spp.

carnivorous species (Fig. 22). By comparison, their lacinial teeth were much shorter and less stout, and were subtended by regular rows of bristles that formed a heavy brush along the mesal lacinial margin. Their mandibles resembled the general outline of carnivorous species from a ventral aspect, but when viewed apically, the apical and subapical teeth were distinctly bicusped and spatulate. The brush and chisel-like mouthparts in both species may facilitate feeding on loosely deposited materials, such as detritus and diatoms, as well as small animals, by aiding the removal of these substances from leaf surfaces.

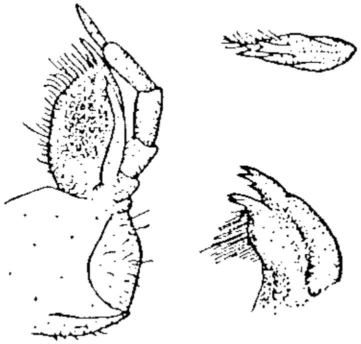
Prey Preference

Food selection represents a key aspect of community trophic studies that attempt to quantify feeding dynamics by consumer groups. Comparisons are usually made between the proportions of food items that occur in the consumer's diet and in the environment. Determination of food selection is central to any quantitative description of food habits, and can be utilized to test predictions of optimal foraging theory (sensu Pyke et al. 1977) and to also address questions that concern niche relationships between consumers, such as the potential for interspecific competition. For example, if preferences for major food categories are shown to be different between species within

Figure 22. Nymphal mouthparts of herbivorous/omnivorous systellognatha, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Illustrated structures include the right maxilla (ventral view) and mandible (apical and ventral views).



Isoperla namata



Isoperla mohri

a microhabitat, then one may cite this as evidence for food resource division, and further test for competitive interaction using both experimentation and close observation. Prey electivity by predaceous stoneflies was examined here to assess the importance of differential prey preference as a mechanism that might account for the high degree of temporal overlap of systellognathan stoneflies in leaf packs.

A myriad of electivity indices have been derived for use in feeding studies (see Cock 1978; Lechowicz 1982). Several stonefly workers (Siegfried and Knight 1976a; Fuller and Stewart 1977,1979) have employed Ivlev's quotient, E (Ivlev 1961). While this index reflects the degree of difference between prey composition in the predator's diet (r) and in the habitat (p) and is easy to compute, it does not allow testing computed values for significant departure from random feeding, (i.e. E=0), nor comparisons of preference between prey taxa if their densities differ, since maximum and minimum electivity values can vary with prey density (Cock 1978). It should be noted, however, that an estimation of electivity by any diet/environmental comparisons is somewhat indeterminate, unless the actual availability of prey for feeding by a predator has been determined. This usually requires a greater knowledge of physiology and behavior of the predators and prey than is usually the case.

In my analysis of preference, I employed a modified forage ratio and its natural log (Q) as proposed by Jacobs (1974):

$$\text{Log10 } Q = \frac{r\ (1-p)}{p\ (1-r)}$$

where:

r= proportion of a given prey type in the diet, and

p= proportion of the same prey type in the environment.

By taking the natural log of Q, computed electivity values will vary about 0 (random feeding), from positive infinity (positive electivity) to negative infinity (avoidance or prey unavailability). Gabriel (1978) has pointed out that log10 Q can be statistically tested for significant deviation from 0 by calculating the standard error, such that:

$$\text{SE Log10 } Q = \sqrt{\frac{1}{n_1\ r(1-r)} + \frac{1}{n_2\ p\ (1-p)}}$$

where:

n_1 = total number of prey in the diet, and

n_2 = total number of food items (animals) in the environmental sample.

Log10 Q may then be transformed to a z value (i.e. a standard normal deviate) and be subsequently tested for significance:

$$Z = \frac{\text{Log10 Q observed} - \text{Log10 Q expected}}{\text{SE Log10 Q}}$$

where: Log10 Q expected = 0 (in this example).

Comparisons between the computed z value and the proportions of z values in a normal distribution (z table) can be made to determine the exact probability of difference between the observed and expected values (Gabriel 1978).

Site-specific electivity values (Log10 Q) for each stonefly predator and the six most important prey taxa, (i.e. prey most frequently consumed) are shown in Table 6. Only those Log10 Q values marked with asterisks were significantly different from 0 ($\alpha = 0.05$). At both sites, the stoneflies as a group predominatey fed at random on the most abundant (and available) animal prey, indicating a

Table 6. Site-specific log10 Q values (electivity) for predaceous stoneflies and their major prey, Upper Little Missouri River, Arkansas, June 1980-May 1981. Dashes indicate prey not present in diet.

Site	Jun		Jul		Aug		Sep		Oct		Nov		Dec		Jan		Feb		Mar		Apr		May	
	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Clioperla clio																								
Baetidae							-	-	-	-	-	.18	-	-	-	-	.00	-	.30	-.39				
Allocapnia							-	-	.23	-	.59	.37	.22	.57	.89*	.40	-	-	-	-				
Simuliidae							-	-	-	-	-.19	-1.1	-.38	-1.2	.45*	.12	.11	-.43	.18	-.49				
Corynoneurini							.27	-	.32	-.25	.47	.13	-.06	.18	-.24	-.21	.12	.31*	.08	.37*				
Orthocladiinae							-	-	-.22	.64*	-.12	.48	.36*	.44	-.09	.24	.06	.18	-.07	-.06				
Isoperla namata																								
Baetidae									-	-	-	-	-	.97	.69	-	-	-	.32	-	.06	-.16		
Allocapnia									-	-	-	-	-	-	-	-	-	-	-	-	-	-		
Simuliidae									-	-	-.26	-	-.70	-.32	-.48	-.15	-.52	-.24	.36	.19	.34	.62*		
Corynoneurini									-	-.48	-	-.76	-.14	.03	-.11	-.10	-.08	-.01	-.60	-.27	-.36	-.50*		
Orthocladiinae									-	.07	.99	-	.73	.57	.29	.43	.39	.40	.06	.34	.33	.71*		
Helopicus nalatus																								
Baetidae														-	-	-		.65	-	-				
Allocapnia														-	-	-		-	-	-				
Simuliidae														-.15	.62	1.1*		.22	1.1*	.45				
Corynoneurini														-.61	-.57	-.89		-1.4	-	-				
Orthocladiinae														.52	-.05	-.26		.99*	.11	.81				
Perlesta spp.																								
Baetidae	-.28	-.52*																	-	-	-	-	-.69	-.86
Allocapnia	-	-																	-	-	-	-	-	-
Simuliidae	.21	.06																	-	-.43	-.92	-	.06	.30
Corynoneurini	-.17	-.27																	-	-.64	-.05	-.14	.06	-.04
Orthocladiinae	.34*	.76*																	-.77	-.24	.24	.69*	.26	.21
Neoperla spp.																								
Baetidae	-.98	-		.85			-	.34	-	-	-		-				-		-	-	-.48	-1.7	-	-.37
Allocapnia	-.24	-		-			-	-	-.37	-	-		-				-		-	-	-	-	-	-
Simuliidae	-.71	.12		-			-	-	-.17	-	-		-				-		-	-	-.17	-	-1.0	-.14
Corynoneurini	-.40	.61		1.0			1.1	.31	-.12	-.26	.64		.56				.03		-.10	-.37	-.15	-.28	-.09	-.38
Orthocladiinae	-.41	.09		.75			-	.28	.12	-	.65		.32				.02		-	.51	.30	.51*	.51	.60*

* = significant selection($\alpha = 0.05$).

Table 6 continued.

Site	Jun		Jul		Aug		Sep		Oct		Nov		Dec		Jan		Feb		Mar		Apr		May	
	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Phasganophora capitata (1980 cohort)																								
Baetidae	-				-	-	-	-.89	-	-.42		-		-		-		-	-	-.21	-.16	-.34		.64
Allocapnia	-				-	-	-	-	-	-.50		.15		-		-		-	-	-	-	-		-
Hydropsychidae	-				1.5	-	-	-	-	-		-		-		-		-	-	-	-	-		-
Simuliidae	-				-	-	-	-	-	.07		-		-		-.68		-	-.34	-.43	-	.83*		.35
Corynoneurini	-				.33	-.26	-.27	.51*	.27	.28		.14		-		-.28		-.04	.53	.07	.09	-.71*		-.42
Orthocladiinae	.59				.13	.28	.94	.25	-.01	.08		-.09		.82		.54		.26	.24	.09	.53	.71*		.24
Phasganophora capitata (1979 cohort)																								
Baetidae	-	-.81					.05	-	-	.89	1.3										1.2	-		1.0*
Allocapnia	-	-					-	-	-	-	-										-	-		-
Hydropsychidae	-	-					.72	-	-	1.4	-										-	1.7		-.06
Simuliidae	-	.96					-.01	-	-.03	-	-.66										.22	1.6*		.65
Corynoneurini	-	-					-.29	1.1*	-.32	.22	.46										-	-		-1.3
Orthocladiinae	.59	-					.31	-	.17	-	-										-.20	.58		.28
Acroneuria spp. (1980 cohort)																								
Baetidae	-	-		-																			-	-
Allocapnia	-	-		-																			-	-
Simuliidae	-.53	-		-																			-	-
Corynoneurini	.14	1.1		1.4																			.03	-.18
Orthocladiinae	.93*	.17		-																			.00	.78
Acroneuria spp. (1978-1979 cohorts)																								
Baetidae									.95		.65						-							
Allocapnia									-.35		1.3*						-							
Simuliidae									-		-.99						.48							
Corynoneurini									-.38		-.20						-.11							
Orthocladiinae									.22		-						-							

* = significant selection (α =0.05).

substantial degree of similarity in prey types consumed by sympatric predators. Significant selection (positive and negative) operated in only 10% of the total number of interactions measured between predators and their major prey (27/265). Relative abundance of prey seemed to be roughly indicative of prey availability, since indiscriminate predator feeding predominated and prey present in the diet provided at least a minimum estimate of the organisms that were available to the predators.

There was also substantial overlap between sympatric stoneflies for preferred prey (41%), particularly at Site II (Table 7). Dietary similarity was especially apparent during Apr., when miscellaneous Orthocladiinae and _Simulium_ spp. were among the most abundant insects and were positively selected by at least four stonefly predators (_Isoperla namata_, _Phasganophora capitata_, _Perlesta_ spp. and _Neoperla_ spp.). One month earlier (Mar.) both prey groups had been present in leaf packs at or near their peak numerical abundance, due primarily to recruitment, but had decreased sharply in number by Apr. Preferential feeding and heavy predation by stoneflies on these abundant prey may have been at least partially responsible for the Apr. decline in density. Despite their large contribution to the diets of most stoneflies, Corynoneurini, unlike other orthoclad and simuliid prey, were in most cases negatively

Table 7. Site-specific interactions between stonefly predators and their preferred prey[a], Upper Little Missouri River, Arkansas, June 1980 - May 1981. Brackets under predator categories indicate months when prey were shared.

	PREY TAXON	PREDATOR	MONTH
Site I	*Allocapnia* sp.	C. clio	JAN
		Acroneuria spp.[c]	NOV
	Simuliidae	C. clio	JAN
		H. nalatus	MAR
	Orthocladiinae	Perlesta spp. Acroneuria spp.[b]	JUN
		C. clio	DEC
Site II	Baetidae	P. capitata[c]	MAY
		Perlesta spp.	JUN
	Simuliidae	H. nalatus	JAN
		I. namata P. capitata[b] P. capitata[c]	APR
	Corynoneurini	C. clio	FEB
		C. clio	MAR
		P. capitata[b] P. capitata[c]	SEP
	Orthocladiinae	H. nalatus	FEB
		Neoperla spp. I. namata Perlesta spp. P. capitata[b]	APR
		Neoperla spp.	MAY
		Perlesta spp.	JUN
		C. clio	OCT

a= those animals with log10 Q significantly >0 (α=0.05).
b= 1980 cohort.
c= pre-1980 cohort.

selected (I. namata, Phasganophora-1980 cohort, Apr., Site II) or randomly ingested, by virtue of their numerical dominance over other insect prey.

The general lack of dietary specialization for major prey indicates that the stoneflies were trophic opportunists on all insects that were vulnerable to predation (i.e. were abundant and of suitable size). Ontogenetic shifts in prey types consumed by stoneflies were more a function of actual changes in size thresholds or seasonal availability of prey than growth-related shifts in specific prey preferences. Low prey preferences were also observed for Plectrocnemia conspersa and Sialis fuliginosa in an iron-rich stream (Hildrew and Townsend 1976), in which predator numbers were correlated with prey density, and prey were consumed in proportion to environmental abundances.

The manner in which stonefly predators forage may help explain why significant prey selection seemed rare in the leaf packs. Stoneflies generally detect prey mechanically using tactile cues from their antennae (Hynes 1941; Kovalak 1978; Peckarsky 1979), and more heavily utilize prey with the greatest probability of encounter. Thus, stoneflies that forage randomly would tend to select prey groups that were most abundant (e.g. Chironomidae, recruited Simuliidae and Baetidae), largely irrespective of prey or predator size, unless prey were highly mobile and could not be captured. It does follow that larger-bodied prey (e.g. Trichoptera, most Ephemeroptera) on an individual basis would be more easily detected because of their size (Siegfried and Knight 1976a), but in the leaf packs these insects were usually uncommon and were probably less vulnerable to predation than smaller insects.

Indiscriminate feeding on abundant prey by stoneflies probably represents the most efficient and "prudent" use of food resources in leaf packs. In their discussion of optimal foraging theory, Pyke et al. (1977) described an optimal diet as one that would maximize the net energy gain of a consumer, and which considered food value, foraging duration, and handling/assimilative costs as variables that act as constraints in attaining such a diet. With such high densities of chironomids and other small insects in the leaf packs, it seems likely that as a group, each of these prey may be more easily encountered, captured, and used as food than larger counterparts, despite the fact that smaller prey are lower in food quantity per unit effort. It is also reasonable to suggest that high densities of small prey are more easily handled and ingested by stoneflies, and may actually represent a more cost-effective food choice. Clearly, this foraging tactic should only operate efficiently for predators (of moderate to large size) experiencing high prey densities since choice or preference of uncommon, small prey with relatively small areas of discovery would be energetically costly.

Predator-Prey Size Relationships

I examined prey size utilization data to determine if predators shift their food habits toward larger prey with growth. Predator head width (i.e. maximum transverse distance across the head), was used to express stonefly size, since others have indicated that it correlates well with mouth gape and potentially with the maximum consumable prey size (Devonport and Winterbourn 1976). Since the diets of predators did not generally differ between sites, I pooled prey size data from both sites for each species, and followed the assumption that stoneflies of a given size class possess equivalent prey size thresholds and ranges of prey items actually ingested. For those predators that consumed prey exponentially with growth (i.e. large stoneflies-Clioperla clio, Helopicus nalatus, Phasganophora capitata, and Neoperla spp.), sizes were log transformed to straighten the line of best fit.

For all stoneflies except Helopicus nalatus, possibly the result of small sample size, there was a significant positive correlation between the size of the predator and its prey (Kendall rank correlation, Zar 1974) (Figs. 23 & 24). That is, as the stoneflies grew they tended to select progressively larger prey, in either a linear or exponential manner, with consumption of the larger prey sizes being usually restricted to the largest stoneflies. This size-dependent relationship has also been noted in predaceous mayflies (Tsui and Hubbard 1979), damselflies (Thompson 1978), dobsonflies (Devonport and Winterbourn 1976) and other stoneflies (Sheldon 1968; Devonport and Winterbourn 1976; Allan 1982). Malmquist and Sjostrom (1980) postulated that such ontogenetic shifts to large prey groups may increase foraging efficiency, (i.e. produce a greater catch per unit effort) and lessen time to emergence, which could increase the likelihood of successful mating during the reproductive season. Research by Allan (1982) on perlodid stonefly feeding habits in a Colorado stream, indicated that positive correlations between sizes of predators and prey were more dependent upon juxtaposed life cycles and less related to active selection. In this situation, mayflies (Baetis spp.) became important food items for larger predators during recruitment, when mayfly prey were more plentiful. Sheldon (1969) also felt that life history synchronization between predators and prey was an important factor in prey size shifts by predators. Juxtaposed predator-prey life cycles

Figure 23. Predator-prey size relationships for *Clioperla clio*, *Isoperla namata*, and *Helopicus nalatus*, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Plotted points represent mean prey size ingested + one standard deviation. Numbers at the top of each SD line indicate the number of prey measured in that predator size class. N equals the sample size of predators.

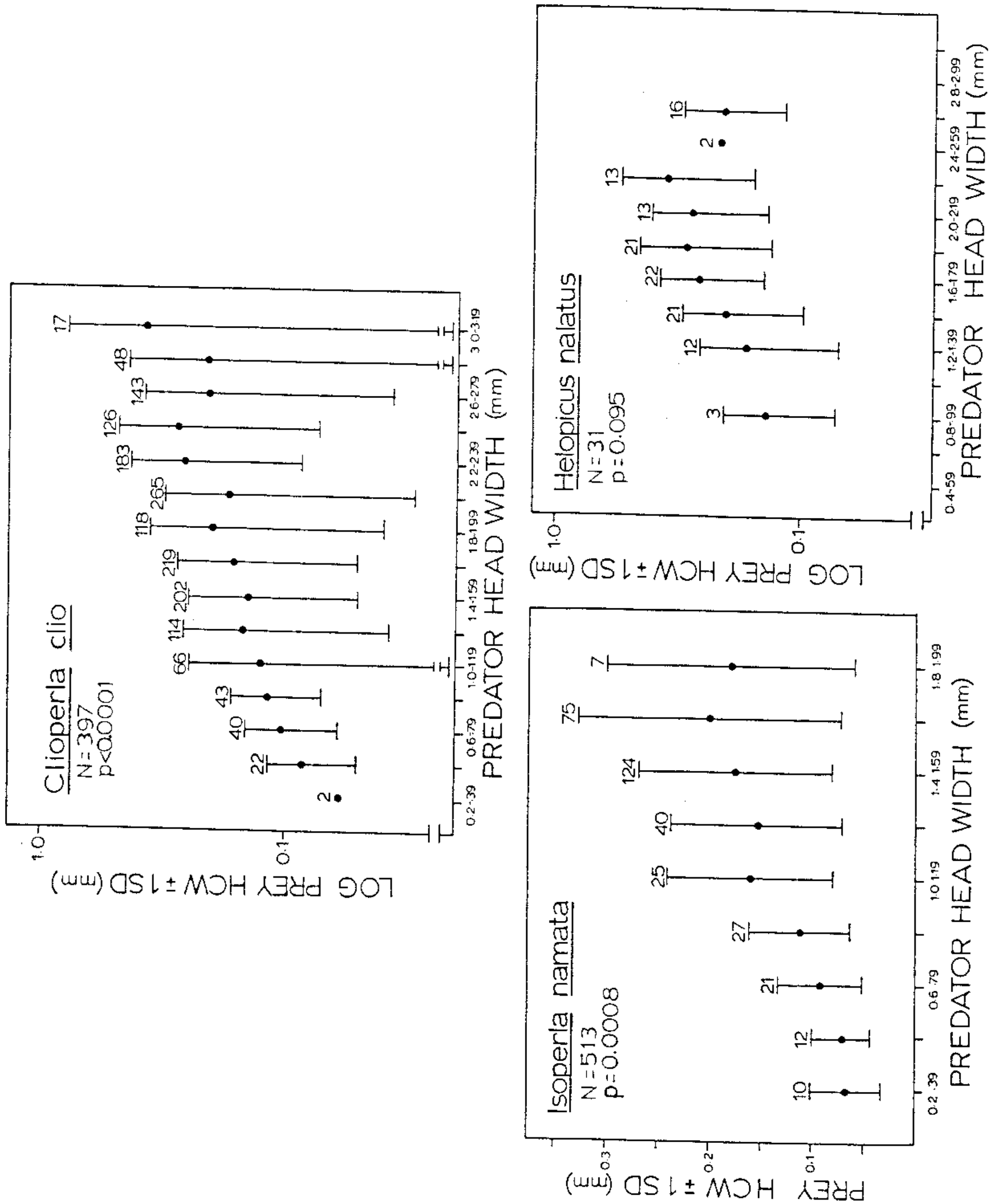
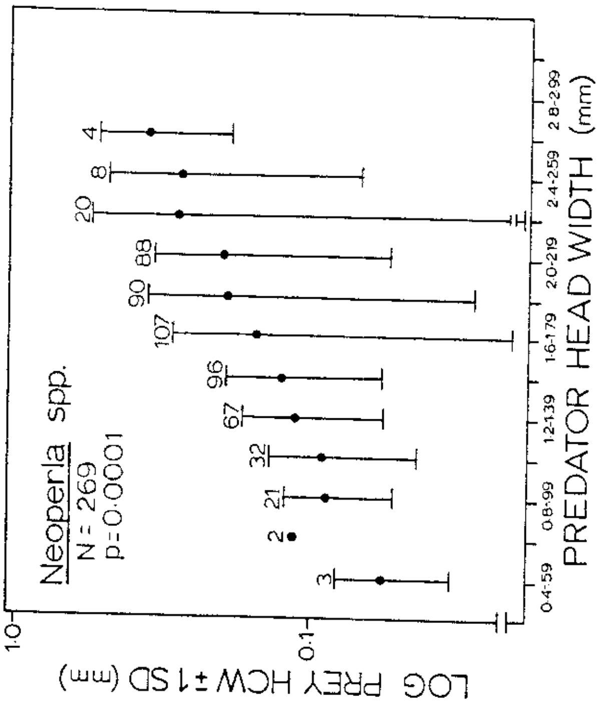
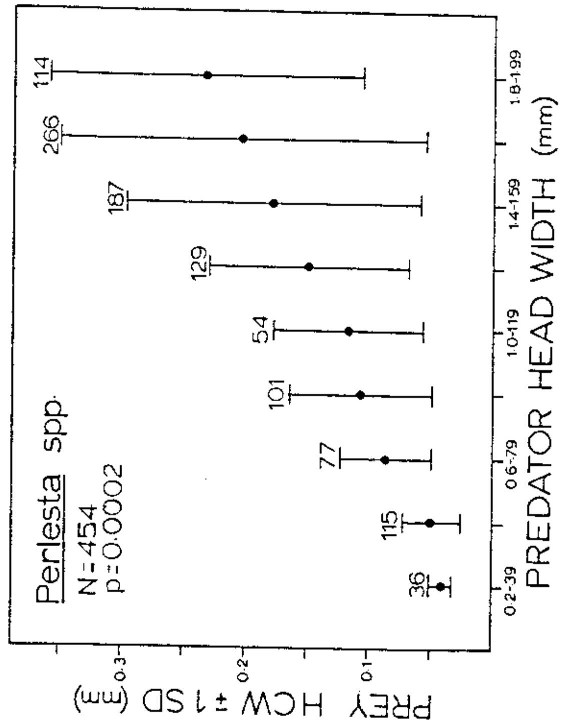
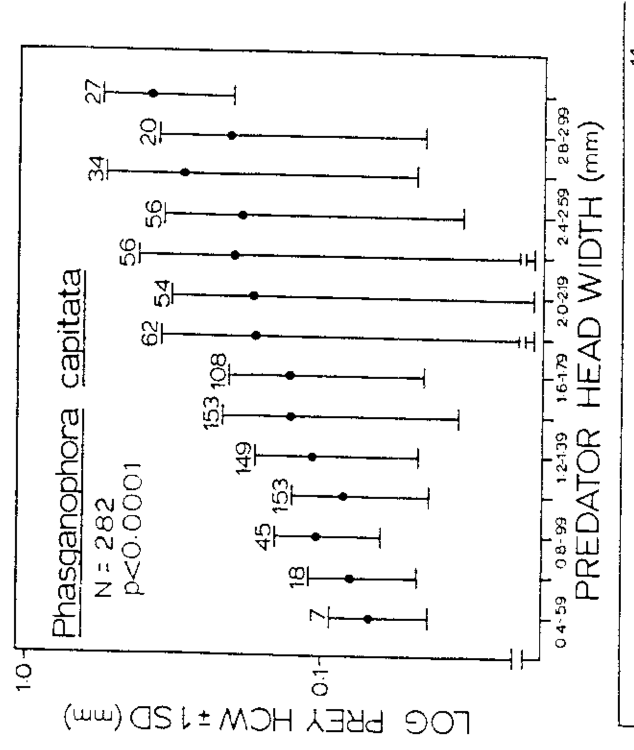
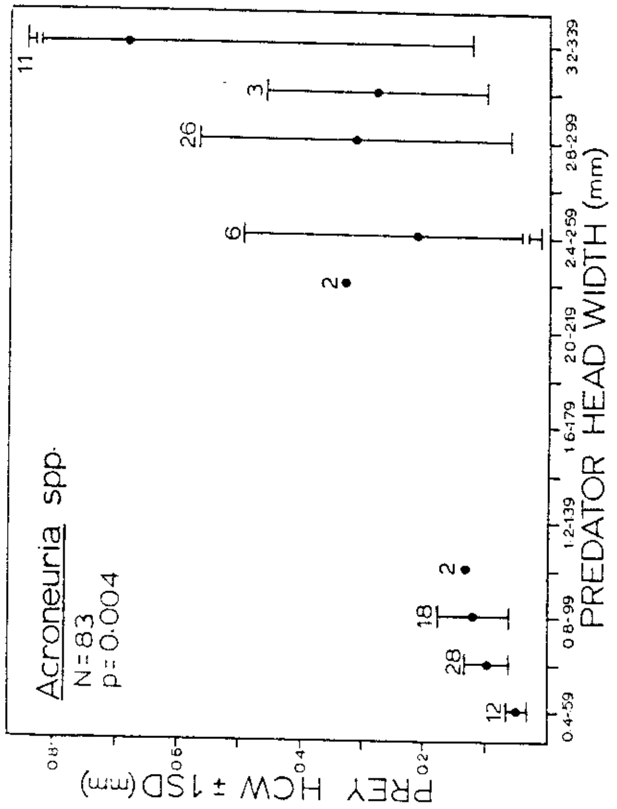

Clioperla clio
N=397
p<0.0001
LOG PREY HCW ± 1 SD (mm)
1.0
0.1
2
22
40
43
66
114
202
219
118
265
183
126
143
48
17
0.2-.39
0.6-.79
1.0-1.19
1.4-1.59
1.8-1.99
2.2-2.39
2.6-2.79
3.0-3.19
PREDATOR HEAD WIDTH (mm)
Isoperla namata
N=513
p=0.0008
PREY HCW ± 1 SD (mm)
0.3
0.2
0.1
10
12
21
27
25
40
124
75
7
0.2-.39
0.6-.79
1.0-1.19
1.4-1.59
1.8-1.99
PREDATOR HEAD WIDTH (mm)
Helopicus nalatus
N=31
p=0.095
LOG PREY HCW ± 1 SD (mm)
1.0
0.1
3
12
21
22
21
13
13
2
16
0.4-.59
0.8-.99
1.2-1.39
1.6-1.79
2.0-2.19
2.4-2.59
2.8-2.99
PREDATOR HEAD WIDTH (mm)

Figure 24. Predator-prey size relationships for *Phasganophora capitata*, *Neoperla* spp., *Acroneuria* spp., and *Perlesta* spp., Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1891. Plotted points represent means ± one standard deviation. Numbers at the top of each SD line indicate the number of prey measured in that predator size class. N equals the sample size of predators.


Neoperla spp.
N = 269
p = 0.0001
LOG PREY HCW ±1 SD (mm)
1.0
0.1
3
2
21
32
67
96
107
90
88
20
8
4
0.4-.59
0.8-.99
1.2-1.39
1.6-1.79
2.0-2.19
2.4-2.59
2.8-2.99
PREDATOR HEAD WIDTH (mm)


Perlesta spp.
N = 454
p = 0.0002
PREY HCW ±1 SD (mm)
0.1
0.2
0.3
36
115
77
101
54
129
187
266
114
0.2-.39
0.6-.79
1.0-1.19
1.4-1.59
1.8-1.99
PREDATOR HEAD WIDTH (mm)


Phasganophora capitata
N = 282
p<0.0001
LOG PREY HCW ±1 SD (mm)
1.0
0.1
7
18
45
153
149
153
108
62
54
56
56
34
20
27
0.4-.59
0.8-.99
1.2-1.39
1.6-1.79
2.0-2.19
2.4-2.59
2.8-2.99
PREDATOR HEAD WIDTH (mm)


Acroneuria spp.
N = 83
p = 0.004
PREY HCW ± 1SD (mm)
0.2
0.4
0.6
0.8
12
28
18
2
2
6
26
3
11
0.4-.59
0.8-.99
1.2-1.39
1.6-1.79
2.0-2.19
2.4-2.59
2.8-2.99
3.2-3.39
PREDATOR HEAD WIDTH (mm)

in the Little Missouri River did not seem as influential a factor for determining which prey sizes were selected by stoneflies. While some mayflies (e.g. *Pseudocloeon* spp., *Baetis* spp.) and blackflies (e.g. *Simulium* spp., *Prosimulium* spp.) did develop synchronously with some stonefly predators, multi-sized chironomids from many cohorts and species predominated in the leaf packs and in most predator diets throughout the year, which meant that suitably sized prey were always available to all but the earliest stonefly instars.

As evidenced by the increased variation in prey sizes eaten, larger predators possessed a broader diet than smaller individuals (Figs. 23 & 24). These stoneflies continued to ingest numerous small-sized prey, usually chironomids, along with larger taxa, such as mayflies, simuliids, caddisflies and euholognathan stoneflies. In many cases, minimum prey sizes were similar for most predaceous instars irrespective of size. Such behavior would allow these predators the option of selecting the largest ingestible sizes as well as small prey that are relatively abundant, thereby minimizing foraging costs.

For preferential size selection to occur, predators would need to shift their prey requirements with growth (i.e. incorporate progressively larger prey and eliminate smaller items from the diet). Three benthic studies have reported such growth-related selection for particular prey sizes by predators (e.g. damselflies, Thompson 1975; caddisflies, Hildrew and Townsend 1976; and stoneflies, Siegfried and Knight 1976a). Since the stonefly predators in the Little Missouri River did not shift their prey size spectra to exclusively larger-bodied groups, but instead relied on a wide array of prey sizes, selectivity did not occur. Rather, prey selection was based upon prey availability and the tendency for predators to select groups they were most likely to encounter. Thus, within the range of prey each stonefly could effectively handle, prey availability, not size, seem to most directly influence prey choice by predators.

CHAPTER V

CONCLUSIONS

Many systellognathan stoneflies spent either a portion or all of their nymphal life in natural leaf packs. At certain times, these populations were sympatric and occurred in relatively large numbers. The primary leaf pack-inhabitants as judged by those species collected throughout their life cycles, were *Clioperla clio*, *Isoperla namata* and *Perlesta* spp. They exhibited rapid growth cycles and a pronounced degree of seasonal overlap. A second group of stoneflies, *Neoperla* spp., *Phasganophora capitata*, were only occasionally abundant in leaf packs, being common during late spring and summer, but relatively rare from autumn through winter. The appearance of other species, *Acroneuria* spp., *Helopicus nalatus* and *Isoperla mohri*) was sporadic in leaf packs and not strongly tied to season.

In favorable stream environments, with stable or benign physical conditions, predation by systellognathan stoneflies may be a significant factor influencing the abundance and distribution of benthic prey organisms (Peckarsky 1982), in conjunction with other important biotic factors. Siegfried and Knight (1976b) and Allan (1982) presented quantitative data that corroborate this hypothesis, and both suggested that substantial predation pressure may be exerted by stoneflies on prey populations. If competition between sympatric stoneflies is keen for limited prey, one would predict that in time these predators would become segregated along one or a series of resource axes that would permit coexistence.

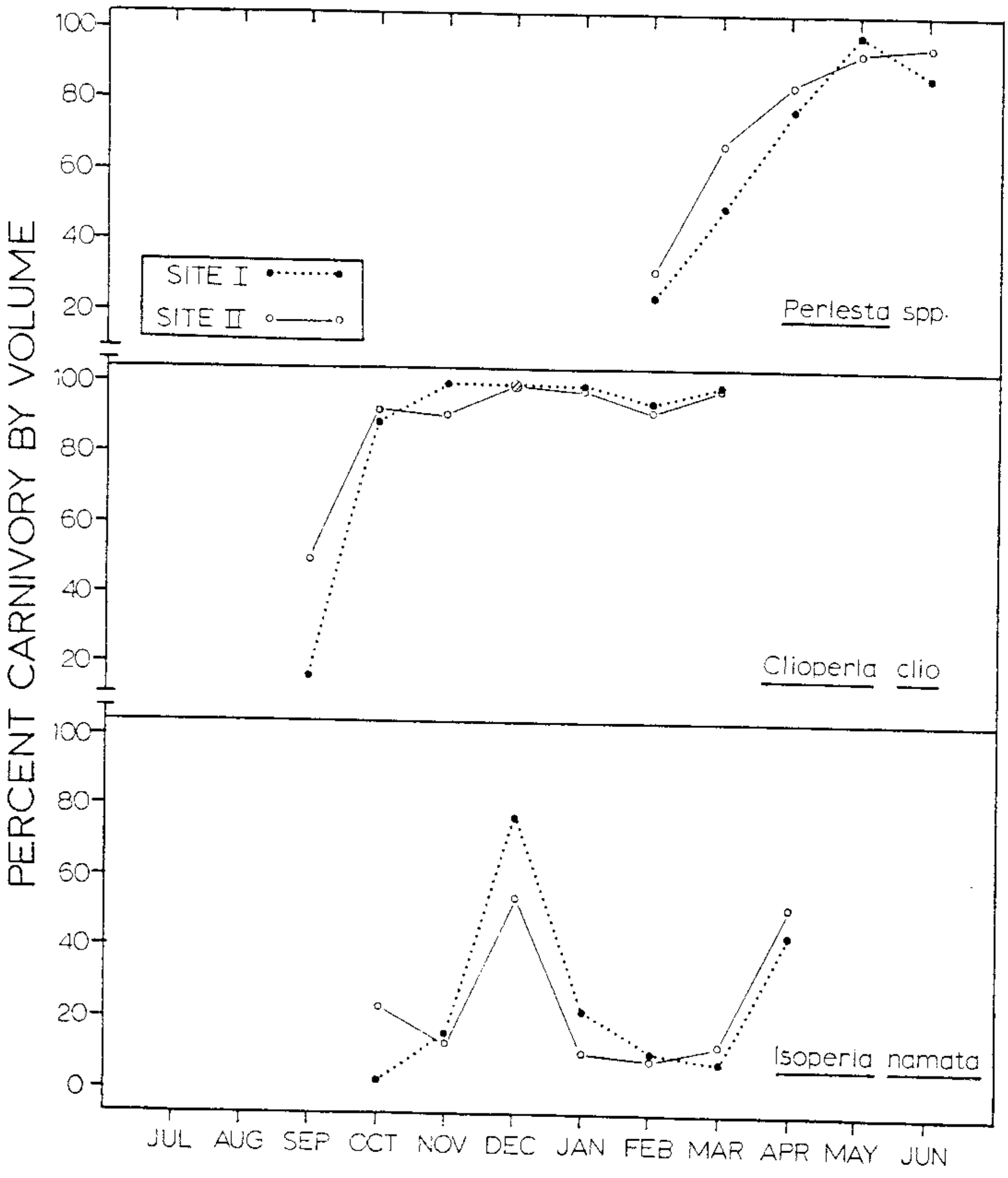
Interspecific competition may occur for similar prey types and/or sizes, as well as for foraging space by stoneflies within the leaf pack itself. Since there appeared to be no spatial partitioning of this microhabitat, (i.e. I saw no evidence to suggest the species were restricted to different regions of the leaf packs) space, though it may have set an upper limit on the maximum number of predators that could co-occur, was not a factor that permitted coexistence of stonefly populations.

With respect to food, there was generally a high degree of dietary similarity between co-occurring stoneflies. Although carnivorous species tended to take larger-bodied prey taxa with growth, all relied primarily on abundant chironomids through most of their life cycles. However, densities of predators with similar diets varied greatly throughout the study; thus, the actual significance of this overlap as an inferential factor for competition is questionable.

Despite high prey overlap, differential food use between sympatric stoneflies was in some cases a viable mechanism that potentially ameliorated competition in the Little Missouri River. Stonefly predators that were primary leaf pack inhabitants were usually segregated in diet. Life cycle timing was an important factor that minimized interactions between _Clioperla_ and _Perlesta_, by reducing temporal overlap to only two months (Feb., Mar.). During this interval, these populations were very different in size, and consequently ingested dissimilar sizes and often types of prey. Trophic interactions between _Clioperla_ and _I. namata_ were probably more acute, since both species were sympatric over most of their life cycles and were closer in body size. Types and sizes of animal prey consumed were generally similar each month between species. However, _I. namata_ relied minimally on animal prey (by volume) during times when it co-occurred with _Clioperla_, and consumed mostly detritus and diatoms in all but two months (Dec., Apr.).

Fig. 25 illustrates the seasonal feeding patterns for _Perlesta_ sp. _Clioperla_ and _I. namata_. Both _Perlesta_ spp. and _Clioperla_ showed predictable ontogenetic shifts in diet from herbivore-detritivores, and ultimately to obligate carnivores, as mature nymphs. By comparison, _Isoperla_

Figure 25. Monthly variations in percent carnivory (% animal matter ingested) for the primary leaf pack-inhabiting systellognathan stoneflies, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Plotted points are means.


PERCENT CARNIVORY BY VOLUME
SITE I
SITE II
Perlesta spp.
Clioperla clio
Isoperla namata
100
80
60
40
20
0
JUL
AUG
SEP
OCT
NOV
DEC
JAN
FEB
MAR
APR
MAY
JUN

namata exhibited facultative omnivory, with its age-specific diet perhaps less related to development and more to actual changes in prey availability. The advantages of a facultative trophic strategy such as this are best implemented in environments that fluctuate widely in food resource abundance (Glasser 1982), such as leaf microhabitats. Prey distributions in leaf packs have been shown to be contagious, varying in accordance with season, predominant leaf species (Hart and Howmiller 1975; Short et al. 1980), and probably the existing physical regimes (discharge, amount of leaf material present etc.). An unstable prey resource poses a serious problem for obligate carnivores. However, flexible species like I. namata that are capable of existing in a less-than-optimal prey environment, have the option to shift their diet to a less preferred food (detritus/diatoms) when prey are scarce, and specialize on animals during times when these are easily acquired.

The irregular shifts in feeding by Isoperla namata may have resulted from density-dependent trophic interactions with Clioperla nymphs for limited prey. Owing to its usually larger size, potentially greater mobility and specialized predaceous mouthparts, Clioperla may have been the competitively superior species, and possibly depressed prey resources below usable levels for I. namata when the two species were sympatric and abundant. A lower *Clioperla* density in Apr., due to emergence, may have rendered prey more available to *I. namata*, which would explain its shift to omnivory at this time. The Dec. rise in carnivory may have also resulted from lower *Clioperla* densities at both sites (Fig.8), possibly the result of excessive stream flow (Fig.2). Reductions in numbers of *Clioperla* from Nov. to Dec. were more decided in Site II (29%) than Site I (8.5%). However, reductions in total predator densities were approximately similar between sites during this interval, since abundances of *I. namata* actually increased at Site II and declined sharply at Site I. This may suggest that the food habits of *I. namata*, (i.e. the degree of omnivory) are subject not only to densities of sympatric predators, such as *Clioperla*, but to actual prey abundance levels as determined by the feeding activities of the total predator assemblage, including individuals of its own species.

Stoneflies that seasonally inhabited leaf packs, (e.g. *Phasganophora capitata*, *Neoperla* spp., *Acroneuria* spp.) provided an opportunity for winter-adapted stonefly residents to occupy greater amounts of leaf pack space, and to possibly forage with less interference. Retarded growth and lower densities of these perlids during autumn and winter months may have acted in a positive manner to allow a more efficient use of prey populations by Clioperla, I. namata and Perlesta spp., and as a consequence to maintain relatively higher abundances through nymphal life.

The spring-early summer leaf pack reinhabitance by perlid predators, particularly Neoperla spp., marked the only period when contemporaneous stonefly populations were consistently overlapping in diet and were abundant. During this interval (Apr., May, Jun.) approximate densities, prey sizes and most prey types in the diets of Neoperla and Perlesta spp. were usually similar, since both stoneflies foraged randomly and were roughly equal in body size. However, Perlesta fed more heavily on simuliid prey than Neoperla during May and Jun., which may have provided adequate prey partitioning to facilitate coexistence. Although Phasganophora capitata and Acroneuria spp. were also more frequent at these times, their impact on other sympatric predators was minimal, due to a combination of substantially lower densities compared with other stoneflies, and some prey size segregation.

This and other similar studies that imply competition between benthic predators from indirect evidence only, (i.e. high dietary overlap, microhabitat shifts etc.) are subject to question for several reasons. For example, it is generally not known how frequently prey become a limited resource in streams. Other key parameters such as predator behavioral interactions and actual microhabitat preferences are too often neglected by investigators, either because they cannot be accurately measured, are considered unimportant, or there is a lack of sufficient time or resources for their study. It has been suggested that competition and its ability to structure communities is extremely variable in environments that experience frequent physical disturbance (Peckarsky 1982). A knowledge of how frequently predator populations are at equilibrium in these variable environments is central to understanding the role biotic factors play in community organization (Wiens 1977). In streams, it is likely that such disturbance (e.g. floods) can significantly influence predator densities, especially in leaf packs, and in turn, affect the levels at which these mobile insects compete for similar resources. Although most predaceous aquatic insects are generally considered to be vagile and are able to rapidly recolonize denuded leaf substrates after a spate, it is reasonable to suggest that during some seasons, high discharge may keep the species below the saturation densities necessary for competition to be important (and thus be detected). This, coupled with subtle variations in microhabitat and food use, and prey size division by predators, may provide a plausible explanation why competition has remained an elusive element in stream research.

APPENDIX A

Species list and mean densities of animals collected from natural leaf packs, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Densities are expressed as numbers per gram dry mass of leaf pack (x 10^2). No samples were taken in July at Site I. (N=5).

TAXON	JUN		JUL		AUG		SEP		OCT		NOV		DEC	
SITE:	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Ephemeroptera	21.3	0		29.3	0	5.9	0	0	0	2.8	0.2	0	0	3.8
Attenella attenuata	11.3	77.3		1.0	0.6	0	0	1.1	0	0	0	0	0	0
Eurylophella bicolor	8.0	0.9		0	0	0	14.2	0	3.9	18.7	0.3	6.0	15.4	8.7
Paraleptophlebia sp.	1.0	3.0		0	1.1	4.4	2.8	0	1.1	8.9	0.5	2.9	2.4	15.9
Leptophlebia sp.	0	0		0	0	0	0	0	0	0	0	0	0	0
Baetidae	560.6	776.7		323.3	111.3	249.1	454.1	353.8	2.8	41.7	52.4	13.6	19.6	13.8
Baetis amplus	0	51.5		8.7	0	0	0	0	0	0	0	0	0	0
Baetis pygmaeus	61.1	19.6		8.1	11.6	90.4	25.3	138.5	21.7	93.9	7.7	47.1	0.9	0
Pseudocloeon spp.	34.1	250.5		33.7	16.7	24.3	23.8	6.6	35.9	8.5	1.7	0.9	0	0
Centroptilum rufostrigatum	123.1	1384.8		207.1	49.6	174.7	236.0	180.1	11.6	11.6	2.7	1.6	0	0.5
Siphlonurus sp.	0	0		1.0	0	5.9	1.8	1.0	0	0	0	0	0.3	1.7
Isonychia rufa	5.2	0		126.3	11.1	64.3	11.5	128.4	15.5	20.7	3.0	41.0	3.5	19.7
Heptageniidae	73.2	216.6		1504.8	14.3	450.3	37.7	379.1	0	16.9	0	26.5	4.2	2.2
Stenonema mediopunctatum	41.5	14.3		575.1	17.4	123.1	17.7	248.6	27.3	64.4	11.8	66.6	1.8	7.9
Stenonema sp.A	2.2	2.1		1.2	2.3	4.1	0	0.4	0	1.8	0	1.2	0	0
Stenonema femoratum	0.3	0		0	0	0.5	0	0	0.4	6.9	0.2	2.3	0.3	0.2
Stenonema sp.	3.4	5.9		471.6	0	156.4	0	478.6	0	20.5	0	0	0	0
Heptagenia spp.	6.5	4.8		0	22.4	2.7	30.1	1.0	4.1	2.3	9.5	0.4	2.4	1.7
Stenacron interpunctatum	11.2	1.8		9.6	0.5	1.5	2.0	0	0.4	2.7	0.5	2.3	0	0
Caenis spp.	117.9	94.1		71.1	13.1	149.1	30.7	27.7	0.4	25.6	0	9.5	4.9	2.1
Tricorythodes atratus	0	8.2		3903.8	6.1	1812.7	15.6	1057.9	1.1	42.9	0.7	52.0	0	4.8
Aeshnidae	0	0.3		0.9	0.6	1.3	0	1.0	0	0.2	0	0.7	0	0
Libellulidae	0	0		8.1	0	0	0	0	0	0	0	0	0	0
Gomphidae	0	0		0	0	0	2.0	6.8	0	5.3	0	0	0.6	0
Hagenius brevistylus	0	0		0	0	1.5	0	0	0	0	0	0	0	0
Zygoptera	0	24.0		8.0	0	8.1	2.0	27.1	0	0	0	0	0	0

Appendix A continued.

	JAN		FEB		MAR		APR		MAY	
SITE:	I	II	I	II	I	II	I	II	I	II
Ephemeroptera	0	0	0	0	0	0	0	0	0	0
Attenella attenuata	0	0	0	5.6	0	12.6	0	3.8	1.4	9.8
Eurylophella bicolor	1.1	1.7	35.4	6.1	11.2	13.0	6.9	7.1	22.0	0.2
Paraleptophlebia sp.	8.5	6.1	10.2	19.0	28.6	33.8	64.2	33.6	2.1	0
Leptophlebia sp.	0	0.3	0	0	0	0	0	0	0	0
Baetidae	45.6	33.6	43.8	29.3	194.2	258.6	264.1	138.6	292.3	253.2
Baetis amplus	3.4	0	0	0	0	0	0	0.9	0	9.3
Baetis pygmaeus	86.9	37.6	35.5	39.4	32.9	48.1	163.1	107.1	234.0	53.3
Pseudocloeon spp.	0	35.8	47.3	14.9	3.0	8.4	444.7	226.3	15.4	9.5
Centroptilum rufostrigatum	0	0	0	0	0	0.8	33.8	118.5	124.9	118.2
Siphlonurus sp.	0	0	0	0	0	0	0	0	0	0
Isonychia rufa	2.2	9.4	2.2	5.0	2.0	5.6	8.2	24.5	4.4	7.6
Heptageniidae	8.3	9.0	7.2	0	4.6	17.6	0	2.6	18.6	64.1
Stenonema mediopunctatum	8.2	15.1	1.9	8.8	7.9	11.0	20.2	16.8	7.0	3.6
Stenonema sp.A	0	0	0.4	0.3	0.3	2.2	1.2	4.3	0.6	5.3
Stenonema femoratum	0	0.8	0	0.3	0	0	0	0	0	0
Stenonema sp.	0	0	0	0	0	0	0	0	0	0
Heptagenia spp.	0.3	0	8.9	0	1.7	0.9	1.4	0.4	1.5	0
Stenacron interpunctatum	0	0	0.6	0	0	0	0	0	3.2	0
Caenis spp.	4.9	2.8	0.4	3.4	0.7	11.1	2.6	15.3	33.7	50.0
Tricorythodes atratus	0	6.5	0	8.2	0	14.5	0	20.7	0	5.0
Aeshnidae	0	0	0	0	0	0	0	2.6	0	0.2
Libellulidae	0	0	0	0	0	0.3	0	0	0	0
Gomphidae	0.4	0	0.7	0.3	4.4	0.2	0	0.2	0.5	0.3
Hagenius brevistylus	0	0	0	0	0	0	0	0	0	0.5
Zygoptera	0	0	0	0	0	0	0	0	0	0

Appendix A continued.

SITE:	JUN I	JUN II	JUL I	JUL II	AUG I	AUG II	SEP I	SEP II	OCT I	OCT II	NOV I	NOV II	DEC I	DEC II
Hetaerina sp.	0	0.6		4.8	0	8.8	0	0.5	0	1.5	0	1.1	0	0
Agrion sp.	0	0		0.9	0	0	0	0	0	0	0	0	0	0
Coenagrionidae	0	0		0	0.6	20.0	0	0.5	0	0	0	0	0	0
Allocapnia sp.A	100.0	58.6		25.6	0.5	0	1.0	0	1.9	0.4	2.5	0.4	1.0	1.9
Allocapnia sp.B	0	0.9		0	0	0	0	0	4.4	10.2	0.2	12.8	131.3	233.2
Capniidae	35.6	15.1		0	0.6	4.0	0	0	662.1	152.1	182.8	705.2	0	0
Leuctridae	0	0		0	0	0	0	0	0	0	0.2	0.6	0	0.2
Misc. Euholognatha	0	0		0	0	0	3.5	0	0	0	0	0	0	3.3
Misc. Systellognatha	0	2.4		0	0	0	0	0	0	0	0	0	0	0
Amphinemura delosa	0.5	2.8		0	0	0	0	0	0	0	93.5	40.4	64.1	22.1
Prostoia completa	0	0		0	0	0	0	0	0	0	0	0	0	0
Taeniopteryx burksi	0	0		0	0	0	0	0	327.6	172.0	64.9	148.0	28.4	60.1
Strophopteryx spp.	0	0		0	0	0	0	0	2.3	3.1	11.2	9.6	0.2	5.4
Perlidae	12.6	0		58.4	0	24.8	0	7.6	0	0	0	0	0	0
Perlesta spp.	75.2	41.3		0	0	0	0	0	0	0	0	0	0	0
Neoperla spp.	5.4	5.4		15.5	0	1.3	3.7	12.8	4.4	3.6	0.9	3.9	0.5	0
Phasganophora capitata	3.4	3.4		1.9	3.1	30.4	11.7	103.9	6.6	11.0	0.9	5.3	0	1.0
Acroneuria spp.	3.3	0.8		10.9	0.6	13.9	0	0	0.8	0	1.3	0	0	0
Perlinella ephyre	0	0		0	0	2.1	0	0	0	0	0	0	0	0
Chloroperlidae	0	0		0	0	0	0	0	0	0.3	0	0	2.1	0
Clioperla clio	0	0		0	0	0	37.3	12.6	41.6	25.3	15.1	15.3	12.9	4.4
Isoperla namata	0	0		0	0	0	0	0	164.5	56.1	81.7	31.1	24.4	38.5
Isoperla mohri	0	0		0	0	0	0	0	0	0	0	0	2.3	0
Hydroperla crosbyi	0	0		0	0	0	0	0	0	0	2.0	0.6	0	0.7
Helopicus nalatus	0	0		0	0	0	0	0	0	0	0.5	0	0	0.6
Trichoptera	7.7	10.6		18,4	0	21.3	0.7	4.8	2.2	2.3	4.6	6.0	2.3	1.7

Appendix A continued.

	JAN		FEB		MAR		APR		MAY	
SITE:	I	II	I	II	I	II	I	II	I	II
Hetaerina sp.	0	0.3	0	0	0	0.9	0	0.5	0	0
Agrion sp.	0	0	0	0	0	0	0	0	0	0
Coenagrionidae	0	0	0	0	0	0	0	0	0	0
Allocapnia sp.A	1.1	4.1	0	0	0	0	0	0	0	0
Allocapnia sp.B	29.7	108.9	0	0	0	0	0	0	0	0
Capniidae	0.4	9.2	6.3	10.0	332.6	180.2	362.8	134.2	53.6	79.2
Leuctridae	0	0	0	0	0	0	0	0	0	0
Misc. Euholognatha	0	0	7.4	0	0	0	0	0	0	0
Misc. Systellognatha	0	0	0	0	0	0	0	0	0	0
Amphinemura delosa	174.8	83.9	184.7	79.3	305.3	256.1	135.5	65.3	5.5	0
Prostoia completa	29.4	22.1	5.2	15.5	0	0.6	0	0	0	0
Taeniopteryx burksi	23.5	46.5	0	0.3	80.1	43.9	2019.6	372.7	0	0
Strophopteryx spp.	0	4.6	0	0.9	0	0	216.6	173.7	0	0
Perlidae	0	0	0	0	0	0	0	0	0	0
Perlesta spp.	0	0	208.2	27.1	186.6	115.6	165.5	103.5	83.4	41.0
Neoperla spp.	0	0.4	1.8	0.4	2.2	1.4	11.5	20.3	13.7	17.2
Phasganophora capitata	0.4	3.9	0.8	1.8	0.7	4.3	1.8	7.7	0	3.5
Acroneuria spp.	0.4	0	0.4	0	0	0	0.3	0	28.5	16.0
Perlinella ephyre	0	0	0	0	0	0	0	0	0	0
Chloroperlidae	0	0	4.1	0	4.9	0.8	7.5	1.4	1.1	0
Clioperla clio	25.7	22.7	22.4	15.4	3.9	6.5	0.4	0.3	0	0
Isoperla namata	57.7	66.4	84.3	34.7	142.2	90.3	84.9	23.1	0	0
Isoperla mohri	8.6	6.7	2.8	8.1	0	0.2	32.3	11.2	0.3	0
Hydroperla crosbyi	0	0	0	0	0	0	0	0	0	0
Helopicus nalatus	0.8	2.8	0	2.5	0.7	1.6	0	0	0	0
Trichoptera	6.6	0	0	0	0	0	0	0	0	0

Appendix A continued.

	JUN		JUL		AUG		SEP		OCT		NOV		DEC	
SITE:	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Hydropsychidae	159.5	423.6		1254.6	0.8	300.2	1.0	453.0	4.5	22.0	0	0	0	0
Cheumatopsyche spp.	259.4	274.5		359.9	4.1	36.3	10.4	41.9	6.6	33.9	0.7	32.3	3.4	13.6
Hydropsyche spp.	122.3	109.8		171.8	0	30.6	20.3	72.9	0	0.3	0	0	0	0.5
Chimarra spp.	175.0	47.8		11.9	3.2	0	1.7	40.5	7.5	31.5	0.2	5.1	14.4	8.0
Dolophilodes sp.	0	0		0	0	28.4	0	0	0	0	0	0	0	0
Wormaldia sp.	0	0		0	0	0.7	0	0	0	0	0	0	0	0
Leptoceridae	1.6	7.7		18.5	0	0	0	0	0	0	0	0	0	0
Oecetis spp.	0.3	0.9		31.1	0.8	47.4	3.9	60.8	0.3	0	0	0.9	0	0.2
Nectopsyche sp.	0	0		0	0	0	0	2.1	0	0	0	0.4	0	0
Lepidostoma sp.	1.3	1.0		2.1	0	0.5	0	0	0	0	0	1.0	0.6	0.8
Polycentropus centralis	0.5	0		1.9	0	0	0	0	0	0	0	0.9	0	0
Micrasema rusticum	0	0		14.8	0	3.9	0	0.5	0	0	0	0.3	0	2.6
Oxyethira spp.	0	40.3		117.0	0	47.3	2.0	14.4	0	0	0	3.3	0	0
Hydroptila spp.	18.6	211.0		211.8	4.4	195.4	0	33.8	0	0	0	0	0	0
Mayatrichia ayama	0.2	125.9		81.2	0	56.7	0	6.3	0	0	0	0	0	0
Hydroptilidae	8.2	0		0	8.6	0	30.1	0	2.5	0	4.2	15.3	0	0
Helicopsyche limnella	1.3	1.5		0	9.2	7.4	31.4	66.8	0.3	2.6	0	0.9	1.3	0.2
Agapetus medicus	6.1	0		0	0	0	0	0	0	2.6	4.7	13.5	25.2	0.8
Neophylax sp.	0	0		0	0	0	0	0	0	0	0	0	0.3	0
Pycnopsyche lepida	0	0		0	0	0	0	0	18.6	20.0	16.7	17.7	12.3	2.8
Rhyacophila sp.	0	0		0	0	0	0	0	0.3	0.4	0	0	10.2	4.5
Simulium spp.	856.7	2703.7		529.1	12.0	74.3	389.3	25.9	225.4	56.1	8.8	6.7	0.8	0.7
Prosimulium spp.	0	0		0	0	0	0	0	0	0	2544.5	1204.7	642.2	1145.3
Dixa sp.	41.5	5.9		0	5.5	41.5	57.3	16.4	0.3	0	0	0	0	0
Empididae	115.2	105.6		209.4	1.1	30.1	19.0	265.1	6.5	35.2	2.5	26.3	1.9	2.6
Bezzia-Probezzia sp.	3.0	2.7		1.0	1.3	7.8	1.7	1.4	0	0.8	0.7	10.6	0.5	0.2
Atherix sp.	0	28.7		6.0	0	1.9	0	0	0	0.2	0	0.5	0	0.2

Appendix A continued.

	JAN		FEB		MAR		APR		MAY	
SITE:	I	II	I	II	I	II	I	II	I	II
Hydropsychidae	0	0	3.5	0	0	0	2.5	3.4	152.7	327.7
Cheumatopsyche spp.	9.5	24.4	10.6	24.3	7.7	29.2	3.0	23.3	64.1	399.1
Hydropsyche spp.	0	0.3	0.3	1.0	0.4	1.0	0.5	0.2	0	0.2
Chimarra spp.	1.9	4.1	5.0	6.9	1.6	5.7	2.3	8.4	79.6	261.7
Dolophilodes sp.	0	0	0	0	0	0	0	0	0	0
Wormaldia sp.	0	0	0	0	0.3	0	2.4	0.2	0	0
Leptoceridae	0	0	0	0	0	0	0	0	0	0
Oecetis spp.	0	0	0	0	0	1.0	0	0	0	0.3
Nectopsyche sp.	0	0	0.3	0	0	0	0	0	0	0
Lepidostoma sp.	0.6	2.8	2.5	2.1	10.9	2.4	6.7	3.0	7.2	9.6
Polycentropus centralis	0	0	1.3	0.4	0	0	0.2	0.4	0	0.3
Micrasema rusticum	0	1.4	0	0	0	0	0	0	0	4.0
Oxyethira spp.	0	0.7	0	0.3	0	0	0	0	0	0
Hydroptila spp.	23.4	3.8	49.4	0	5.9	0.3	4.1	0	13.3	9.1
Mayatrichia ayama	0	0	0	0	0	0	0	0	0.3	4.7
Hydroptilidae	0	0	0	0	0	0	0	0	0	0
Helicopsyche limnella	0	0	0	0.3	0	0	0.4	1.0	1.4	2.9
Agapetus medicus	32.0	13.3	45.2	8.9	8.9	3.8	7.1	0	0	0
Neophylax sp.	14.4	1.0	8.9	1.6	4.6	0.3	0	0	0	0
Pycnopsyche lepida	13.2	6.2	10.4	3.2	4.1	0.7	0.7	0.2	0	0
Rhyacophila sp.	10.2	9.3	22.3	1.4	9.2	2.7	4.0	0.9	0	0
Simulium spp.	0	0	0	0	532.4	1155.1	905.1	447.2	1902.6	1700.4
Prosimulium spp.	1278.3	1685.2	1770.6	1553.7	711.4	831.0	3.3	2.0	0	0
Dixa sp.	0	0	0	0	0	0	0	0.2	0	0
Empididae	25.7	20.4	38.8	15.0	82.9	11.4	8.9	6.5	18.5	6.3
Bezzia-Probezzia sp.	0.4	0.4	0.7	0	0	0	1.0	0.4	7.0	0.3
Atherix sp.	0.3	0.7	0.3	1.0	0	0	0	0	0	4.5

Appendix A continued.

	JUN		JUL		AUG		SEP		OCT		NOV		DEC	
SITE:	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Fericoma sp.	0	0		0	0	0	0	0	0	0	0	0	0.3	0
Antocha sp.	0.2	1.9		0	0	0	0	0	0	0	0	0	0	0
Tipula abdominalis	2.8	0.5		0	0	0	0	0.4	22.3	12.4	5.5	10.8	4.9	1.0
Tipulidae	0	0		0	0	0	0	0	0	0	0	0	0	0
Forcipomyia sp.	0	0		18.8	12.2	12.9	31.6	1.9	0.4	0.2	0	0	0	0
Pararygyractis sp.	0.2	0.3		0	0.9	0	0	1.1	0	0.4	0	0.3	0	0.2
Tanypodinae	290.4	280.1		362.9	21.1	507.8	86.0	606.8	30.3	78.2	16.3	120.8	24.1	18.9
Corynoneurini	816.9	361.2		609.0	143.8	3552.5	1050.8	4937.8	2301.6	5028.0	372.6	1600.0	575.2	635.8
Tanytarsini	229.1	262.2		672.2	17.5	559.1	42.8	1426.2	3.9	63.0	0.9	96.5	37.0	23.0
Chironomini	28.5	13.2		38.6	33.2	379.5	76.3	91.7	54.4	67.3	17.3	96.2	9.4	11.3
Cryptochironomus sp.	0	0		2.1	0	5.1	0	9.7	0	0.6	0	0.3	0	0.2
Misc. Orthocladiinae	1308.7	1095.4		441.7	13.0	687.4	79.1	566.2	2564.6	927.7	447.6	615.7	910.2	718.3
Corydalus cornutus	0.9	4.3		317.5	6.2	108.3	3.7	19.4	0	1.1	0	1.1	0	0
Nigronia sp.	0.7	0.2		0	0.6	0	0	0	0	0.9	0	1.2	0.2	0.2
Rhagovelia flavicinta	0	0		0	13.0	15.7	0	0.5	0	0	0	0	0	0
Merragata brevis	10.9	11.6		13.4	28.3	5.3	2.9	6.3	0	0	0	0	0	0
Psephenus herricki	3.4	1.4		1.9	8.5	106.1	14.8	11.0	2.0	1.2	0	0.6	0	0.2
Ectopria nervosa	0	0		0	0	0	0	0	0	0.2	0	0	0	0
Elmidae	2.6	6.0		440.6	21.3	1197.9	33.7	410.1	0	0	0	2.2	2.3	0
Microcylloepus pusillus	5.8	48.9		384.8	7.7	511.8	19.7	752.0	0.3	22.2	0	9.1	0	0.4
Optioservis sandersoni	0.6	0		0	0	0	0	0.4	0	0.2	0.9	0	0.8	0
Macronychus glabratus	0	0		1.9	0	0	0	0	0	0	0	0	0	0
Stenelmis spp.	0.4	5.1		0	0	0	4.8	0	0	0.2	0	0.5	0	0.2
Stenelmis beameri	0.5	0		0	0	0	0	0	0	0	0	0	0	0
Stenelmis bicarinata	0.7	1.0		0	0	2.1	0.7	0	0	0.2	0	0.9	0	0
Stenelmis knobeli	0	0		3.8	0	0	0	0.6	0	0	0	0.3	0	0

Appendix A continued.

	JAN		FEB		MAR		APR		MAY	
SITE:	I	II	I	II	I	II	I	II	I	II
Pericoma sp.	0	0	0	0	0	0	0	0	0	0
Antocha sp.	0	0	0	0	0	0	0	0	0.4	0
Tipula abdominalis	7.0	7.4	7.4	1.5	4.3	1.2	5.8	2.4	1.1	0.7
Tipulidae	0	0	2.3	0	0	0	2.0	0	2.1	0
Forcipomyia sp.	0	0	0	3.8	0	0	0	0	0	0
Pararggyractis sp.	0.4	0	0	0	0.3	0	0	0	0	0
Tanypodinae	77.6	42.5	134.9	55.4	96.9	64.0	81.4	62.7	235.6	380.9
Corynoneurini	2155.4	5284.7	2243.0	5261.5	1583.8	5717.4	3875.3	6747.4	4260.9	6739.0
Tanytarsini	38.8	32.1	68.6	43.7	91.3	102.0	87.5	71.5	596.7	646.5
Chironomini	33.8	64.5	119.5	94.2	113.7	219.7	96.9	191.8	981.1	1222.4
Cryptochironomus sp.	0	0	3.5	0	0	0	0	0	0	0
Misc. Orthocladiinae	2400.0	1825.0	1545.4	1052.8	2113.2	3876.1	2104.8	1125.4	2255.1	2192.0
Corydalus cornutus	0	1.3	0	0.6	0	1.3	0	2.9	0.7	1.6
Nigronia sp.	1.8	0.8	0.6	1.2	5.0	0.6	0.3	0.5	0.4	0.8
Rhagovelia flavicinta	0	0	0	0	0	0	0	0	0	0
Merragata brevis	0	0	0	0	0	0	0	0	0	0
Psephenus herricki	0	0.3	0	0.3	0	5.4	4.1	2.3	3.2	0.5
Ectopria nervosa	0	0.4	0	0	0	0.6	0	0	0	0.3
Elmidae	0	0.8	0	0	0	0	0	0	0	0
Microcylloepus pusillus	0	0.7	0	0.8	0	22.9	24.2	76.7	9.0	15.1
Optioservis sandersoni	0.3	0.3	2.2	0	2.1	0	0.9	0	0	0
Macronychus glabratus	0	0	0	0	0	0	0	0	0	0
Stenelmis spp.	0	0	3.9	0.6	0.4	0.3	1.8	0.7	0.4	0.2
Stenelmis beameri	0	0	0	0	0	0	0	0	0	0
Stenelmis bicarinata	0	0	0.4	0.3	0	0.2	0	2.7	0	1.8
Stenelmis knobeli	0	0	0	0	0	0	0	0	0	0

Appendix A continued.

	JUN		JUL		AUG		SEP		OCT		NOV		DEC	
SITE:	I	II	I	II	I	II	I	II	I	II	I	II	I	II
Hydrophilidae	0	0.3		0	1.0	0	0	0	0	0	0	0	0	0
Helichus spp.	0	1.4		9.6	0	0	0	0	0	0	0	0	0	0
Helichus fastigiatus	0	0		0	0	0.4	0	0.5	0	0.7	0	0.4	0	0
Helichus basalis	0	0		0	0	0.4	0	3.1	0	1.1	0	0	0	0
Hydracarina	336.2	327.2		1192.5	102.1	1001.4	164.1	674.2	104.0	117.0	78.6	75.9	65.5	30.5
Lirceus sp.	17.3	4.0		0	0	0	0.8	0	4.2	12.6	5.0	2.5	7.9	1.6
Amphipoda	0	0		0	0	0	0	0	0	0	0	0	0	0
Hebetancylus excentricus	0.8	33.8		992.3	23.1	1251.9	45.1	1489.1	3.0	38.8	1.0	13.0	1.1	5.4
Harpactacoidea	62.2	60.6		0	0	3.7	6.2	6.7	19.6	54.9	36.0	69.3	38.8	10.8
Calanoidea	0	0		0	0	0	0	0	0	0	0	0	0	0.3
Cladocera	12.3	23.0		8.7	0.5	0	5.0	0	1.6	0	0	0	2.3	1.7
Orconectes spp.	4.3	0.3		1.0	1.1	0.5	0.8	0	0.9	0.2	0	1.1	1.7	0.7
Planorbidae	0	0		9.8	0	0	0	0	0	0.2	0	0.6	0	0.2
Ostracoda	1.6	0		0	0	20.5	2.5	0	0	0.5	0	0	3.9	0.2
Bivalvia	0	0		0	0	0.5	0	0	0	0.6	0	0	0	0
Tricladida	0	0		0	0	4.0	0	75.0	0.4	0.8	0.2	1.1	0	0
Desmognathus brimleyorum	0	0		0	0	0	0	0	0.4	0	0	0	0.8	0
Etheostoma radiosum	0	0		0	0	0	0	0	0	0	0	0	0.2	0

Appendix A continued.

	JAN		FEB		MAR		APR		MAY	
SITE:	I	II	I	II	I	II	I	II	I	II
Hydrophilidae	0	0	0	0	0	0	0	0	0	0
Helichus spp.	0	0	0	0	0	0	0	0	0	0
Helichus fastigiatus	0	0	0	0	0	0	0.5	0.2	0.7	0
Helichus basalis	0	0	0	0.5	0	0	0	0	0	0
Hydracarina	93.7	29.9	219.8	64.2	498.7	235.7	241.4	195.0	149.6	229.0
Lirceus sp.	3.7	0	4.6	0.3	2.5	0	25.1	0	13.1	2.0
Amphipoda	0	0	0.6	0	0	0	0	0	0.4	0
Hebetancylus excentricus	1.1	2.6	1.5	0	0.7	4.7	1.3	0	8.8	8.0
Harpactacoidea	94.0	40.9	226.8	47.7	593.2	351.9	819.1	838.1	311.4	555.4
Cladocera	0	0	3.7	0	7.8	0	12.8	2.6	22.8	4.0
Calanoidea	0	0	0	0	0	0	0	0	0	0
Orconectes spp.	0	0	0.7	0	0.8	0	0.8	1.0	2.0	0
Planorbidae	0	0.4	0	0	0	0	0	0	0	0
Ostracoda	2.9	0.4	9.3	3.2	0.7	1.5	9.8	8.3	14.3	7.3
Bivalvia	0	0	0	0.5	0	0	0	0	0	0
Tricladida	0.7	0.7	0	0	0.4	0.3	0	0	0	0
Desmognathus brimleyorum	0	0	0.3	0.2	0	0.3	0	0	0	0
Etheostoma radiosum	0	0	0	0	0	0	0	0.2	0	0

APPENDIX B

Composite list of organisms identified from stonefly foreguts, Upper Little Missouri River, Montgomery County, Arkansas, 6 June 1980 - 21 May 1981. Names in parentheses are subtaxonomic categories or commonly used terms.

Phylum	Class	Order	Family	Subfamily	Tribe	Genus species
Protista	Rhizopodea	Testacida	Arcellidae			*Arcella sp.*
			Difflugiidae			*Difflugia sp.*
Rotatoria	Monogonata					
Nematoda						
Arthropoda	Crustacea	Cladocera				
		Copepoda (Harpactacoidea)				
		Ostracoda				
	Arachnoidea	(Hydracarina)				
	Insecta	Collembola (Arthropleona)				
		Ephemeroptera	Baetidae			*Baetis spp.* *Pseudocloeon sp.* *Centroptilum sp.*
			Ephemerellidae			*Attenella attenuata*
			Leptophlebiidae			*Paraleptophlebia sp.*
			Siphlonuridae			*Isonychia sp.*
			Caenidae			*Caenis sp.*
			Tricorythidae			*Tricorythodes sp.*
			Heptageniidae			*Heptagenia sp.* *Stenonema spp.*
		Plecoptera	Capniidae			*Allocapnia sp.*
			Leuctridae			*Zealeuctra sp.*
			Taeniopterygidae			*Taeniopteryx burksi*
			Nemouridae			*Amphinemura delosa*
			Perlidae			*Phasganophora capitata* *Neoperla sp.* *Perlesta sp.*
			Perlodidae			*Isoperla sp.*

Appendix B continued.

Phylum	Class	Order	Family	Subfamily	Tribe	Genus species
Arthropoda	Insecta	Trichoptera	Hydropsychidae			*Cheumatopsyche sp.* *Hydropsyche sp.*
			Philopotamidae			*Chimarra sp.*
			Glossosomatidae			*Agapetus sp.*
		Lepidoptera	Pyralidae			*Parargyractis sp.*
		Diptera	Tipulidae			*Tipula sp.* *Antocha sp.*
			Simuliidae			*Simulium sp.* *Prosimulium sp.*
			Chironomidae	Tanypodinae		
				Orthocladiinae	Corynoneurini	*Corynoneura sp.*
						(Misc. species)
					Tanytarsini	
					Chironomini	*Cryptochironomus sp.*
						(Misc. species)
		Coleoptera	Elmidae			*Microcylloepus pusillus*
Mollusca	Gastropoda		Ancylidae			*Hebetancylus excentricus*
Chlorophyta	(Chlorophyceae) (Filamentous algae)	Zygnematales	Desmidiaceae			
Chrysophyta	(Chrysophyceae)	Pennales	Fragilariaceae Cymbellaceae Naviculaceae			

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