ECOLOGICAL STUDIES OF TRICHOPTERA IN THE FLATHEAD RIVER, MONTANA

DISSERTATION

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By

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Life histories, trophic dynamics, abundances, and microdistribution of Trichoptera were investigated in the Flathead River, Montana, from January 1977 through August 1979. Thirty-six Trichoptera species representing 9 families were collected from 5th order tributaries and the 6th order Mainstream River.

Two morphologically and ecologically distinct *Arctopsyche grandis* (Banks) larvae (Type I with a head stripe, and Type II without a head stripe) were found throughout the drainage except in lower order streams. Type II larvae grew more rapidly and attained a larger final instar size than Type I. In areas where *A. grandis* biomass was greatest, Type I larvae were over 10 times more abundant than Type II. Type II larvae selected microhabitats characterized by larger interstitial spaces; Type I larvae were more common in tightly compacted substrata. Food items selected by both larval phenotypes differed between sites. Larvae of both phenotypes were reared in laboratory streams. Type I larvae were male or female, but all Type II were female. I concluded that the presence of Phenotype II larvae increases resource utilization and species fitness.

Three Hydropsychinae species, Symphitopsyche cockerelli (Banks), Symphitopsyche oslari (Banks), and Hydropsyche occidentalis Banks, sequenced larval growth within a univoltine life cycle. Growth patterns were sequenced so that no two species had major growth periods at the same time. Arctopsyche grandis was the dominant hydropsychid in 3rd and 4th order valley tributary streams. Hydropsychinae were more abundant than A. grandis in the unregulated North and Middle Forks. In the Mainstream River below the confluence of the regulated South Fork, A. grandis larvae were significantly more abundant than in unregulated sections and the Hydropsychinae species were infrequently collected. Ratios of abundance between A. grandis and Hydropsychinae were similar in this river section to the lower order tributary streams. Reversal in expected sequence of macroinvertebrate species distribution along the stream continuum was attributed to a decrease in accumulated temperature and the increase in large particle, particulate organic matter, >1000 µm, in the partially altered Mainstream River.

Larvae of Brachycentrus americanus (Banks) occured primarily in 5th and 6th order tributaries and the Mainstream River. Larvae were contageously distributed, preferring substrates in nonturbulent flow. Several hundred individuals were occasionally observed in congregations along sticks or tree roots protruding from the rubble substrata in random and widely spaced locations. Five larval instars were sequenced in a univoltine life cycle, but two distinct cohorts were evident. The first larval cohort grew primarily in the late summer and fall and emerged in June. The second cohort grew primarily in the spring and early summer and emerged in late August and early September. I concluded that the larval growth and sequencing of two cohorts was most likely in response to the biannual maxima of periphyton production.

Dicosmoecus gilvipes (Hagen) had a two year life cycle, but most growth occured during the first summer. This is the first reported record of a two year life cycle for this species. Fifth instar larvae overwintered in diapause and became active during the following early summer. Early larval instars occured primarily in depositional areas at the edge of riffles or in pools and backwater areas. Late instar larvae were most frequently observed on and within the rubble substrata near riffles. Rarely were larvae of this species collected in areas of strong current. In late summer, last instar larvae entered a prepupa diapause for 4 to 6 weeks prior to metamorphosis. Adults began emerging in late August and persisted into October.

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CHAPTER I

INTRODUCTION

Theoretical and Conceptual Background Related to Trichoptera Life Histories in Lotic Habitats

Biota of running waters have been the subject of many studies throughout this century (Banks, 1900; Gallepp, 1977; Lloyd, 1921; Milne, 1934-36; Odum, 1956; Vorhies, 1909). Yet, only recently has a holistic approach to study of stream ecosystem structure and function become established (Cummins, 1974; McIntire and Colby, 1978; Hynes, 1970; Whitton, 1975). Studies which merely inventory community composition are of limited value, because they do not address biological processes manifest in lotic dynamics and contribute little to general theory of lotic ecosystems. Studies which are restricted to ecosystem function are likely to result in generalizations which lack thorough understanding and present an oversimplification of lotic ecosystem processes. I have maintained a holistic approach throughout this study in order to delineate both structure and function of major lotic environment components.

In general terms, a stream can be perceived as an open-ended dynamic system in which different types and sources of nutrients and organic substances drive the biological components. As resources change along a continuous drainage basin, community structure and consequently forms of resource utilization also change (Wiggins and MacKay, 1978). Evolution of a large number of species, each exploiting different microhabitats and consuming different energy sources, has resulted in a complex system of resource partitioning. The consequence of fine partitioning of stream resources is that frequently benthic macroinvertebrates are closely tuned to their environment. Environmental controls regulate community structure and species composition. Presence of certain species, in turn, may reflect or characterize the environment.

A basic element of lotic ecosystems is the dependence of higher order communities on upstream processes. Successive stream order communities require downstream movement or "leakage" (Cummins, 1979) of nutrient and organic matter from the preceeding stream order. Headwater streams are predominantly influenced by allochthonous detritus from the terrestrial environment through which the stream flows (Cummins and Klug, 1979; Fisher and Likens, 1973; Petersen and Cummins, 1974; Sedell et al., 1973). Heterotrophic communities are characteristic of these low order streams. The macroinvertebrate fauna consists primarily of shredders which feed upon and reduce the size of large coarse particulate organic matter (LCPOM) and collectors which feed on comparatively fine particulate organic matter (FPOM). Even in streams with considerable photosynthetically derived biomass, organic processing may largely occur in the detrital component (Minshall, 1978). Autochthonous production generally increases in importance progressively down the longitudinal gradient of the river as stream canopy is reduced. Although autotrophy is increased, the mid-sized river continues to receive a significant proportion of total carbon flux from upstream. Collectors of fine particulate matter and grazers which consume attached microbial growth dominate macroinvertebrate communities in these river segments.

Net spinning caddisfly larvae, Hydropsychoidea, and morphologically adapted filter feeders (e.g. Brachycentrus sp.), which filter and concentrate particulate matter, prevent material from being washed down stream. Retention of particulate organic matter results in an incorporation of that material into the metabolism of stream biota (Anderson and Sedell, 1979; Wallace, Webster, and Woodall, 1977). Thus, stream ecosystem energy and nutrient utilization is increased. Nutrient spiralling (Webster, 1975) in which nutrients such as particulate organic matter are stored, cycled, and released is a fundamental feature in lotic ecosystems. Continuous ecological changes along a drainage basin gradient, such as community composition and forms of resource utilization, are embodied in the river continuum concept (Vannote et al., 1979).

Based on the premise suggested by Wiggins and Mackay (1978) that the genus represents an ecological, as well as morphological type, Trichoptera have had great evolutionary potential and ecological success. Trichoptera comprise more genera than the other three wholly aquatic insect orders (i.e. Plecoptera, Ephemeroptera, and Odonata) and have exploited a broader range of habitats and food materials. They have adapted to cool and warm lotic, lotic erosional and depositional, seepage, temporary and lentic waters. They also are comparatively evenly represented in Cummins (1973) classification of trophic categories. Consequently, Trichoptera are particularly significant in the study of running water ecosystem structure and function, especially in reference to the concept of gradational changes in communities and/or trophic categories along the river continuum.

The Flathead Basin contains a broad spectrum of aquatic habitats distributed over a wide array of altitudes. It also contains many headwaters to medium-sized rivers that remain virtually free from cultural activities, yet also regulated stream sections. The Flathead Basin, therefore, is an ideal site for the comparative study of structural and functional aspects of riverine ecology.

Derivation of Research Problem

Stanford and Potter (1976) described a river-lake ecosystem concept of the Flathead River Basin. Hydrodynamic influences, interdependent processes, parameters controlling biomass dynamics, and trophic hierarchy were emphasized. They suggested that aquatic insects play a central role in the processing and flow of energy and nutrients through the lotic portions of the ecosystem. Previous limnological studies of the Flathead River and tributaries (Gaufin et al., 1972; Stanford and Gaufin, 1974; Stanford, 1975) centered on the occurrence, life histories, and basin zoogeography of Plecoptera and their role in the stream ecosystem. Stanford (1975) reported 42 species of Plecoptera present in Mainstream River benthic communities. Based on preliminary study, Trichoptera and Ephemeroptera were presumed to be significant components of the Flathead Basin. Trichoptera, Ephemeroptera, and Plecoptera often play important roles in the structure and function of lotic environments particularly in pristine ecosystems (Hynes, 1970; Whitton, 1975; Merritt and Cummins, 1978). Therefore, important structural and functional constituents of Flathead lotic environments remained to be quantified.

As part of a larger, holistic research project of the structure and function of the Flathead River-Lake Ecosystem (see Stanford, Hauer, and Stuart, 1979), I investigated the ecology of the Trichoptera. Temperature, substrata, and the quantity and availability of organic matter were examined in relationship to trichopteran distribution, role in ecosystem processes, and position in community structure.

Trichoptera, or caddisflies, are a relatively small order of approximately 10,000 species with a cosmopolitan distribution (Wiggins, 1977). Caddisfly larvae often compose a significant portion of zoobenthic biomass (Cushing, 1963; Anderson, 1967), and have been recognized as an integral part of lotic communities for several centuries. The term cod-worm or caddis first appeared in Izaak Walton's Compleat Angler (1653). However, caddisflies remain comparatively poorly known at the species level due to insufficient taxonomic study. Investigations of ecosystem structure in general have been hampered by taxonomic problems. Although the macroinvertebrate community in lotic environments are dominated numerically and functionally by immature stages of aquatic insects (Minshall, 1968), taxonomy is based largely on adult characters. Larvae (and pupae in Trichoptera) are often virtually indistinguishable at the species level. This has often led to ecological studies treating caddisflies at the generic or higher level.

Many recent studies have been directed toward an understanding of trichopteran ecology (Anderson and Bourne, 1974; Anderson and Wold, 1972; Cloud and Stewart, 1974; Fraley, 1979; Gordon and Wallace, 1975; Lehmkuhl, 1970; Mecom, 1972; Resh, 1976). My research, however, is the first in which life histories, abundance, detailed distribution, and basin-wide distribution have been investigated for an entire trichopteran community. This is especially significant in light of the paucity of knowledge of large cordilleran rivers. These data also contribute substantially to the overall goal of describing ecosystem structure and function in the Flathead River system.

Research Objectives

The purpose of this research was to 1) document Trichoptera species composition in the riverine portion of the

Flathead River; 2) document the life history dynamics of dominant Trichoptera species; 3) determine the relationship between temperature and Trichoptera species distribution; 4) determine specific thermal criteria necessary for the sequencing of trichopteran life histories; 5) document organic matter flux and its relationship to dominant Trichoptera species. Verification of Trichoptera community structure and function necessitated quantification of life histories, growth patterns, and abundance. Functional interrelationships of key species to specific environmental factors; such as temperature, temporal sequencing of hydrographic events, and dissolved and particulate compounds were documented to identify important parameters which directly influence stream biota.

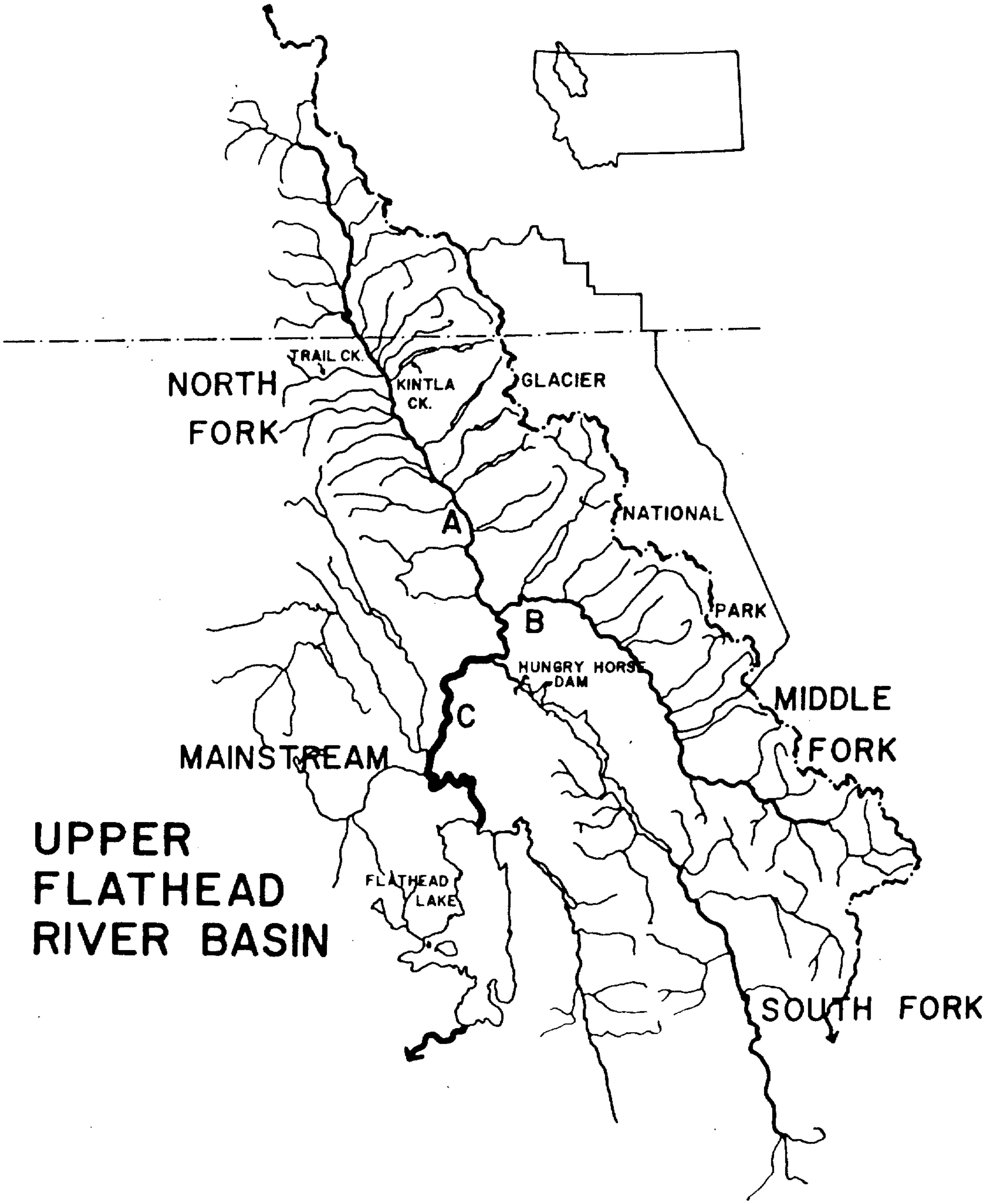
CHAPTER II

STUDY AREA

The Flathead River Basin is located along the west slope of the continental divide in northwestern Montana and southeastern British Columbia (Fig. 1). The basin is underlain by Pre-cambrian sediments, which have experienced a broad regional uplift combined with faulting to establish a series of northwest oriented mountain ranges and valleys. There are three major tributaries of the Flathead River; the North Fork (draining 4009 sq. km, mean annual flow of 85 cms), the Middle Fork (draining 2921 sq. km, mean annual flow of 84 cms), and the South Fork (draining 4307 sq. km, mean annual flow 101 cms). After confluence of the three forks, the river flows through the relatively flat alluvial flood plain of the Flathead Valley and discharges into the north end of Flathead Lake. Elevation in the basin ranges from in excess of 3048 m of several mountains in the Livingston Range, to the approximately 884 m elevation of Flathead Lake. The North, Middle, and South Fork valleys support nearly continuous coniferous forest.

The climate of the basin is predominantly a Pacific maritime type. Winter weather is periodically influenced by polar continental air masses spilling westward over the continental divide. Occasionally winter temperatures are

Fig. 1. Map of Flathead River Basin; location of sampling sites are indicated.


TRAIL CK.
NORTH FORK
KINTLA CK.
GLACIER
NATIONAL
A
PARK
B
HUNGRY HORSE DAM
MIDDLE FORK
C
MAINSTREAM
UPPER FLATHEAD RIVER BASIN
FLATHEAD LAKE
SOUTH FORK

less than -40°C. Climatic variation is largely determined by terrain.

Pleistocene glaciation extensively influenced basin topography; many moraine deposits, kettle lakes, and areas of glacial outwash occur throughout the lower part of the valley. A large part of Glacier National Park, known for its several active glaciers, u-shaped valleys, cirque basins, and horn-type mountains, is contained within the North and Middle Fork drainages.

The North Fork, which begins in the southeastern corner of British Columbia, flows in a southeast direction. The North Fork Valley is broad and rounded. Many of the tributary creeks from Glacier National Park to the east flow through large (> 4 km long), deep glacial lakes. Many of the creeks from the Whitefish Range to the west have a high gradient and boulder substratum. The Middle Fork originates in the Bob Marshall and Great Bear Wildernesses and flows northwest in excess of 180 km where it is joined by the North Fork about 7 km upstream of the South Fork confluence. The Middle Fork frequently courses through narrow canyon sections over large boulder and bedrock substrate. Although both rivers erode extensive deposits of glacial clays, the Middle Fork carries a larger sediment load, particularly during spring runoff. Fine particulate organic matter, composed of both allochthonous and autochthonous materials, is closely associated with the clay sediments in a colloidal matrix. The organically rich sediments are transported downstream and are deposited on and within the substrata of both rivers. Because the Middle Fork carries a higher sediment load than the North Fork, more interstitial spaces in the rubble are partially filled with fine sediments, course sands, and gravel. The annual spring flood, in which discharge typically increases from 10 to 100 times mean low flows, is a major hydrographic event. The flood transports large quantities of inorganic and organic material from the sediments and captured from the flood plain. The redistribution of organics and the scouring and displacement of periphytic growth are key ecosystem processes.

The Middle Fork, possibly because of valley slope and narrow canyon areas, does not clear as rapidly as the North Fork after runoff and becomes turbid periodically through the year following rainstorms. Both rivers, as well as the Mainstream, are characterized by cobble and small boulder substrata. Alluvial deposits are extensive in the flood plains, creating large areas of hyporheic habitat (Stanford and Gaufin, 1974).

The South Fork flows out of the Bob Marshall Wilderness in a northwest direction approximately parallel to and 20 km west of the Middle Fork and joins the combined waters of the North and Middle Forks forming the Mainstream River. Approximately 6 km above confluence with the combined waters of the North and Middle Forks, the South Fork is impounded by 153 m high Hungry Horse Dam establishing 55 km long Hungry Horse

Reservoir. The South Fork below the dam has been significantly altered due to hypolimnial discharges (Stanford and Ward, 1979); flow may fluctuate between 7.5 cms and 300 cms diurnally. Substrata has become heavily armoured similar to other regulated rivers (Stanford and Ward, 1979). Hypolimnial discharges have resulted in an isothermal temperature regime. Substantial growths of *Gomphonema* and *Ulothrix* cover the surface of the substrata. Trichoptera no longer occur in this river segment due to frequent dewatering of a large portion of the river channel and severe alteration of thermal regime and trophic dynamics.

The Mainstream River below the confluence of the South Fork has a rubble substrate and abundant riffles. This reach of the river is influenced during late summer, fall, and winter by hypolimnetic discharges from Hungry Horse Reservoir. Summer and fall temperatures are suppressed 2-3°C and winter temperatures are warmed 1-2°C. Thermal regima of the North and Middle Forks have a summer maxima of approximately 20°C $\pm$ 1°C. These tributaries typically freeze over in late Dec. or early Jan. A brief period of moderate temperature in which daytime temperatures $> 40^{\circ}C$ usually occur in late Jan. or early Feb. resulting in loss of ice cover. The rivers seldom refreeze after this late winter thaw. The Mainstream River also differs considerably from the North and Middle Forks in that periphytic algae are sloughed by the abraiding and sluicing effect of diurnally altered discharges from Hungry Horse Dam. This has resulted in large particle POM in the seston of this river section. The range of specific physico-chemical parameters illustrates the differentiation of the river segments (Table I: from Stanford, Hauer and Stuart, 1979).

The 5th order tributary rivers and 6th order Mainstream are open-canopied; riparian vegetation is dominated by Douglas-fir (Pseudotsuga menziesii), grand fir (Abies grandis), and aspen (Populus tremuloides). Algal growth; primarily Gomphonema, Synedra, Navicula, Ulothrix, and the cold water species Hydrurus foetidus, is closely tied to the hydrographic regime. Standing crops of attached algae generally increase during spring until the annual spring runoff. During peak flow, periphyton typically is scoured by stream bed movement and abraided by suspended materials. Algal growth is re-established in the summer, continues into fall, and is terminated by short photoperiod and icing conditions during winter.

Table I. Range of physico-chemical data from seven locations on the Flathead River, Montana.

	T°	POC mg/l	DOC mg/l	TOC mg/l	TSS mg/l	pH	TP µg/l
N. Fk. at Polebridge	0-17	.071-4.49	.122-3.68	.268-8.17	0.5-325	6.59-8.5	5-15
N. Fk. at Camas Ck.	0-17	.033-3.60	.343-3.12	.391-.672	0.5-269	6.45-8.5	3-14
M. Fk. at Walton R. S.	0-17	.068-5.08	.135-3.30	.203-8.28	0.3-377	7.1-8.2	6-20
M. Fk. at W. Glacier	0-17	.035-7.68	.039-2.94	.103-10.6	0.4-800	6.9-8.2	7-17
River just above S. Fk. confluence	0-17	.038-3.31	.264-2.13	.342-5.40	0.3-346	6.5-8.1	6-15
S. Fk. below dam	2-5.5	.027-.576	.916-1.99	.963-2.26	0.1-3.4	6.47-8.1	3-15
Mainstream at Presentine	0-17	.049-5.73	.333-2.95	.382-8.68	0.7-404	7.0-8.2	5-11

Table I Continued

TKN $\mu g/l$	NO_3 $\mu g/l$	Ca mg/l	Mg mg/l	Na mg/l	K mg/l	SiO_2 mg/l	Cond.
40-110	30-90	20-55	5.0-8.8	1.2-1.8	0.3-0.4	1.3-6.7	110-274
20-85	20-90	20-45	4.0-8.8	1.3-2.2	0.3-0.4	2.8-5.7	100-272
20-120	10-130	30-41	4.0-10.0	1.3-2.2	0.3-0.8	4.2-7.7	124-239
20-90	40-170	25-41	4.0-8.9	1.2-1.9	0.3-0.4	2.2-8.3	110-228
20-180	40-120	30-50	4.0-7.8	1.3-1.8	0.3-0.6	2.0-5.9	102-288
30-100	30-90	18-30	3.0-6.8	0.5-2.0	0.2-0.5	2.2-4.7	100-210
30-100	20-120	20-48	3.0-8.2	1.1-2.8	0.2-0.5	2.7-6.9	120-183

CHAPTER III

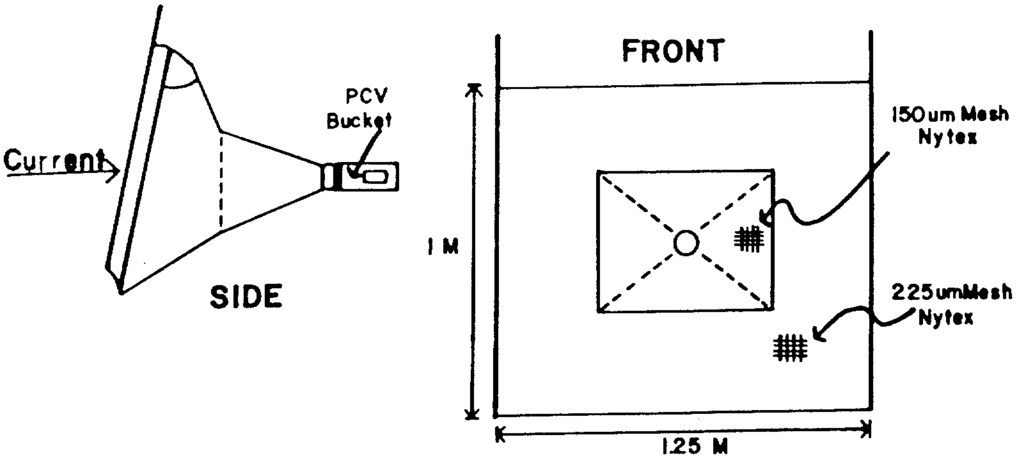
METHODS AND MATERIALS

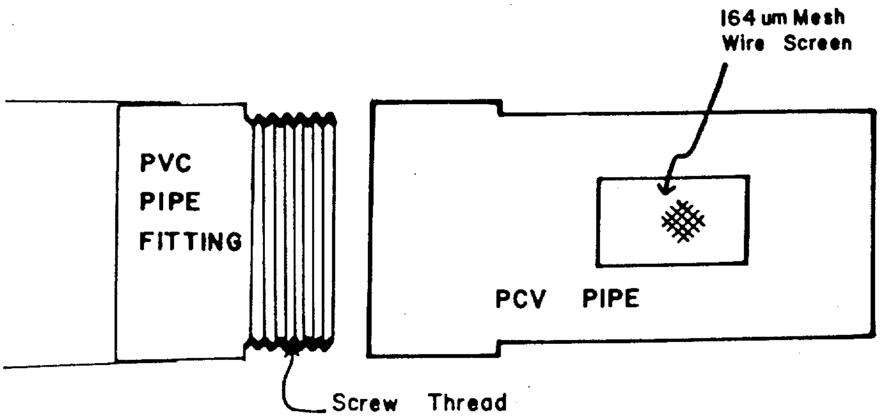
Three stations were established for collection of quantitative, time-series data: Station A was located on the North Fork ca. 20 km above confluence with the Middle Fork; Station B was located on the Middle Fork ca. 15 km above confluence with the North Fork; and Station C was located on the Mainstream River ca. 15 km downstream from the South Fork confluence. In addition, qualitative samples were obtained in a variety of smaller tributary streams throughout the drainage including Trail Creek and Kintla Creek (Fig. 1).

Immature and adult stages of Trichoptera were collected in 1977-79 using both quantitative and qualitative techniques to establish microdistributional relationships and levels of abundance and to provide sufficient number of individuals to document life history events.

Due to low macroinvertebrate standing crops and presence of large rubble in the substrata, often larger than 25 cm dia., standard Surber and Hess samplers were not suitable. Therefore, larval caddisflies were quantitatively collected using a modified kick-net (Fig. 2). The outer flat surface of the 1 m x 1.2 m net was constructed of 225 μm mesh Nitex. The center of the net was fashioned into a long, conical-shaped tube and was constructed of 150 μm mesh Nitex. At the

Fig. 2. Diagram of modified kick-net.


Current
PCV
Bucket
SIDE
FRONT
1 M
150um Mesh
Nytex
225umMesh
Nytex
1.25 M


164 um Mesh
Wire Screen
PVC
PIPE
FITTING
PCV PIPE
Screw Thread

end of the net was a 1.5 l PVC bucket. The bucket had a 125 µm stainless steel wire mesh on one side to drain water and could be unscrewed from a fitting permanently attached to the end of the net. To obtain a sample, the net was positioned perpendicular to the current immediately downstream from a 0.5 m^2 quadrat. Individual rocks >10 cm in dia. were lifted from within the quadrat into the net and washed of all zoobenthos. Any insects clinging to the outer perimeter of the net were washed by hand into the tubular section. The sample collection was concluded by vigorously disturbing the remaining substratum within the quadrat for 15 seconds. All macrozoobenthos were washed into the bucket end of the net, then transferred into Kahle's fluid. Samples were later sorted in the laboratory and insects were stored in 70 percent ethanol. Larvae inhabiting pools were collected qualitatively by visual searching, fixed in Kahle's fluid, then later transferred into 70 percent ethanol.

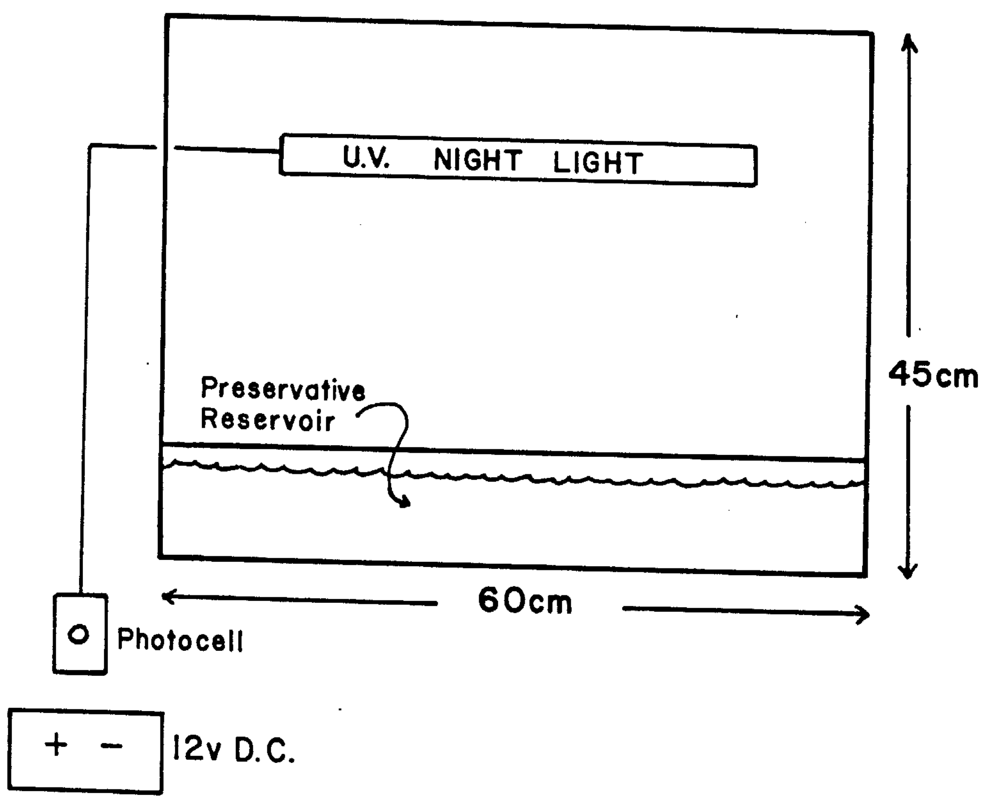
Larval collections were made monthly from Aug. through Apr.. High water prevented quantitative sampling during spring runoff in late Apr., May, and Jun.. Diving gear enabled qualitative collections of larvae and pupae during the runoff period. Instar determinations were made using the technique described by Mackay (1978), which essentially consisted of separating larvae of each species into different size classes prior to measurement.

Several hundred larvae of frequently-collected species were reared in the laboratory in circular plexiglass chambers containing gravel and rock substrate and a flow-through spring water supply. Temperature was controlled near mean weekly river temperature and light banks run on a timer were set to provide a natural photoperiod. Larvae were fed thawed, commercial, frozen brine shrimp. Field-collected larvae were reared through pupation in the laboratory streams. Pupae were also collected from the river. Larval-adult association was accomplished by dissection of mature pupae, which had larval sclerites in the cocoon and completely formed, hardened, and colored genitalia (see Vorhies, 1909; Milne, 1938; Ross, 1944).

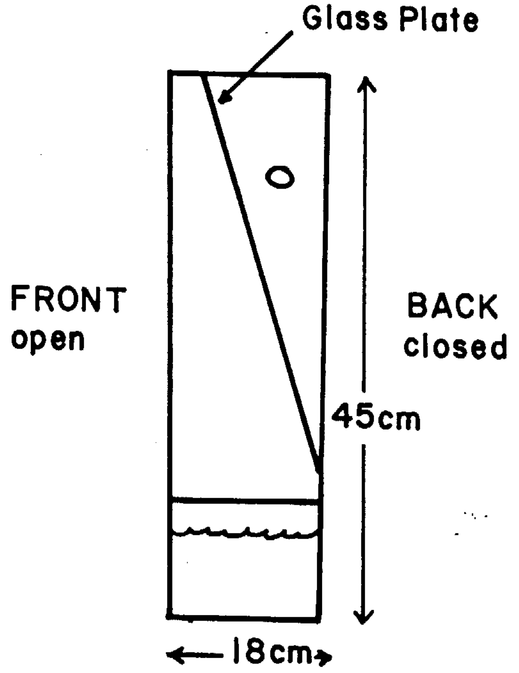
Adult caddisflies were collected using three methods: 1) active search using a sweep net, aerial insect net, and by searching under rocks along river banks and on bridge supports; 2) night lighting with a U.V. collecting light in which attracted adults were aspirated off a white reflecting cloth; and 3) a remote trap employing a U.V. collecting light. The remote trap (Fig. 3) consisted of a 45 cm x 60 cm open front box containing a reservoir filled with 10 percent formalin solution. Above the reservoir a U.V. collecting light was operated behind a glass plate. Attracted flying insects would strike the glass plate and fall into the collecting reservoir. A thin film of oil was placed over the formalin to entrap attracted adult caddisflies. The power source consisted of a 12 volt D.C. battery which was operated by a photosensitive cell, thus turning the light on at night and

Fig. 3. Diagram of U.V. night-light box.

FRONT


U.V. NIGHT LIGHT
Preservative Reservoir
45cm
60cm
Photocell
+ −
12v D.C.

SIDE


Glass Plate
FRONT open
BACK closed
45cm
18cm

off during the day. Traps were deployed at 2 to 6-day intervals at the major sampling sites on the rivers throughout the caddisfly flight period, Apr. - Oct.. All species collected were either associated by rearing in the laboratory, or by unequivocal serial collections of all life stages in the field. Dr. Glenn B. Wiggins of the Royal Ontario Museum, Toronto, verified my identifications.

I followed the procedure of Mecom and Cummins (1964) for gut analysis of Arctopsyche grandis. The alimentary canal from crop to the mesenteron was removed from last instar larvae. Contents of the proventriculus were suspended in 15 ml of two percent formalin solution and filtered onto a 0.45 μm acetate filter. The filters were placed on microscope slides, dried, and cleared with immersion oil before microscopic analysis.

Temperature data from selected sites were used to determine accumulated heat units (i.e, degree-days). Continuous recording thermographs were maintained by U.S.G.S. on the North Fork and by Montana Department of Fish, Wildlife, and Parks on the Middle Fork, the Mainstream River below the South Fork confluence and Trail Creek, a 4th order tributary of the North Fork.

Particulate organic carbon and total suspended solids (TSS) were collected semi-monthly during runoff and monthly during the fall, winter, and early spring. Organic carbon was determined using an Oceanography International 0524B total carbon system. Water was filtered onto a prefired glass fiber filter. The filter was then placed into an ampule with a strong oxidant and digested. The quantity of CO_2, and thus level of organic carbon, was determined with a non-dispersive I.R. analyzer (Menzel and Vaccaro, 1964). Total suspended solids were determined gravimetrically by filtering one liter of sample water onto a pre-washed tared 0.45 µm pore size Millipore filter. Filters were dried two weeks in an oven then weighed on a Mettler H33 balance.

CHAPTER IV

RESULTS AND DISCUSSION

Species Presence List and Bionomics of Some Infrequently Collected Caddisflies

Larvae of four insect orders, Trichoptera (caddisflies), Plecoptera (stoneflies), Ephemeroptera (mayflies), and Diptera (true flies), dominated the zoobenthos in the Flathead drainage. Stanford (1975) conclusively demonstrated that Plecoptera species composition in the Mainstream Flathead River and its tributaries is exceptionally diversified, with 42 species extant at one site on the Mainstream River. Gaufin et al. (1972) reported 118 Plecoptera species from Montana and Bauman, Gaufin, and Surdick (1977) listed 158 species for the Rocky Mountains. Of these, 100 species are known from Glacier National Park (Stanford, unpubl. data). Therefore, the Flathead Basin contains nearly two-thirds of the known Rocky Mountain Plecoptera species.

Fewer Trichoptera species were found at the same sampling sites used by Stanford (see Fig. 1); a total of 35 species were collected. An additional 27 species were found in the tributary creeks sampled (Table II). Many high altitude streams and most lake and pond systems in the basin remain uninvestigated and, because Trichoptera so successfully inhabit lentic habitats, I anticipate that many species have yet to be collected.

Table II. Collections of Trichoptera from the Flathead River Basin, Montana and southeastern British Columbia.

Taxon	Life Stage Collected	Preferred Habitat	Frequency
Philopodamidae			
Dolophilodes pallidipes	A	SC	R
Wormalida sp.	A	SC	R
Polycentropodidae			
Polycentropus sp.	L	SC,LC	R
Hydropsychidae			
Arctopsyche grandis	L,P,A	LC, R	A
Parapsyche elsis	L	SC	C
Hydropsyche occidentalis	L,A	R	R
Symphytopsyche cockerelli	L,A	LC, R	A
Symphytopsyche oslari	L,A	LC, R	A
Rhyacophilidae			
Rhyacophila acropedes	L,P,A	SC,LC,R	R
Rhyacophila alexanderi	A	SC	R
Rhyacophila angelita	L,A	SC,LC,R	C
Rhyacophila bifila	L,A	R	C
Rhyacophila coloradensis	L,P,A	SC,LC	C
Rhyacophila hyalinata	L	SC	R
Rhyacophila oreta	L	SC	R
Rhyacophila unimaculata	A	SC	R
Rhyacophila vaccua	L	SC,LC	C
Rhyacophila vagrita	A	R	R
Rhyacophila vao	A	SC	R
Rhyacophila vobara	L	AC	R
Glossosoma			
Anagapetus debilis	L,A	SC	C
Glossosoma alascense	L,P,A	R	A
Glossosoma excitum	A	R	C
Glossosoma verdona	A	R	R
Glossosoma velona	A	R	R
Hydroptilidae			
Agraylea sp.	A	R	R
Hydroptida ajax	L,A	R	C
Stactobiella	A	R	R

Table II. Continued

Brachycentridae			
Brachycentrus americanus	L,P,A	LC, R	A
Micrasema sp.	L	SC	R
Limnephilidae			
Amphicosmoccus canax	L,A	LC, R	R
Anabolia bimaculata	L,A	R	C
Apatania alberta	L,A	R	C
Apatania chasica	A	SC	R
Apatania stigmatella	L,A	R	C
Asynarchus sp.	A	R	R
Chyranda centralis	A	SC	R
Dicosmoecus gilvipes	L,P,A	SC,LC,R	C
Ecclisomyia conspersa	L,A	SC,LC,R	C
Ecclisomyia maculosa	L,A	SC	R
Glyphopsyche irrorata	A	R	R
Goeracea genota	L,A	SP,SC	R
Grammataulius sp.	A	R	R
Halesochila taylori	L	P	C
Hesperophylax incisus	L,A	GL	A
Hydatophylax hesperus	L	AC	R
Imania sp.	L	SP	R
Limnephilus alberta	A	R	R
Limnephilus extenus	A	R	R
Limnephilus spinatus	A	R	R
*Neophylax ricker*i	L,A	LC, R	C
Neophylax splendens	A	SC	R
Neothrema sp.	L	SC	R
Onocosmoecus unicolor	L,A	R	A
Pseudostenophylax edwardsi	L	SC	R
Rossiana montana	L,A	R	C
	A	SC	R
Lepidostomatidae			
Lepidostoma cascadensis	A	SC	R
Lepidostoma pluviale	L,A	R	C
Leptoceridae			
Ceraclea cancellata	A	R	C
Cerales tarsipunctata	A	R	C
Triaenodes sp.	L	P	C

Life Stage Collected - A = adult; P= pupa; L = larva.

Preferred Habitat- SC = small creek; LC = large creek; R = river; AC = Alpine creek; GL = glacial lake; SP = seepage spring; P = pond.

Frequency - A = abundance; C = common; R = rare.

Although the Flathead River is diverse in macrozoobenthos composition, it is comparatively unproductive. Stanford (1975) reported consistently low densities of Plecoptera and I found hydropsychid larvae densities typically less than 1000 m^{-2}. In contrast, Cushing (1963) recorded standing crops of over 37,000 m^{-2} benthic insects in the Montreal River, Sask.; 95 percent of these were compodeiform larvae, primarily from the trichopteran family Hydropsychidae. Coulter (1980) found a similarly high density of Hydropsychidae in the Brazos River, Texas below a hypolimnial release hydroelectric facility. The comparatively low level productivity of the Flathead River may be partially explained by low level particulate organic matter in the stream seston (see Chapter IV, section 3).

Analyses of life histories, basin distribution, microhabitat distribution and relative abundance of trichopteran species which were comparatively abundant in river benthos collections (i.e., *Arctopsyche grandis*, *Symphitopsyche cockerelli*, *Symphitopsyche oslari*, *Hydrospyche occidentalis*, *Brachycentrus americanus*, and *Dicosmoecus gilvipes*) are detailed in sections beginning on page 60. Data concerning species less frequently collected, but which were, nevertheless, important components of the zoobenthic community, are reported in this section. Much of these data concern bionomics of species for which little previous knowledge existed, even though these or closely related taxa, are known to be distributed widely over the nearctic region. Adult collections of infrequently-occuring riverine species of Trichoptera, 29 species from 6 genera, are given in Table III.

Family Rhyacophilidae

Rhyacophila is the largest genus in the Trichoptera, nearly 500 species are distributed throughout the Holarctic and Oriental regions. In excess of 100 species are known in North America (Wiggins, 1977). According to Ross (1956), the Rhyacophilidae established one of the phylogenetic lines of Trichoptera and, because of their primitive nature, are believed to occupy the same cool mountain stream habitats of the ancestral trichopteran.

Five Rhyacophila species (Table III) were collected from the North and Middle Forks and Mainstream Flathead River. This was therefore the most diverse trichopteran genus collected. Comparison of collections from creeks versus rivers indicated that Rhyacophila spp. were more abundant in 1st to 4th order streams than in the main tributaries. All quantitative collections (n = 25) from Kintla Creek, a tributary of the North Fork, yielded a range of 24 to 2 individuals m^{-2}. Quantitative collections from Coal Creek, also a North Fork tributary, contained a maximum of 30 Rhyacophila spp. m^{-2}. Less than one-half of the quantitative collections from the North and Middle Forks and Mainstream River contained any Rhyacophila larvae.

R. angelita was collected from the North and Middle Forks but not in the Mainstream River (Table II). This species was

Table III. Collections of infrequently observed adult Trichoptera at three sites on the Flathead River Montana.

	A	B	C	Total
Rhycophilidae				185
Rhyacophila acropedes Banks	1			
Rhyacophila angelita Banks	62	73		
Rhyacophila bifila Banks	30	9	7	
Rhyacophila coloradensis Banks		1		
Rhyacophila vagrita Milne	2			
Glossosomatidae				535
Glossosoma alascense Banks	34	204	270	
Glossosoma excitum Ross			15	
Glossosoma velona Ross		1		
Glossosoma verdona Ross		6	5	
Hydroptilidae				520+
Agraylea Curtis				
Hydroptila ajax Ross			1	
Stactobiella Martynov	15		500 +	
	4			
Limnephilidae				649
Amphicosmoecus canax Ross	33	1		
Anabolia bimaculata Walker	4	2		
Apatania alberta Nimmo	60	1	2	
Apatania stigmatella Zetterstedt	2		211	
Asynarchus Mclachlan			1	
Ecclisomyia conspersa Banks		3		
Glyphopsyche irrorata Fabricius	2			
Grammataulius Kolenati	2			

Table III. Continued

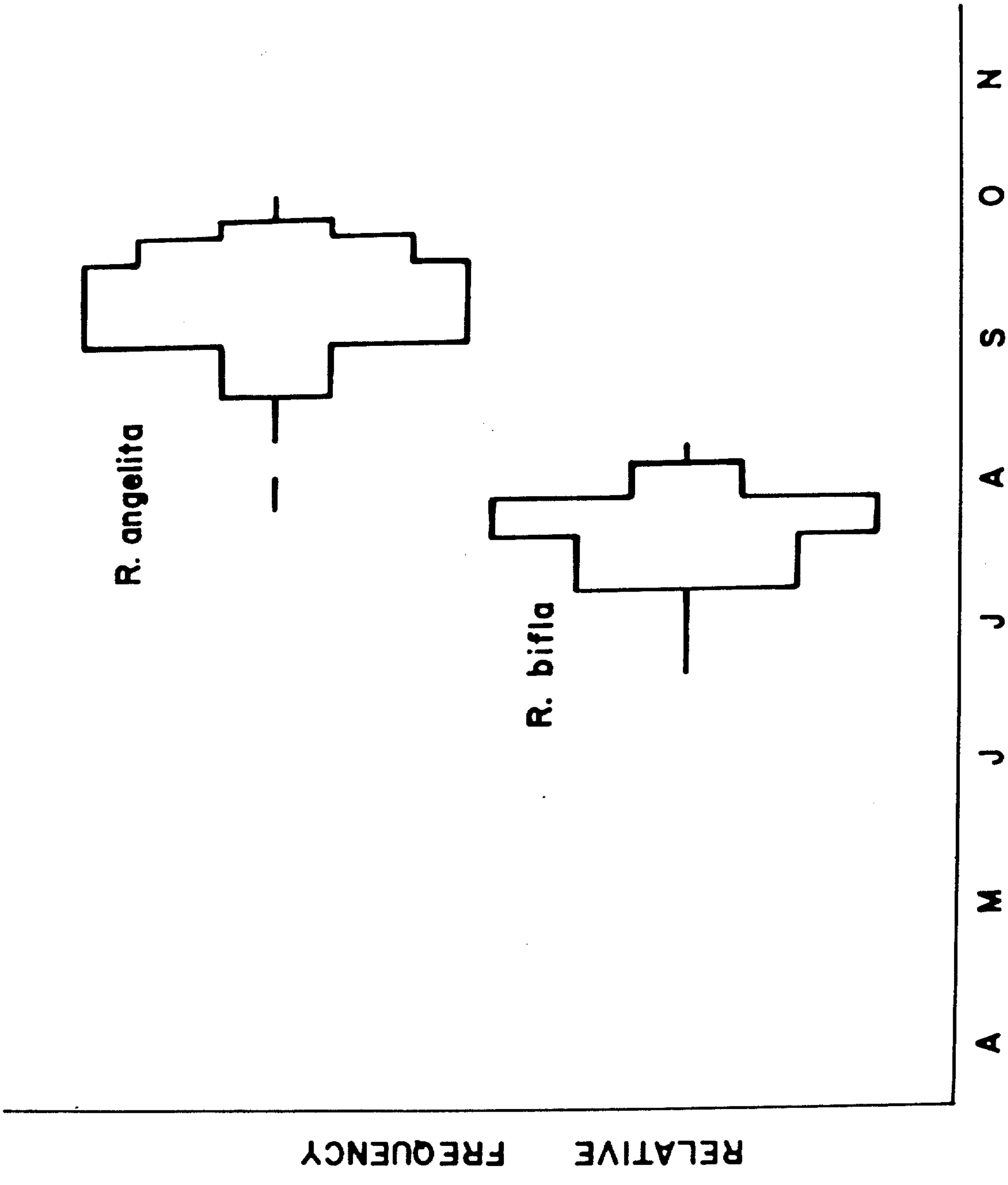
Limnephilus alberta Denning	2			
Limnephilus externus Hagen	6	2		
Limnephilus spinatus Banks			4	
Neophylax rickeri Milne	56	17		
Onocosmoecus unicolor Banks	29	140	18	
Psychoglypha subborealis Banks	7			
Lepidostomatidae				160
Lepidostoma pluviale Milne	21	109	30	
Leptoceridae				109
Ceraclea cancellata Bettem			7	
Ceraclea tarsipunctata Vorhies	10	14	78	
				2158

a major component of the zoobenthos in the Kintla drainage, a tributary of the North Fork (Hauer, Zimmerman, and Stanford, 1979), and larvae were collected frequently from several other creeks. Larvae were collected in the large rubble of riffles. Adults emerged over an extended period during the late summer and fall (Fig. 4). There was an early emergence of a few individuals in mid-Aug., but a peak in emergence occured during late Sep. and early Oct.. Adults were readily collected with a U.V. light at night. During the day, adults were collected on bridges and shoreline rubble, particularly on warm, sunny autumn afternoons.

A few *R. bifila* larvae were collected in the main tributary sampling sites and adults were often found resting along the North Fork (Table II) during Jul. and Aug.. This species was not collected from any tributary creeks. Larvae always occured in riffle areas, although unlike *R. angelita*, they were collected from closely compacted substrates as well as from large rubble. A few adults appeared in mid-Jul., but peak emergence did not occur until Aug. (Fig. 4). Adults have been reported to be crepuscular or nocturnal (Smith, 1968b) and were attracted to U.V. night light. However, individuals were also collected among riparian vegetation and on bridges and shoreline rubble during the day.

R. acropedes and *R. vagrita* were infrequently collected as adults, but were occasional components in benthic collections from the North Fork. Similarly to *R. angelita*, *R. acropedes*

Fig. 4. Adult flight period of *Rhyacophila angelita* and *Rhyacophila bifila*. Maximum width of bar graph represents peak emergence.


R. angelita
R. bifla
A
M
J
J
A
S
O
N
RELATIVE FREQUENCY

was collected frequently from 3rd and 4th order segments of Kintla Creek. Larvae were also frequently collected from other high gradient creeks. The only adult male to be collected from main tributary sites was from the North Fork during a night lighting collection on 20/VII/78. R. vagrita was not collected from the creeks, and no significant information on the bionomics of this species was obtained, except for a single collection on 30/VIII/78 from the North Fork (Table III).

Larvae of R. coloradensis were infrequently collected in the river segments, but were commonly found in 2nd and 3rd order tributary creeks. They were especially common around large boulders, which caused turbulent water flow. A single adult was collected on the Middle Fork at Site B on 12/IV/77. Environmental conditions remained harsh for adult caddisflies at that time, as the snow-covered shoreline persisted, and water temperatures were approximately 0°C at night and only 1 to 2°C during day. In tributary streams R. coloradensis adults were found in shoreline vegetation during Jul. and early Aug.. Mating pairs were frequently observed in sheltered areas along the stream banks.

Family Hydroptilidae

The North American fauna of the hydrophtilid genera inhabit a wide range of lotic and lentic habitats (Wiggins, 1977); however, because of their small size, they are infrequently collected, and little study has been devoted to Hydroptilidae bionomics. Three species were collected from the tributary rivers and Mainstream (Table III). All collections were very infrequent for both larvae and adults. A few late instar *Hydroptila sp*. were in qualitative collections from the Mainstream River sampling site during the summer. Larvae were always in close association with the filamentous green algae *Ulothrix*. Nielsen (1948) indicated that a European *Hydroptila sp*. fed on filamentous algae by piercing the cells and eating the contents.

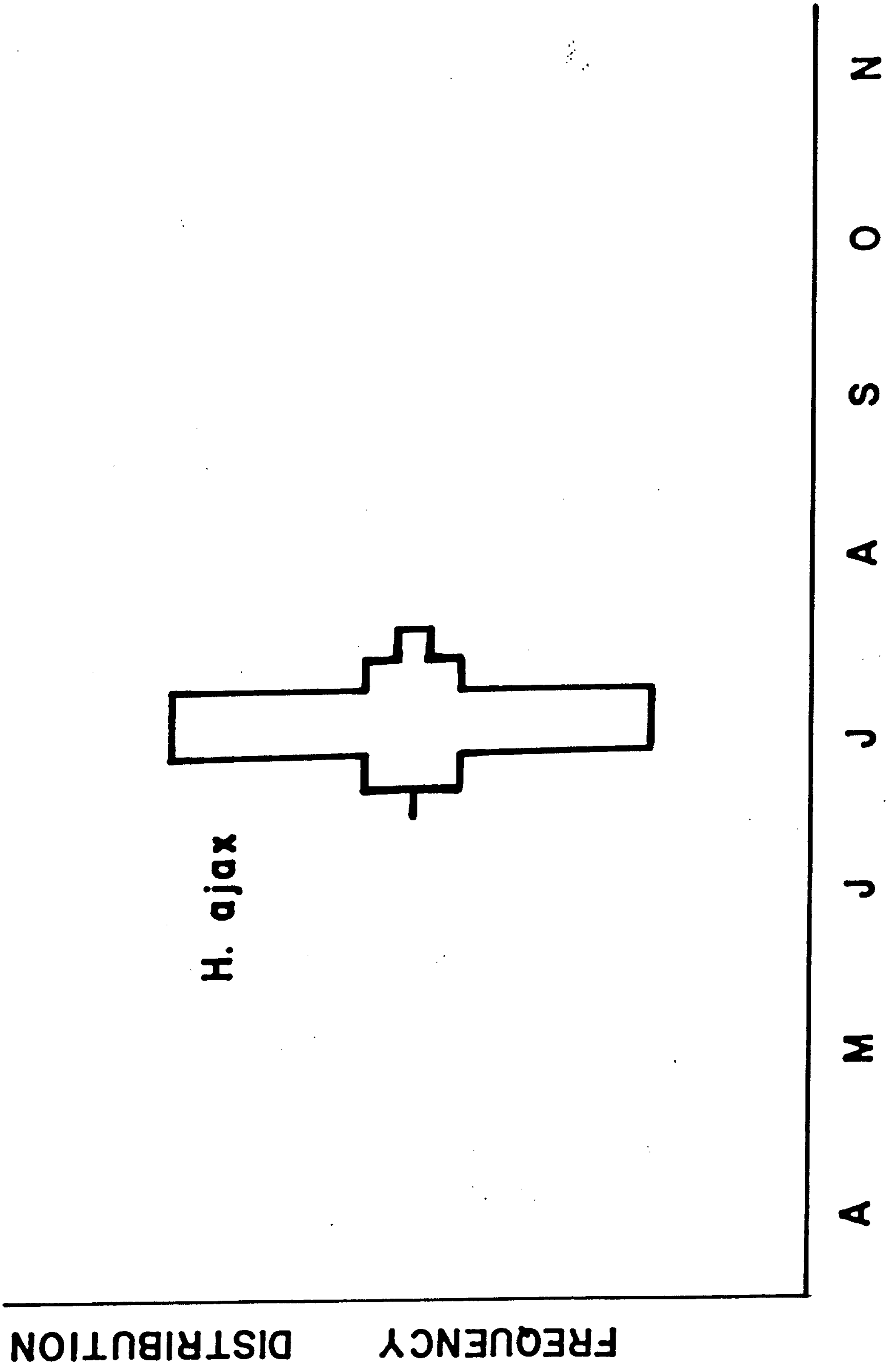
Adults of *Hydroptila ajax* were collected throughout Jul. at the Mainstream River sampling site (Fig. 5). Mid-Jul. appeared to be the time of peak emergence. On the evening of 14/VII/78, over 500 individuals were collected during a one-hour night light collection. During the day, a few adults were collected among the shaded boughs of overhanging Douglas-fir trees.

Only five adult females of the other hydroptidid genera were collected. A single *Agraylea sp*. was taken from the Mainstream sampling site with a night light (14/VII/78), and four females of *Stactobiella sp*. were collected on the North Fork with a night light (9/VIII/78).

Family Glossosomatidae

Glossosoma spp. occur over much of the Holarctic and Oriental faunal regions. Four of the approximately 25 known North American species were collected from the river segments. *Glossosoma spp*. were abundant in quantitative samples from the

Fig. 5. Adult flight period of Hydroptila ajax. Maximum width of bar graph represents peak emergence.


FREQUENCY DISTRIBUTION
H. ajax
A
M
J
J
A
S
O
N

three river sites. Larvae were also abundant in most creek samples. However, I was unable to separate specific life histories, since the larvae are indistinguishable at the species level. It is for this reason, and not a lack of larval specimens for study, that the *Glossosoma* are discussed as a group here.

I observed occasional high concentrations of larvae on the upper surfaces of the boulder substrata of the North Fork, especially during the spring prior to runoff (max. = 673, $\bar{\mu}$ = 280.8, s.d. = 222.8 m^{-2} in quantitative samples). In the North Fork, they were frequently observed on the under surface of boulders in the substratum interstitial space. A thin microbial film coated the rocks in these areas and presumably was grazed by the glossosomatid larvae. The Middle Fork and Mainstream substrata were more compacted than that of the North Fork. Consequently, *Glossosoma spp*. were not observed on the undersides of the surface layer rubble in these river segments, during spring Middle Fork $\bar{\mu}$ = 71.2; s.d. = 30.4 m^{-2}; Mainstream River $\bar{\mu}$ = 118.4, s.d. = 96.6 m^{-2}. Although *Glossosoma spp*. larvae occupied the interstitial spaces in the substrate of the North Fork, larvae usually were observed on the top and sides of large stones (>10 cm dia.) where diatoms and associated bacterial and fungal growth was abundant. Larvae were spatially precluded from areas of heavy diatom or filamentous algal growth. *Glossosoma spp*. were also restricted to erosional areas; deposition of flocculated clay and organic matter on the tops of rocks precluded all *Glossosoma* larvae.

During fall, standing crops of *Glossosoma* were significantly higher ($P < .05$) in the North and Middle Forks than in the Mainstream (Fig. 6). During winter, standing crops in the North and Middle Forks had larger mean abundance than the Mainstream, but differences were not significant. During spring, standing crops of *Glossosoma* were significantly ($P < .05$) greater than in the Middle Fork or the Mainstream.

There was an exceedingly wide range in *Glossosoma* larval development throughout the fall, winter, and spring. During winter and spring, glossosomatid larvae were present in all five instars. Larvae completing growth in late winter or early spring sealed their larval case and entered a diapause prior to larval-pupal apolysis. Diapausing *Glossosoma* collected at this time and reared in the laboratory were *G. alascense*. This species was the most frequently collected and had the widest distribution of the adult glossosomatids (Table III). Adults began to emerge immediately after the peak of spring runoff, at the end of May and first week of Jun.. Peak emergence occured the last week of Jun. and early Jul. (Fig. 7). Adults were active during the day and were collected among riparian vegetation. *G. alascense* adults were readily attracted to the U.V. night light. The species apparently is univoltine in the Flathead Rivers.

G. excitum, *G. velona*, and *G. verdona* were infrequently collected as adults. *G. excitum* was only collected from the Mainstream River. Data from 1977 and 1978 suggested a late

Fig. 6. Seasonal abundance of *Glossosoma spp.* at the three river sites on the Flathead River.

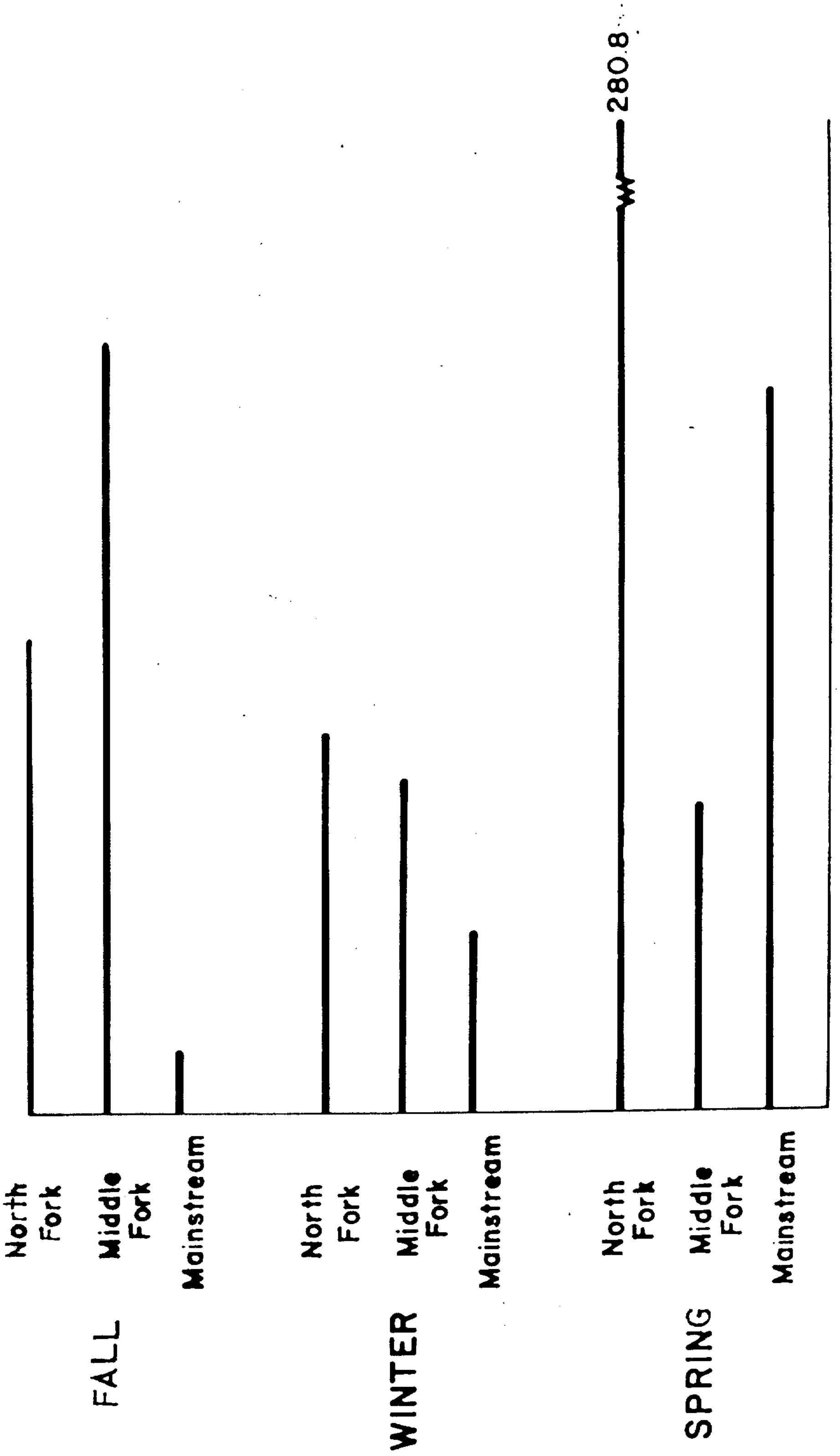
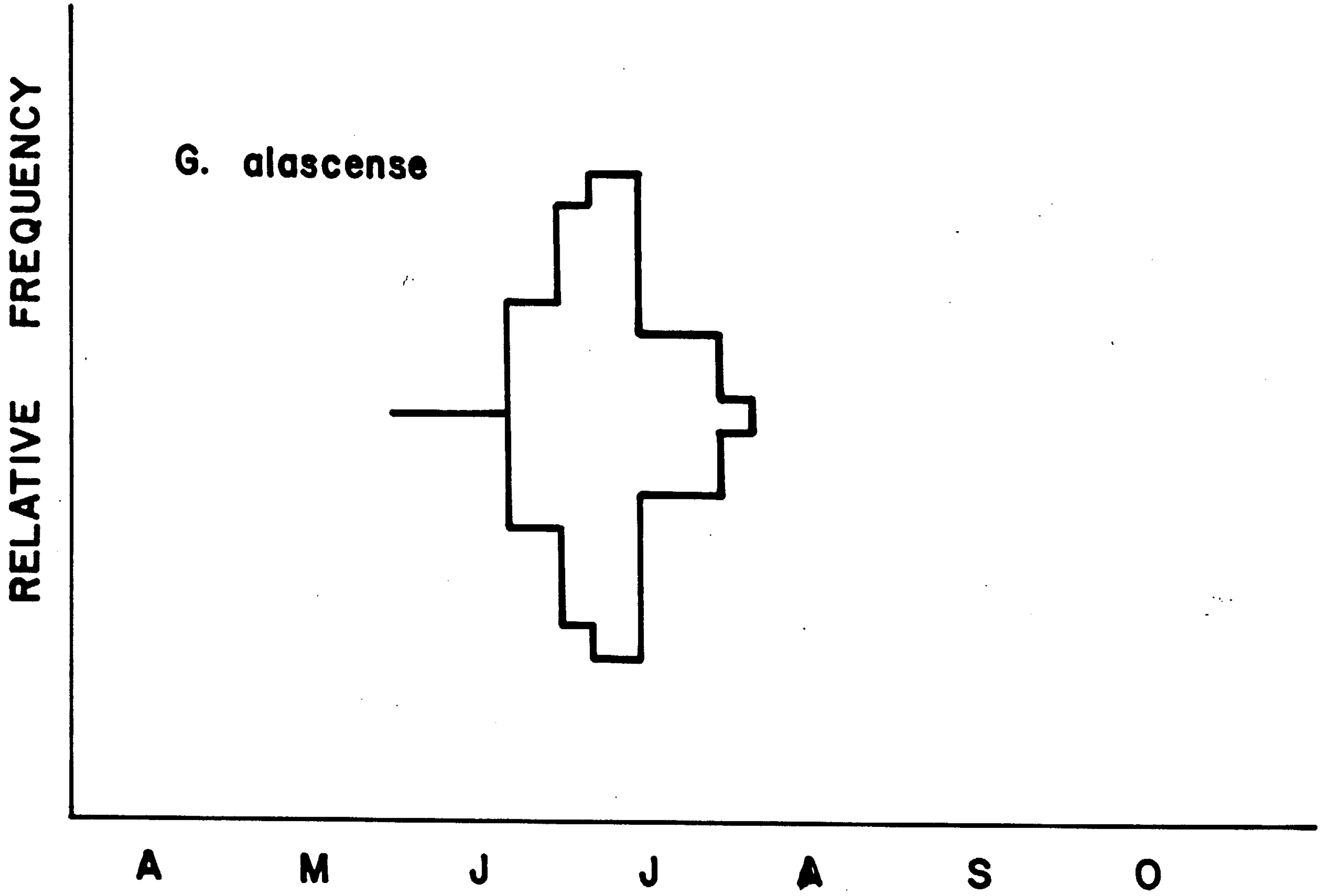

FALL
North Fork
Middle Fork
Mainstream
WINTER
North Fork
Middle Fork
Mainstream
SPRING
North Fork
Middle Fork
Mainstream
20
40
60
80
100
120
140
280.8

Fig. 7. Adult flight period of *Glossosoma alascense*. Maximum width of bar graph represents peak emergence.


G. alascense
RELATIVE FREQUENCY
A
M
J
J
A
S
O

Jun. and early Jul. emergence period. Only a single male of G. verdona was collected along the shoreline rubble during the runoff (14/V/77). G. velona was collected from both the Middle Fork and Mainstream River. Although insufficient data are available to verify adult bionomics, a mid-Jul. emergence period was suggested.

Family Limnephilidae

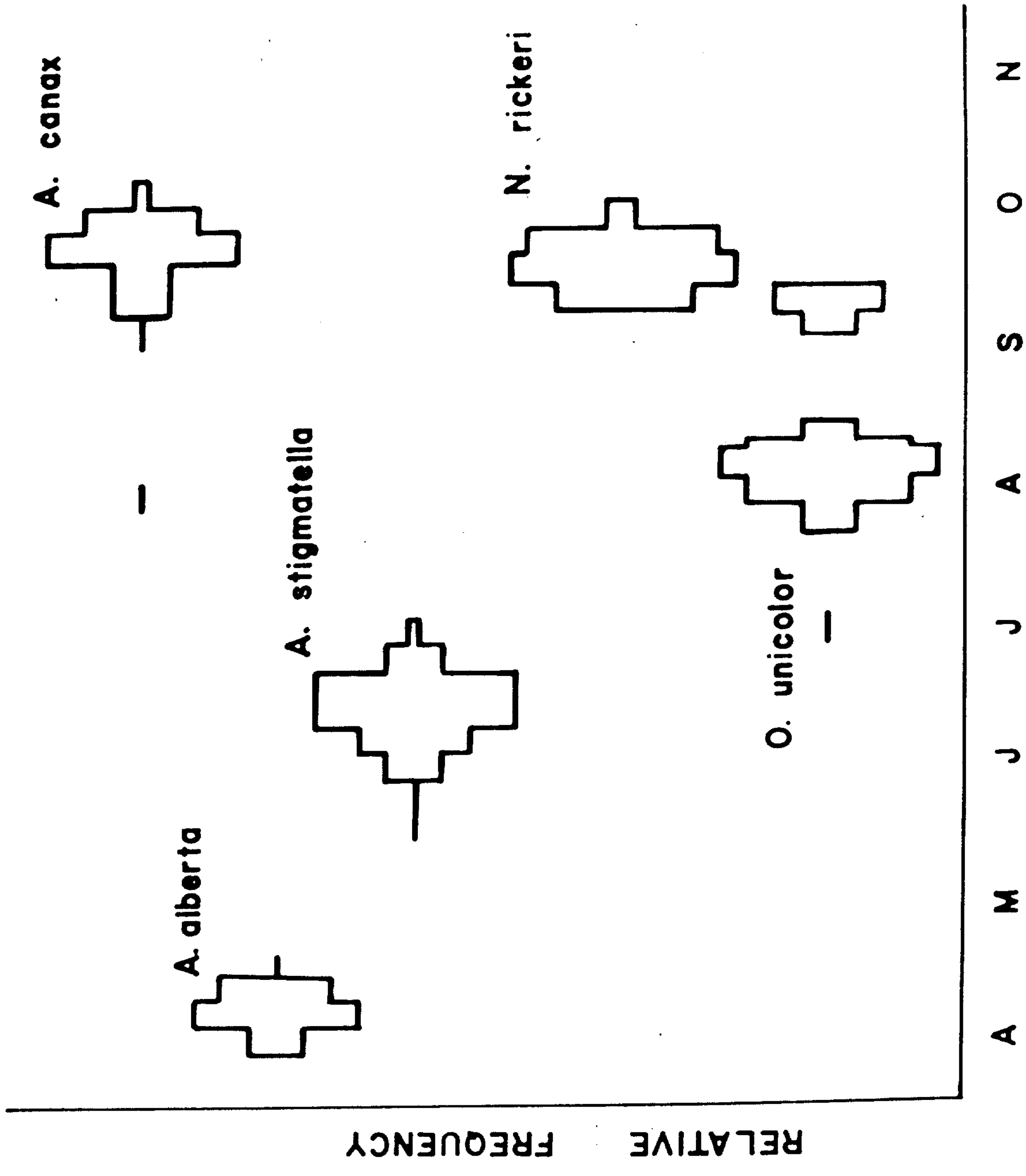
The Limnephilidae is the largest family of Trichoptera in North America (Wiggins, 1977). Larvae occupy a wider range of habitats than any other trichopteran family with genera characteristic of springs, streams, rivers, lakes, marshes, fine organic detritus of spring seeps, temporary streams and pools, and moist terrestrial sites. This family was also the most diverse in the main tributaries and Mainstream Flathead River represented by 13 species from 10 genera. However, none of the species of Limnephilidae were abundant. Several species occured commonly (i.e., Apatania spp., Onocosmoecus sp., Neophylax sp.), but were collected only in later instars. Dicosmoecus gilvipes also did not occur abundantly; however, it was the only limnephilid species to be collected in all instars and, consequently, I was able to define the life history (presented elsewhere).

Amphicosmoecus canax, a mono-specific genus, was predominantly collected from the North Fork. The few larvae collected annually were obtained primarily during peak runoff. During runoff, larvae were typically found clinging to floating debris in backwaters and small whirlpools behind rocks. Several weeks after peak runoff, A. canax larvae were also collected from silt substrates in backwater areas or from small, isolated pools left on the flood plain after the receding of runoff. Both the hollow twig case and the small chunks of wood case as described by Wiggins (1977) were collected. Larvae were in late-instar at time of collection. Adults emerged primarily in late Sep. and Oct., however I did obtain a teneral individual in mid-Aug. (Fig. 8). Adults were active in the late afternoon and at dusk and were frequently observed flying out over the river for long distances, 200 to 300 m. Adults were collected after dusk with the U.V. night light.

Anabolia bimaculata larvae were collected only from the North Fork, although two adult males were collected from the Middle Fork. Larvae were found only in backwater silt substrate areas after runoff. Larvae sealed their case for pupation in early Jul., usually after attaching the case along the stem of emergent vegetation such as Equisetum sp. Larval cases were constructed of elongate conifer needles arranged longitudinally. The case was nearly twice the length of the larvae. Adults from the North Fork were collected between 9/VII/78 and 30/VIII/78, however the single collection of two adult males from the Middle Fork occurred on 25/IX/78.

Apatania spp. were occasionally collected as larvae in benthic samples from riffles. However, in the spring, larvae were found aggregated for pupation. On several occasions, over

Fig. 8. Adult flight period of *Amphicosmoecus canax*, *Apatania alberta*, *Apatania stigmatella*, *Neophylax rickeri*, and *Onocosmoecus unicolor*. Maximum width of bar graphs represents peak emergence.


A. alberta
A. stigmatella
A. canax
O. unicolor
N. rickeri
A
M
J
J
A
S
O
N
RELATIVE FREQUENCY

50 sealed cases were observed on the undersides of a single rock along the edge of the river, usually below a riffle. Pearson and Kramer (1972) explained the clumped distribution of *Oligophlebodes sigma* pupae as a function of many individuals seeking a limited number of suitable pupal environments. This seems unlikely in the case of *Apatania spp.*, since there appeared to be many areas suitable for pupation which were uninhabited. It is likely that, similar to habits of *Brachycentrus occidentalis* reported by Gallep (1974), pupal aggregation was in response to predation or parasitism in which clumped prey require a much greater search effort by potential predators (Olson, 1964). Probability of successful pupation and emergence would, thereby, be enhanced.

The two species of *Apatania* occuring in the Flathead River appeared to be ecologically segregated temporally and spatially. *A. alberta* was the smallest of the limnephilids from the Flathead River and was also the first trichopteran species to emerge each year. Adults were primarily collected from the North Fork (Table III) and emerged within a 3 week period at the end of Apr. (Fig. 8). Emergence generally began after the first high water of the runoff period; river temperatures fluctuated between 1 and 4°C, diurnally. Adults were collected on exposed shoreline rubble and on the south side of bridges on warm, sunny afternoons. *A. stigmatella* was the first trichopteran species to emerge after peak runoff. Adults were collected primarily from the Mainstream River (Table II). Although a few individuals were collected in early Jun., the peak in adult emergence did not occur until the end of Jun. and early Jul. Adults were collected while flying among riparian vegetation or flying in a skipping motion over the water near shore. Adult activity ended rapidly after the peak emergence period (Fig. 8).

Neophylax rickeri larvae were collected primarily from the North Fork, where individuals were found on the surface of large stones presumably grazing diatoms and fine particulate organic matter. Larvae were only found in slow current, along the edge of the river after peak runoff. Larvae were also components of the zoobenthos in the tributary creeks of the North Fork drainage, particularly near the confluence with the river. The larval case was constructed of large rock fragments and gravel, with several large stones along each side. Larvae collected from areas with a faster current constructed cases with larger stones on the sides. Presumably the side stones are used for ballast. Larvae attached their case and entered a diapause in early Aug.. Adults emerged over an approximately 3 week period at the end of Sep. and first half of Oct. (Fig. 8). Adults were collected from riparian vegetation with a sweep net during the day and with a U.V. night light after dusk. This short emergence time is in agreement with that found by Anderson and Wold (1972).

Larvae of _Onocosmoecus unicolor_ were most frequently collected in backwater and slow-current areas after peak runoff, on a wide variety of substrates from submerged branches and twigs to rocks and silt. Nimmo (1971) also reported finding them on a wide variety of bottom types. Late-instar larvae were collected throughout the summer. The larval case was constructed of thin, flat pieces of bark and wood positioned so that the case has a slightly curved shape. Adults were collected at all three main river sampling sites (Table II) and emerged over an extended time period. A few individuals were collected in mid-Jul., adults were not collected again until the second week in Aug.. Peak emergence occured in mid-Aug. followed by a 2-week period of no emergence during the first half of Sep.. A smaller emergence occured during the end of Sep. (Fig. 8). On 9/X/78, two weeks after the cessation of emergence, several larvae in 4th or 5th instar were collected in the North Fork at the base of a riffle. This suggests that this species has either a two year life cycle, or that larvae grow very rapidly from eggs deposited in Aug. and larvae overwinter in late instar.

Psychoglypha subborealis were collected as larvae exclusively crawling across the silt substrate in backwaters and pools left by the spring runoff. Adults emerged in Early Oct., only from the North Fork, and were attracted to the U.V. night light.

Three species of *Limnephilus* were collected as adults; *L. alberta*, *L. externus*, and *L. spinatus*. However, only two *Limnephilus* larvae were collected over the 2.5 year period. Both larvae were collected from the same backwater area on the North Fork on subsequent years. The larvae were collected from grass which had been submerged by high water runoff. The larval cases were made of small twigs and bark with the length of the material positioned radially around the case similarly to that illustrated for *L. indivisus* by Wiggins (1977).

Only adults of *Ecclisomyia conspersa* and *Glyphopsyche irrorata* were collected from the Middle Fork and North Fork, respectively. Also, females of the genera *Asynarchus* and *Grammoltaulius* were collected from the Mainstream River and the North Fork (Table III). No significant information on the bionomics of these species was forthcoming due to these limited collections.

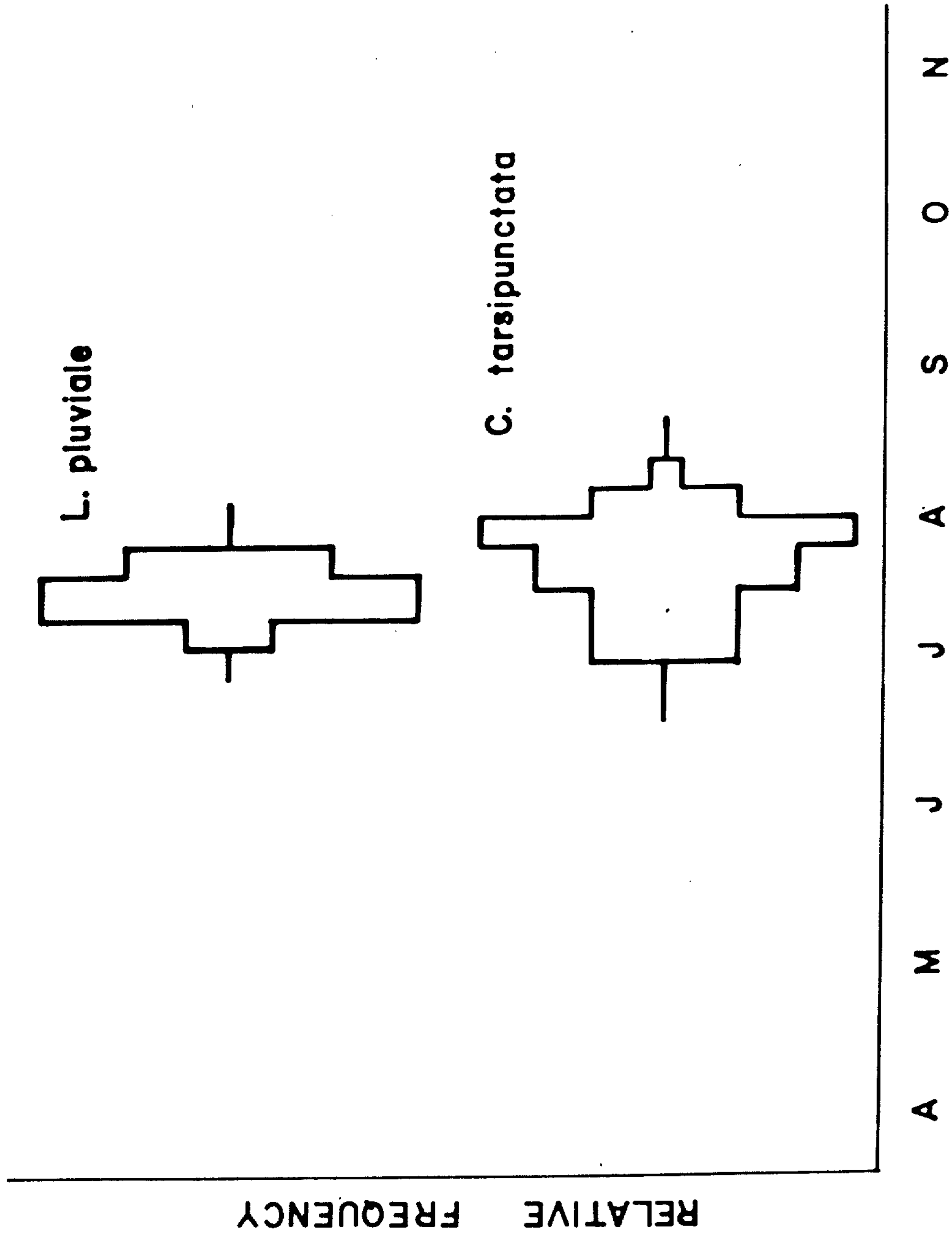
Family Lepidostomatidae

Lepidostoma is a Holarctic genus containing 65 Nearactic species. The one species in the Flathead River, *Lepidostoma pluviale*, was occasionally collected in quantitative benthic samples over a wide range of lotic erosional conditions from areas of slow, even flow near shore to the most turbulent areas in mid-riffle. Ross (1946) reported *L. pluviale* to be the dominant *Lepidostoma* in the eastern ranges of the western montane region. Anderson (1976) states that larvae occur primarily in streams in backwaters, pools, or quiet areas near shore. *Lepidostoma quereina* is known to be a leaf shredder (Grafius and Anderson, 1979); however, I found *L. pluviale* larvae most frequently in association with a fine film of microbial growth that occurred on the sides and under large boulder substrata within the rubble interstitial space. The larval case was composed of uniform mineral particles formed in a slightly tapering, tubular shape. Adults were collected from all three of the main river sampling sites (Table III) and emerged over a relatively short time period from the end of Jul. to early Aug. (Fig. 9). This time period coincides with the annual temperature maxima for the rivers during 1977 and 1978. Adults were collected during the day with a sweep net while resting in riparian vegetation and after dusk with a U.V. night light.

Family Leptoceridae

Approximately 34 species of the genus *Ceraclea*, formerly assigned to *Athripsodes*, occur in the Nearctic region. Two species, *C. cancellata* and *C. tarsipunctata*, were collected as adults from the North and Middle Forks and Mainstream River (Table III). Despite intensive collecting, no *Ceraclea* larvae were obtained. An extensive hyporheic habitat and associated community are significant features of the Flathead River. Several of the plecopteran species (e.g. *Isocapnia spp.*, *Paraperla frontalis*) live nearly their entire nymphal life history within the hyporheic habitat, entering the main channel of the river only during emergence (Stanford and Gaufin, 1974). Since *C. cancellata* and *C. tarsipunctata* were collected only as adults, it is possible that these species could also be members of the hyporheic community

Fig. 9. Adult flight period of *Lepidostoma pluviale* and *Ceraclea tarsipunctata*. Maximum width of bar graphs represents peak emergence.


L. pluviale
C. tarsipunctata
A
M
J
J
A
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RELATIVE FREQUENCY

during the larval part of their life history. The few *C. cancellata* adults were collected from the end of Jun. to mid-Jul.. *C. tarsipunctata* was collected from mid-Jul. through Aug. and had a peak emergence in early Aug. (Fig. 9).

Ecological Segregation of Congeneric Species

Aquatic insects, which frequently dominate the zoobenthos of running water ecosystems, segregate themselves not only distributionally along the stream continuum (Vannote et al., 1979; Wiggins and Mackay, 1978; Cummins, 1975a), but also on different substrates and within different microhabitats (Hynes, 1970; Grant and Mackay, 1969). Spatial segregation, in a pattern of temporally sequenced life histories, permits closely related species to occupy similar riverine habitat. The failure of one species to ensure competitive displacement over another species is largely due to shifts between limiting resources which are perceived as environmental heterogeneity. Thus, the maintenance of diversity or species richness may be considered as a function of a constantly changing intensity and focus of specific environmental parameters (Pielou, 1975; Huston, 1979).

Rhyacophila angelita and *R. bifila* occured primarily in the North and Middle Forks and were occasionally collected in the same benthic sample. There were insufficient numbers of individuals of both species to establish definitive growth patterns; however, I did observe a distinct difference in emergence pattern. *R. bifila* emerged in mid-summer and was completing its adult activity as *R. angelita* began to emerge.

Apatania alberta and A. stigmatella were ecologically segregated both spatially and temporally. A. alberta occured primarily in the North Fork, while A. stigmatella was a part of the Mainstream River community. Also, A. alberta emerged in Apr. and A. stigmatella emerged in Jun. and early Jul.. Consequently, not only was there little spatial overlap, but also there was no overlap of emergence time.

The Flathead drainage possesses an exceedingly diverse set of aquatic habitats resulting in an exceptionally rich faunal composition. Plecoptera have been collected extensively throughout the drainage; in excess of 100 species are known to occur (Stanford, unpubl. data). Trichoptera have not been as intensively collected in habitats outside the Flathead River, but probably because of the diversification of this insect order, will exceed the Plecoptera in total number of species occuring in the basin.

Other studies (Cushing, 1963; Anderson, 1967; Coulter, 1980; Stanford and Ward, unpubl.) have recorded high densities of benthic insects particularly among campodeiform larvae. Cushing reported densities of over 37,000 m^{-2} of benthic insects in the Montreal River, Sask.; 95 percent of these were Hydropsyche sp. and Cheumatopsyche spp. larvae on the Brazos River, Texas, 30 km downstream from a dam. The Flathead River did not approach such high densities of Trichoptera larvae, max. $\approx$ 1500 m^{-2}. However, perhaps because of the comparatively low productivity in combination with resource availability and niche segregation, the Flathead River has developed an exceptionally rich benthic fauna.

Larval Specialization and Phenotypic Variation in *Arctopsyche grandis* (INSECTA: Trichoptera): Ecology and Adaptive Significance

Net-spinning larvae often contribute significantly to zoobenthic biomass and energy processing in running water ecosystems (Cummins, 1974; Wallace, Webster, and Woodall, 1977; Ward and Short, 1978). Although stream size preference (Gordon and Wallace, 1975; Wiggins and Mackay, 1978) and the importance of various environmental factors such as current velocity (Wallace, 1975; Haddock, 1977) have been documented for certain species of hydropsychid larvae, the biology of caddisflies is not well known, especially in western Montana.

Ecological relationships of the large hydropsychid caddisfly, *Arctopsyche grandis* (Banks), were investigated throughout the Flathead Basin. I found *A. grandis* in 3rd and 4th order high mountain streams, as well as in the riffles of the mainstream rivers above Flathead Lake. Larvae were very abundant in the river sections, max. 600 m^{-2}, and were frequently one of the numerically dominant caddisfly species in riffle areas. Although *A. grandis* is widespread in western North America and has been the subject of ecological (Alstad, 1980; Mecom, 1972) and taxonomic study (Smith, 1968a; Givens, 1976), differentiation in larval morphology and possible ecological differences between phenotypes have remained uninvestigated.

Soon after the initiation of my research, it became apparent that two morphologically distinct larvae of *A.*

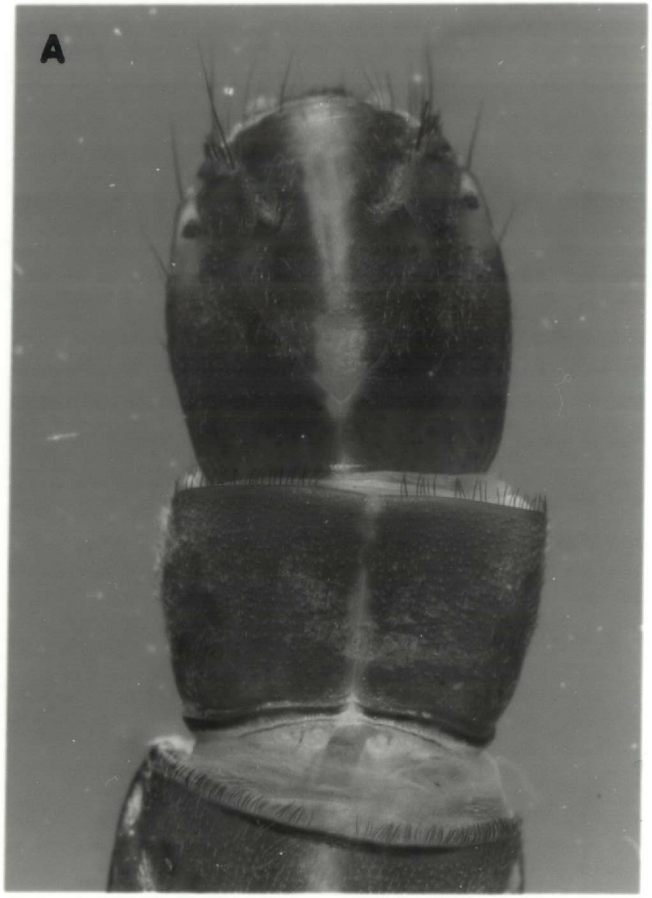
grandis were commonly found in close association. The two morphs had different color patterns and, after close examination, it was apparent that they selected slightly different microhabitats and responded differentially along specific resource gradients within the river system. To fully delineate the means of apparent morphological heterogeneity within the species, I examined growth and emergence, habitat selection, and possible sexual differences between the two larval phenotypes.

Larval Morphology and Life Cycles

A. grandis is the largest of the net-spinning caddisflies in the Flathead Rivers. The two distinct morphological types, designated Phenotype I and Phenotype II, were determined by differences in head and thorax color pattern. The head of Phenotype I larvae is dark brown with a pale yellow mid-dorsal stripe running from the anterior edge of the frontoclypeal apotome posteriorly through the coronal suture and mid-dorsal ecdysical line of the pronotum and mesonontum (Fig. 10a). The head and thorax of Phenotype II larvae are dark brown with no stripe (Fig. 10b). Individuals reared in the laboratory maintained their distinct markings through successive instars. Larvae were rarely collected in which the mid-dorsal line on the head was slightly broken at the constricture of the lateral sutures at the frontoclypeal apotome.

Distribution of larval instars over the annual cycle revealed that A. grandis had five instars (Fig. 11) and a 2

Fig. 10. Two morphological variations of Arctopsyche grandis larvae from the Flathead Rivers, Montana; Phenotype I (A) has a distinct stripe on head and thorax, Phenotype II (B) does not.


A

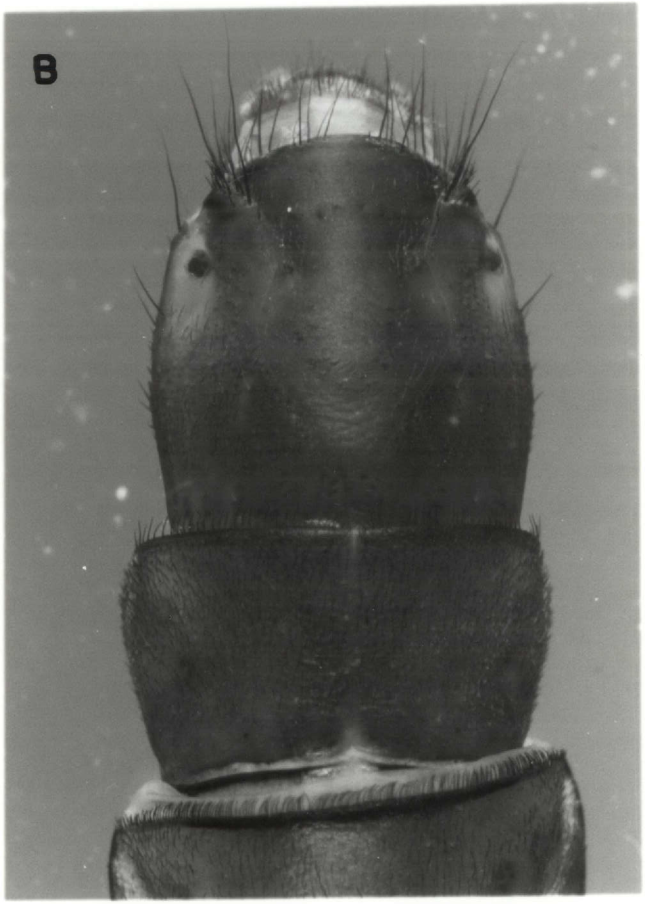
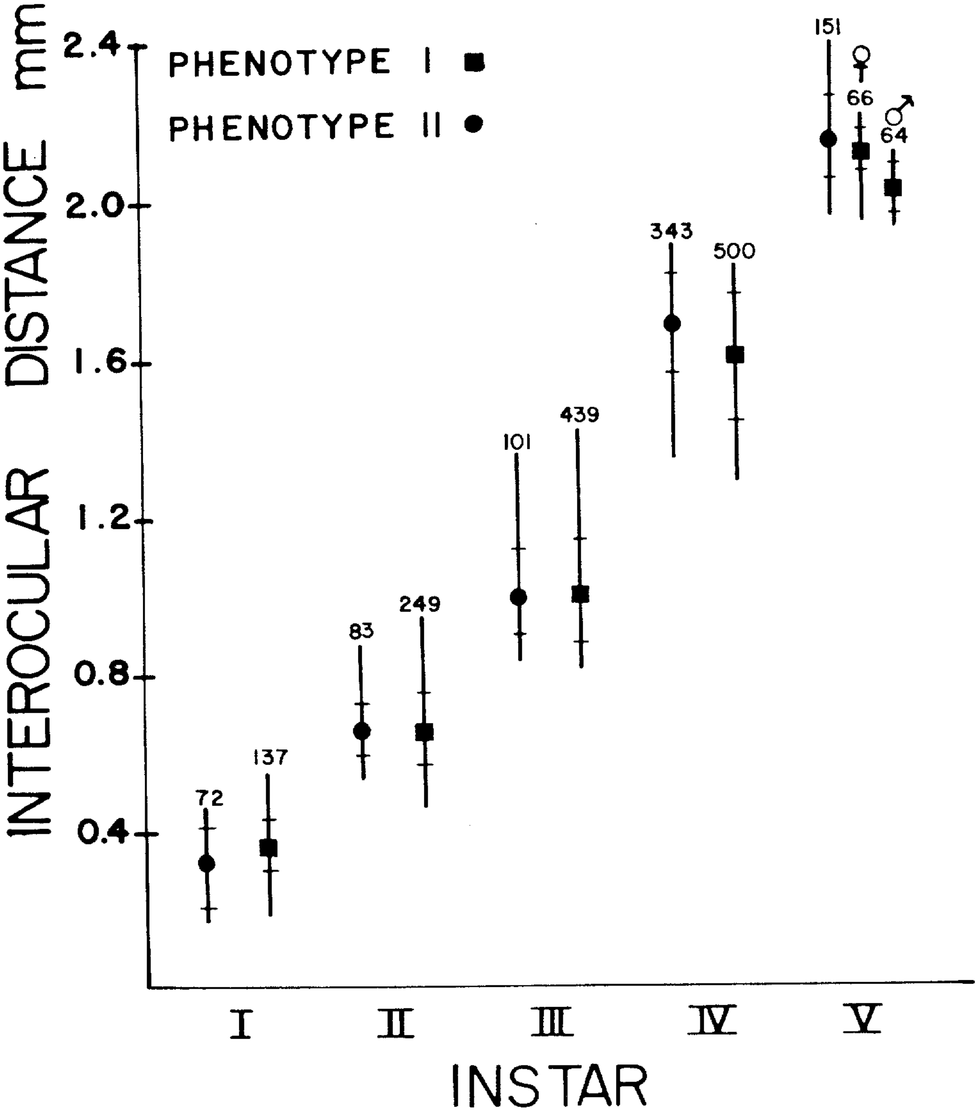

B

Fig. 11. Instar discrimination of Arctopsyche grandis larvae by phenotype; indicating mean, standard deviation, range of head width as a function of interocular distance and number of individuals measured.


INTEROCULAR DISTANCE mm
2.4
2.0
1.6
1.2
0.8
0.4
PHENOTYPE I ■
PHENOTYPE II ●
72
137
83
249
101
439
343
500
151
♀
66
♂
64
I
II
III
IV
V
INSTAR

year life cycle throughout the Flathead Rivers. In the North Fork (Fig. 12), Phenotype II larvae grew rapidly in the autumn, especially 2nd year class larvae, and reached predominantly 5th instar before winter. Phenotype I larvae, in contrast, did not grow as rapidly in fall, overwintering primarily in the 4th instar. In spring, last instar Phenotype II larvae had a mean head width significantly larger than Phenotype I larvae ($P < .01$). In the Middle Fork, Phenotype II larvae grew rapidly in the early fall, as in the North Fork. However, this growth did not continue into late fall, and larvae of both phenotypes overwintered predominantly in 4th instar (Fig. 13). Larval growth for both phenotypes in the Mainstream River was very similar to that of the Middle Fork; however, the final size relationship between Phenotype I and Phenotype II larvae was very similar to that observed in the North Fork (Fig. 14).

Adult females were significantly larger than males. A size frequency distribution of final instar larvae indicated a bimodal distribution of Phenotype I larvae. Phenotype II larvae, however, were normally distributed (Fig. 15). This was interpreted as evidence of ecological, as well as morphological, differentiation.

The adult flight period for A. grandis throughout the Flathead Rivers occured from late Jun. to mid-Aug. (see Figs. 12, 13, and 14). Emergence took place just prior to and at dusk. Teneral adults swam to the surface then horizontally to the river edge, whereupon they crawled out of the river

Fig. 12. Life cycles of the two phenotypes of *Arctopsyche grandis* in the North Fork. Larval instars (I-V), pupae (P), and adult flight period (AF) are indicated.

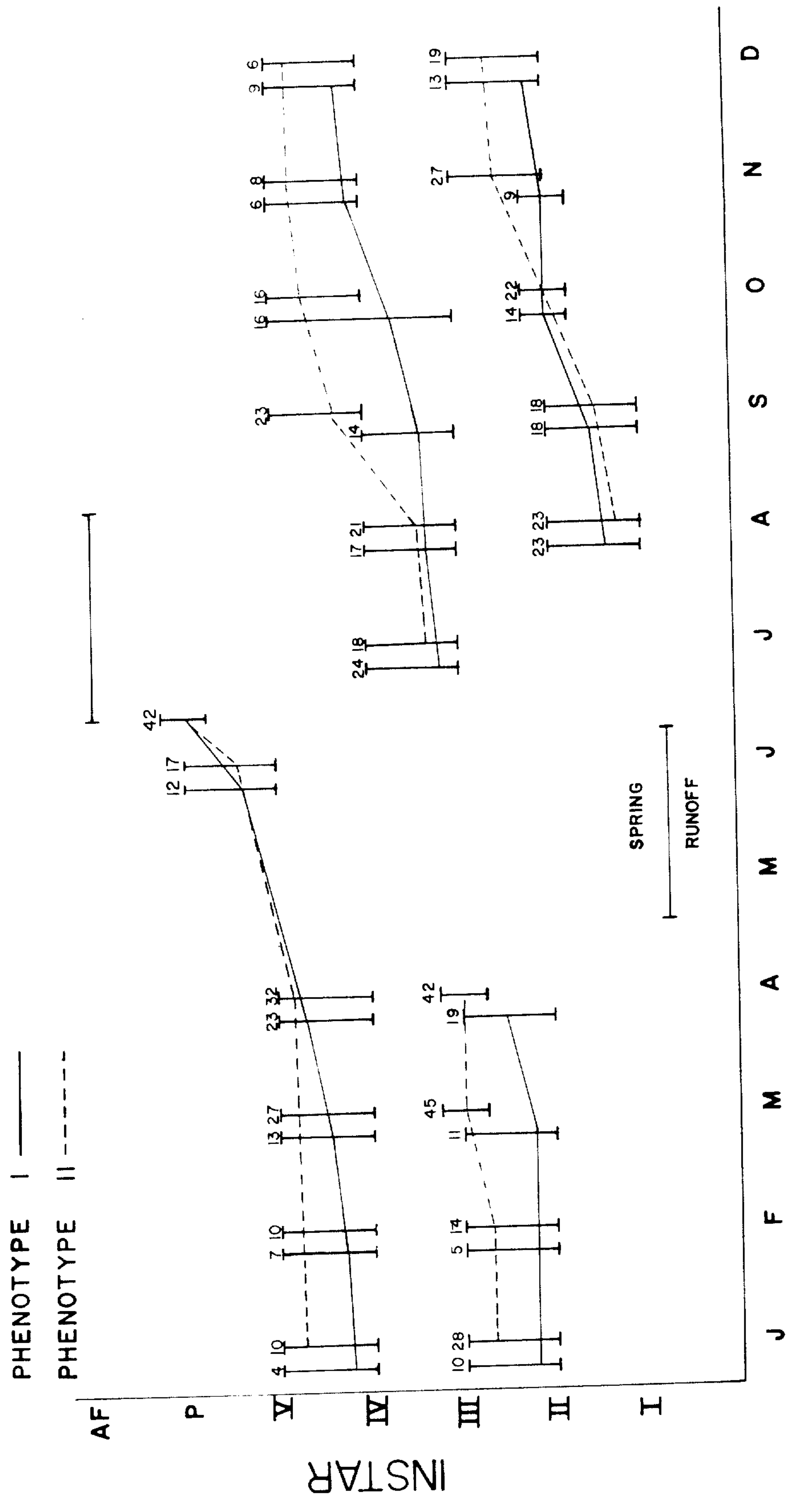

PHENOTYPE I
PHENOTYPE II
INSTAR
AF
P
V
IV
III
II
I
MONTH
J
F
M
A
M
J
J
A
S
O
N
D
SPRING
RUNOFF
4 10
7 10
13 27
23 32
12 17
42
24 18
17 21
23
14
16 16
6 8
9 6
10 28
5 14
11 45
19 42
23 23
18 18
14 22
9
27
13 19

Fig. 13. Life cycles of the two phenotypes of *Arctopsyche grandis* in the Middle Fork. Larval instars (I-V), pupae (P), and adult flight periods (AF) are indicated.

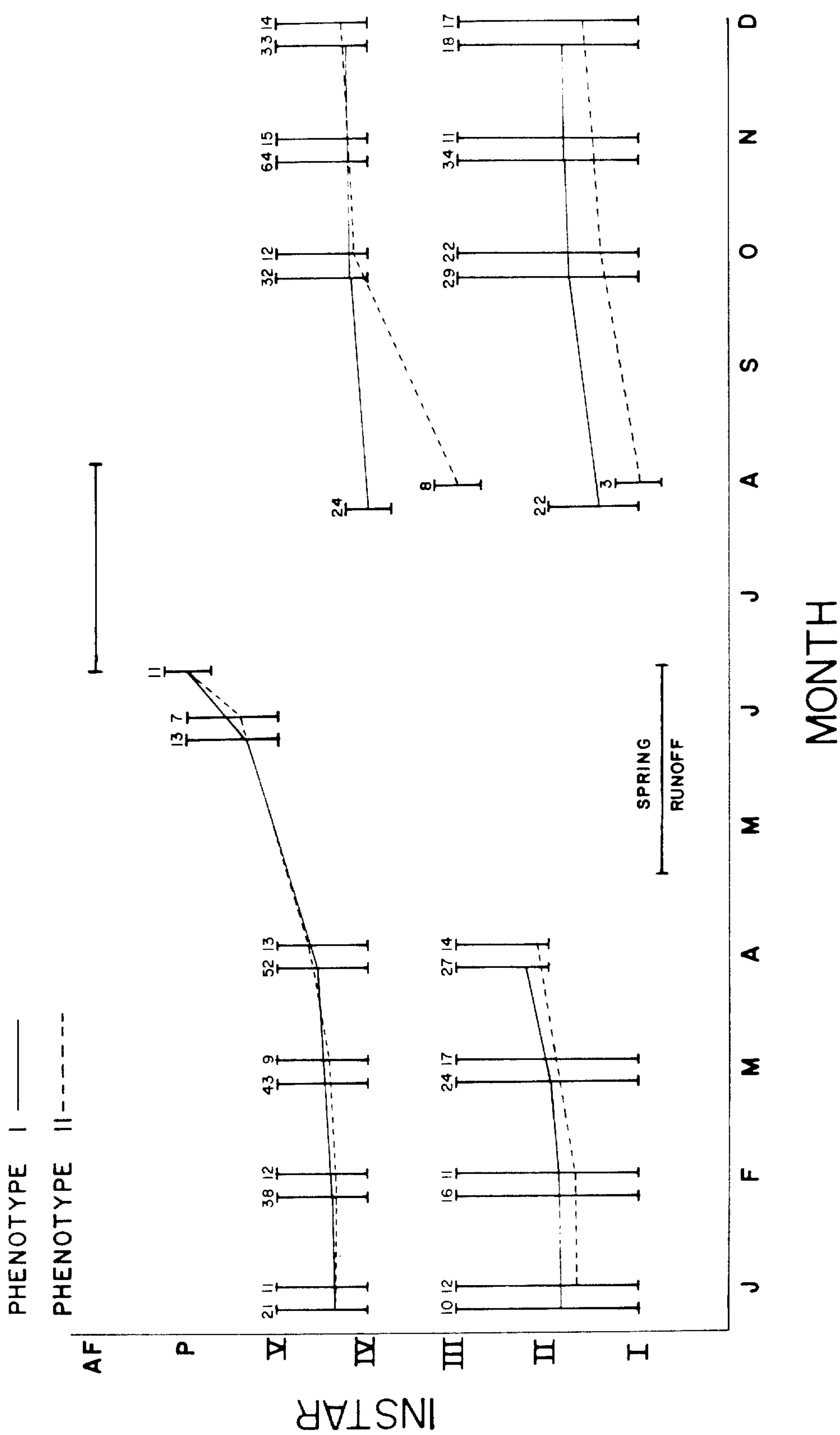

PHENOTYPE I ——
PHENOTYPE II - - - - -
INSTAR
AF
P
V
IV
III
II
I
MONTH
J
F
M
A
M
J
J
A
S
O
N
D
SPRING RUNOFF
21 11
38 12
43 9
52 13
13 7
11
24
8
32 12
64 15
33 14
10 12
16 11
24 17
27 14
22
3
29 22
34 11
18 17

Fig. 14. Life cycles of the two phenotypes of <u>Arctopsyche grandis</u> in the Mainstream River below confluence with the regulated South Fork. Larval instars (I-V), pupae (P), and adult flight period (AF) are indicated.

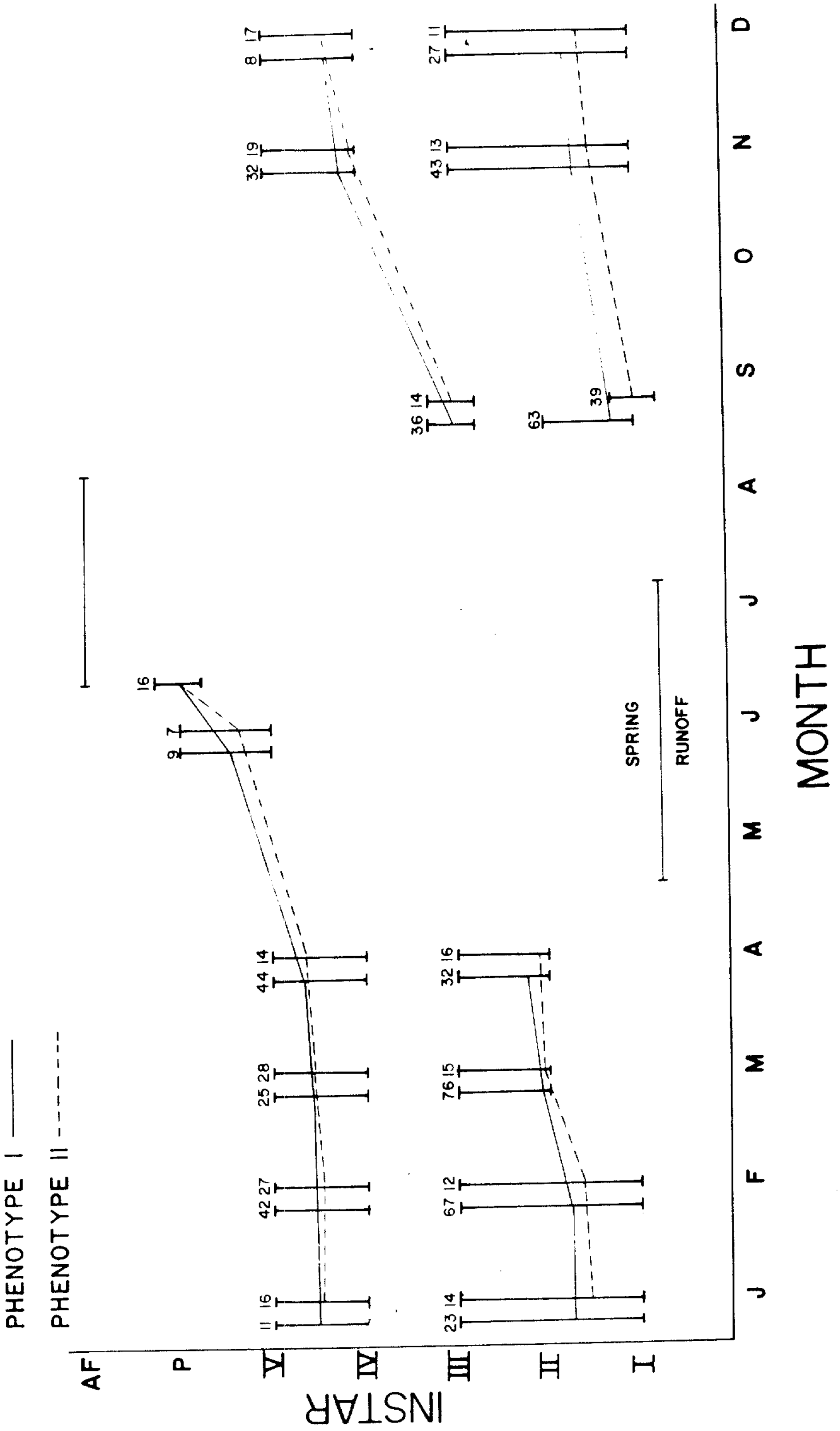
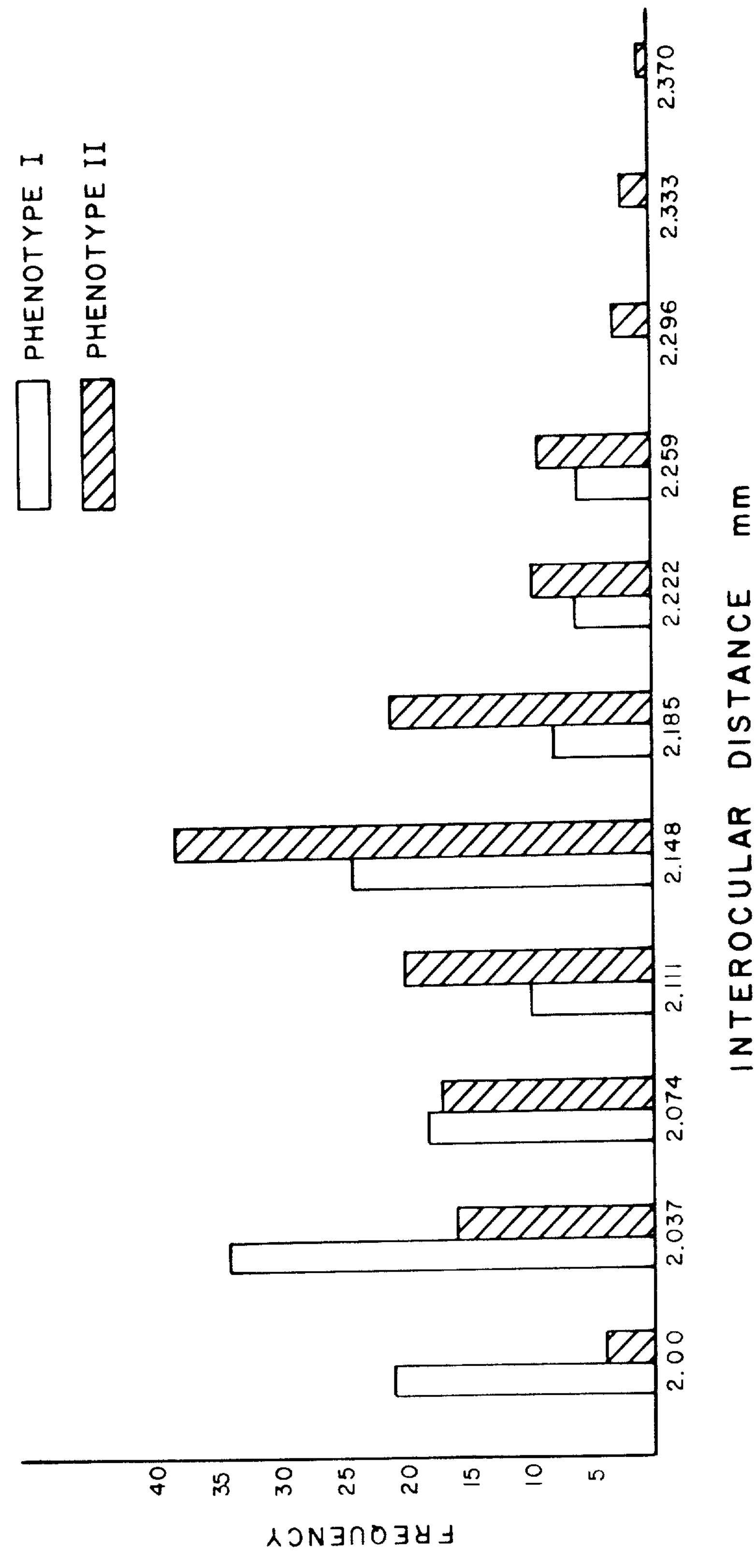

PHENOTYPE I ——
PHENOTYPE II - - - -
INSTAR
AF
P
V
IV
III
II
I
MONTH
J
F
M
A
M
J
J
A
S
O
N
D
SPRING
RUNOFF
11 16
42 27
25 28
44 14
9 7
16
32 19
8 17
23 14
67 12
76 15
32 16
36 14
63
39
43 13
27 11

Fig. 15. Size frequency distribution of final instar in *Arctopsyche grandis* showing differences between the two phenotypes.


PHENOTYPE I
PHENOTYPE II
FREQUENCY
40
35
30
25
20
15
10
5
2.00
2.037
2.074
2.111
2.148
2.185
2.222
2.259
2.296
2.333
2.370
INTEROCULAR DISTANCE mm

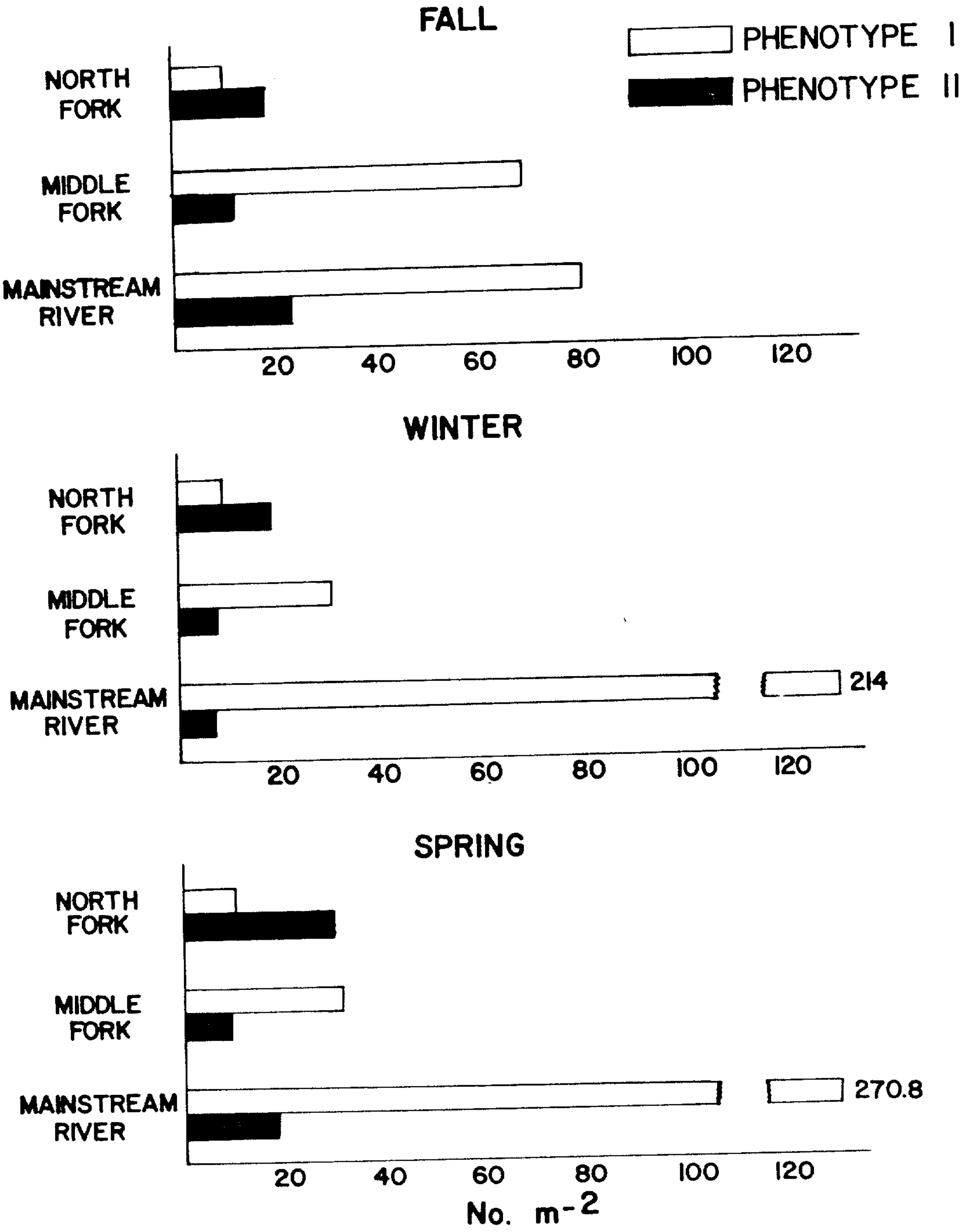
via shoreline rubble and riparian vegetation. During the day, adults were found resting exclusively among the boughs of large Douglas-fir and grand fir scattered along the river bank. Individuals disturbed from a particular tree would fly over the rivers but frequently would return to the same tree. Flight activity was greatest immediately after dusk, and adults were readily attracted to the U.V. night light.

Relative Abundance and Distribution

Phenotype I and Phenotype II larvae of *A. grandis* have responded differentially to the environmental parameters in the different river segments. Phenotype II larvae were dominant in the North Fork; total numbers of individuals m^{-2} were approximately twice that of Phenotype I larvae (Fig. 16). In the Middle Fork and Mainstream, Phenotype I larvae were far more abundant than Phenotype II larvae. The total number m^{-2} of both phenotypes combined was greatest from the Mainstream, followed by the Middle Fork.

A. grandis larval retreats were restricted, at all stations throughout the Flathead Rivers, to the undersides of rocks and within the interstitial space of the rubble substrate. The only locations in the drainage where *A. grandis* larvae were observed building retreats and filter nets on the surface of the substrata were below lake outlet streams draining the large, glacial lakes on the west side of the North Fork. Presumably, this adaptation occured in response to the less rigorous winter environment at these locations; lake outlet

Fig. 16. Seasonal abundance of the phenotypes of *Arctopsyche grandis* at the riverine sampling sites.


FALL
PHENOTYPE I
PHENOTYPE II
NORTH FORK
MIDDLE FORK
MAINSTREAM RIVER
20
40
60
80
100
120
WINTER
NORTH FORK
MIDDLE FORK
MAINSTREAM RIVER
214
20
40
60
80
100
120
SPRING
NORTH FORK
MIDDLE FORK
MAINSTREAM RIVER
270.8
20
40
60
80
100
120
No. m-2

streams rarely developed anchor or surface ice, which heavily scoured the substrate in the main rivers.

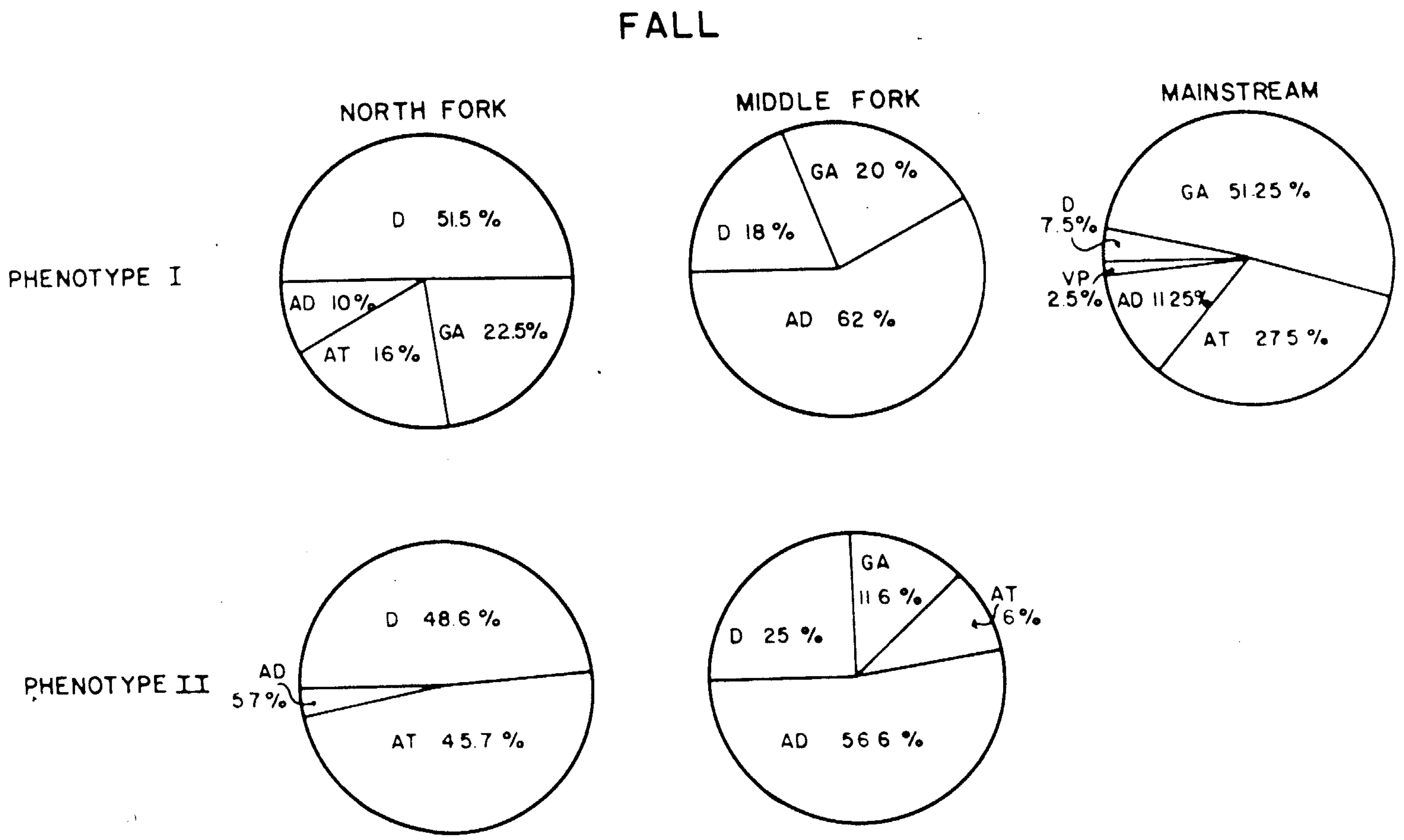
Phenotype II larvae were observed only in very large rubble where the interstitial space between the rocks was not filled with coarse sands and gravel. Such habitat was found throughout the course of the North Fork, but was less frequently observed in the Middle Fork and Mainstream. Phenotype I larvae were also observed in large rubble, but they were found along seams where rocks rested together and the interstitial spaces were limited by gravel, sand, and fine sediments or tightly compacted rocks.

Trophic Relationships

The gut contents of *A. grandis* were comprised primarily of five food types: 1) diatoms, largely *Synedra*, *Navicula*, and *Gomphonema*; 2) green algae, primarily *Ulothrix* and some *Hydrurus*; 3) vascular plant tissue, entirely of terrestrial derivation; 4) animal tissue, from a wide variety of sources (e.g. plecoptera nymphs, *Ephemerella* nymphs, chironomid larvae, and *Glossosoma* and *Hydropsyche* larvae); and 5) amorphous detritus.

During the fall, diatoms comprised approximately 50 percent of the food items for both larval types in the North Fork (Fig. 17). However, Phenotype II larvae consumed 45 percent animal tissue, while the remaining Phenotype I larval gut contents were evenly divided between animal tissue and green algae. Larvae from the Middle Fork consumed large quantities of amorphous detritus, accounting for over 50 percent of gut

Fig. 17. Trophic relationships of *Arctopsyche grandis* by phenotype at the riverine sites during fall. Percent of total food injested by 10 larvae is given with each food category; diatoms, D; green algae, GA; vascular plant tissue, VP; animal tissue, AT; amorphous detritus, AD, in each pie chart.


FALL
NORTH FORK
MIDDLE FORK
MAINSTREAM
PHENOTYPE I
D 51.5 %
AD 10%
AT 16%
GA 22.5%
GA 20 %
D 18 %
AD 62 %
GA 51.25 %
D 7.5%
VP 2.5%
AD 11.25%
AT 27.5 %
PHENOTYPE II
D 48.6 %
AD 5.7%
AT 45.7 %
GA 11.6 %
AT 6%
D 25 %
AD 56.6 %

contents. Larvae from the Mainstream River contained over 50 percent green algae, largely *Ulothrix*.

I observed a distinct shift in the trophic relationships of Phenotype II larvae in the North Fork (Fig. 18) during winter. Diatoms comprised 80 percent of the gut contents and animal tissue decreased as a food item. Winter food habits of larvae from the Middle Fork were similar to those exhibited in the fall. Larvae from the Mainstream changed from consumers of green algae to consumers of diatoms. Animal tissue remained an important food item.

During spring, dominance of animal tissue was observed among all groups with the notable exception of Phenotype I larvae at Station C (Fig. 19). I have no explanation for this observed phenomenon other than the appearance of green algae in the gut contents of the Type I larvae coincided with observed increased *Ulothrix* production at that site. The large amount of animal tissue consumed may be a function of the possible increase in feeding activity and movement of prey species after ice-out, thus making them more susceptible to drift and capture or a more aggressive last instar larvae preparing for pupation and emergence thus maximizing effort and energy input into gonadal tissue. Frequently other aquatic insects, primarily early instar Plecoptera, chironomids, and *Hydropsyche oslari* were found in close association with *A. grandis* retreats. Increasingly aggressive *A. grandis* larvae might have exploited this source of animal tissue.

Fig. 18. Trophic relationships of *Arctopsyche grandis* by phenotype at the riverine sites during winter. Percent of total food injested by 10 larvae is given with each food category; diatoms, D; green algae, GA; vascular plant tissue, VP; animal tissue, AT; amorphous detritus, AD, in each pie chart.

WINTER

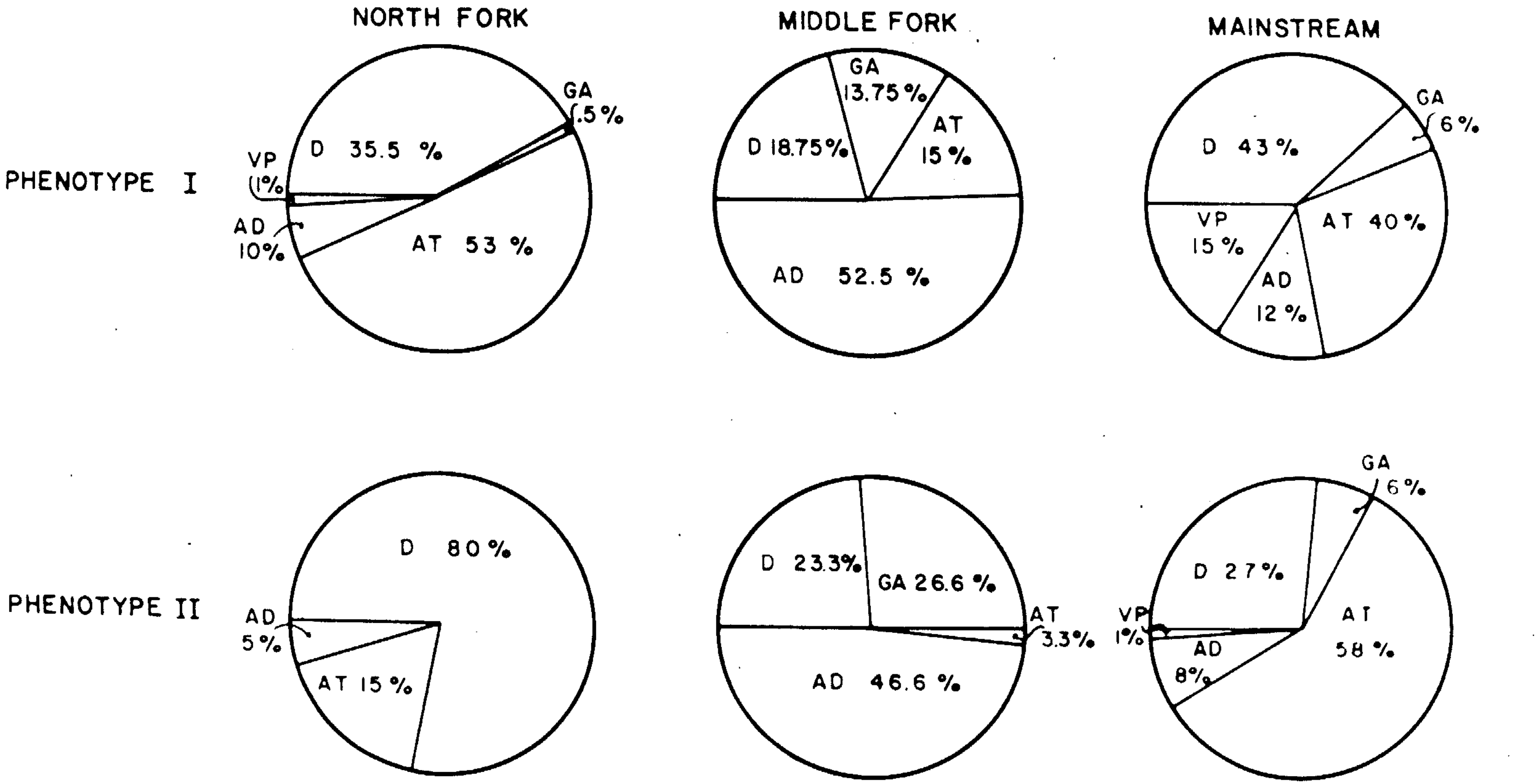
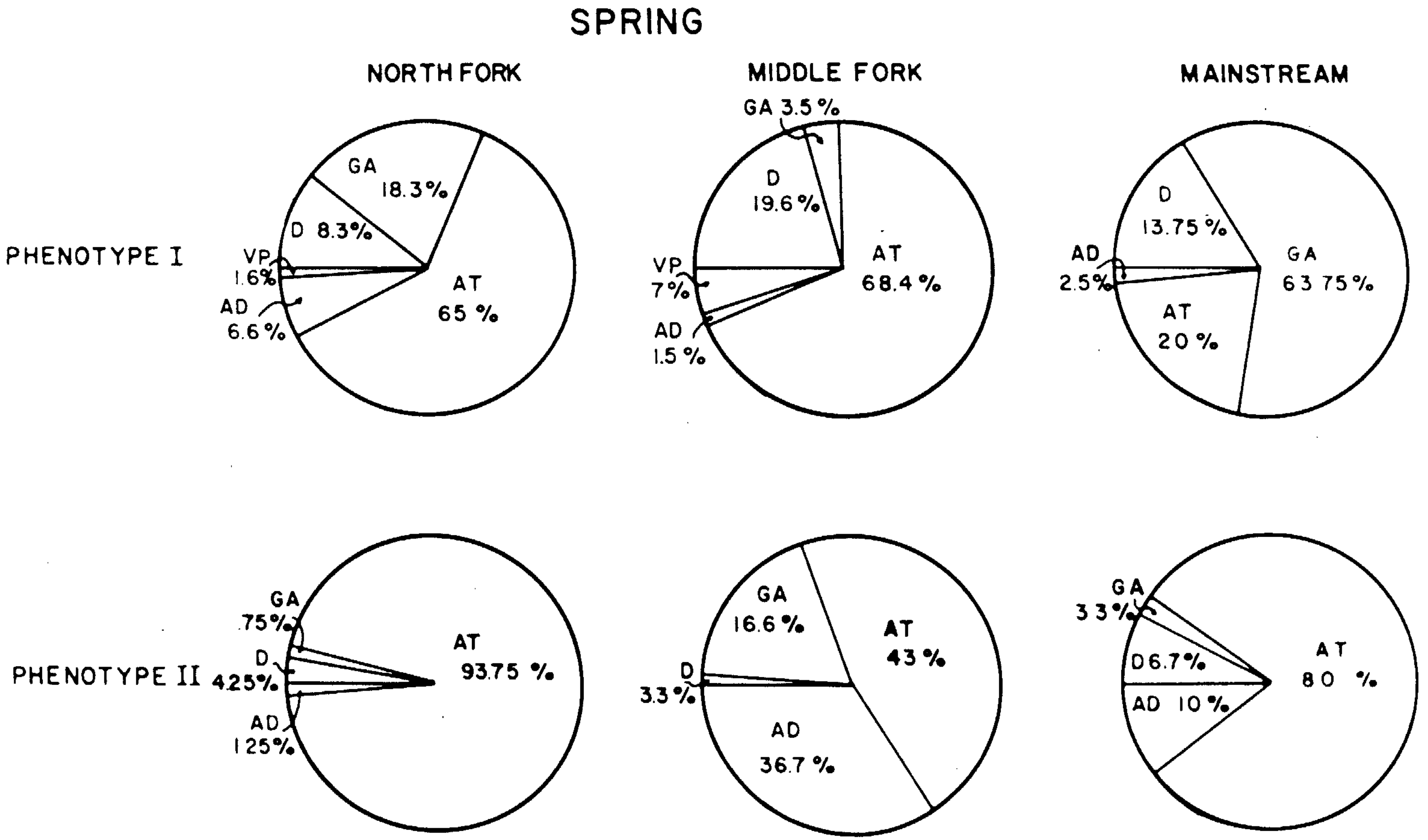

NORTH FORK
MIDDLE FORK
MAINSTREAM
PHENOTYPE I
D 35.5 %
GA .5%
VP 1%
AD 10%
AT 53 %
D 18.75%
GA 13.75 %
AT 15 %
AD 52.5 %
D 43 %
GA 6 %
AT 40 %
VP 15 %
AD 12 %
PHENOTYPE II
D 80 %
AD 5 %
AT 15 %
D 23.3%
GA 26.6 %
AT 3.3%
AD 46.6 %
D 27 %
GA 6 %
AT 58 %
VP 1%
AD 8%

Fig. 19. Trophic relationships of Arctopsyche grandis by phenotype at the riverine sites during spring. Percent of total food injested by 10 larvae is given with each food category; diatoms, D; green algae, GA; vascular plant tissue, VP; animal tissue, AT; amorphous detritus, AD, in each pie chart.



SPRING

NORTH FORK
MIDDLE FORK
MAINSTREAM
PHENOTYPE I
PHENOTYPE II
GA 18.3%
D 8.3%
VP 1.6%
AD 6.6%
AT 65 %
GA 3.5 %
D 19.6 %
VP 7%
AD 1.5 %
AT 68.4 %
D 13.75 %
AD 2.5%
AT 20 %
GA 63 75 %
GA .75%
D 4.25%
AD 1.25%
AT 93.75 %
GA 16.6 %
D 3.3 %
AD 36.7 %
AT 43 %
GA 3 3 %
D 6.7 %
AD 10 %
AT 80 %

Variance between stations for each season was high and reflects natural differences between the trophic structure of the sites. But, within-site differences between phenotypes indicate significant differentiation in food habits. An analysis of mesh size of the filter nets of each phenotype indicated no significant differences, consequently the within-site differences in food ingested must have been a function of food selection by the larvae. This could have been accomplished by positioning nets in different areas or by differential selection of foods collected on the nets. I believe the former is most plausible, because retreats of the two phenotypes were consistently found in different microhabitats.

Larvae-Adult Associations

The investigations of growth rates, microhabitat selection, relative site specific abundance, and trophic dynamics of the *A. grandis* larval phenotypes indicated a divergence of functional relationships. To resolve the specific consequences of the apparently different ecological roles played by the two larval phenotypes it was necessary to firmly determine whether different species were involved or if a sexual dimorphism was occuring.

Twenty-three field-collected larvae were successfully reared to late development pupae in the laboratory microcosms. An additional 35 late development pupae were collected from the North Fork. Thirty-seven of the 58 pupae were from Phenotype I larvae, 21 from Phenotype II larvae. In all 58 specimens, adult taxonomic characteristics, determined from pupae, were typical *A. grandis*. Twenty-one of the 37 Phenotype I pupae were male and 16 female, while all 21 of the Phenotype II larvae were female.

Adaptive Significance

The competitive exclusion principle is one of the mainstays of ecological theory (Pianka, 1974; Huston, 1978), and although complete exclusion has been achieved in simple laboratory systems (Gause, 1934), it is unlikely to occur readily in complex and diverse systems with multiple feedback mechanisms (Hutchinson, 1961). Discrete phenotypic variability coupled with distinct ecological differentiation within a species may result in interactions which encourage ecological divergence.

The tendency for a population experiencing intense intraspecific competition to increase utility along a resource gradient may lead to a phenotypic deviant, which then may exploit an overlapping, yet different, segment of the resource. This should result in a shift in optimal resource use by the deviant. Greater utilization of resources is insured for the species, thereby enhancing its fitness.

A. grandis may have developed the Type II phenotype in response to an abundance of large interstitial space in the riverine segments, which was insufficiently exploited by the "typical" phenotype. However, the deviant phenotype is more restricted in habitat utilization. I found it more abundantly in 5th and 6th order river segments where large interstitial spaces and diatomaceous periphyton characterized the substrate.

This morphological type may require the specific thermal criteria associated with the large, open-canopied river and, thus, is excluded from lower order streams, even though the microhabitat spatial requirements are suitable. Regardless, I believe that the development of the deviant phenotype was in direct response to a niche expansion phenomenon in riverine segments, which has extended the scope of resource utilization. Also, this adaptation has increased the production of females, which probably increases species fecundity. This interpretation is consistent with the hypothesis suggested by Powell and Taylor (1979) that environmental diversity and intraspecific habitat choice establish genotype variability. The apparent genotypic plasticity of this species may well explain its wide distribution among and between drainage basins in western North America.

These findings do not preclude the possibility that Type II males may exist, but were not found. Also, it is possible that Type II females are parthenogenic. These additional questions must be addressed by laboratory rearing of _A. grandis_ Type I and Type II phenotypes through several generations.

Stream Regulation and Ecology of the Hydropsychidae (INSECTA: Trichoptera) in the Flathead River, Montana: A Case for River Continuum Reset

Patterns of community structure and function in relationship to physical factors and river system dynamics along a parameter gradient have developed into the "River Continuum" conceptualization of running water ecosystems (Cummins, 1975a, 1979; Vannote et al., 1979). The myriad of environmental factors such as temperature, substrate, current velocity, dissolved inorganic and organic substances, and food quantity and quality integrate to establish composition and abundance of stream zoobenthos. The physical variables within the stream system integrate into an environmental mosiac which elicit a series of population responses along a continuous downstream gradient. Energy input in the form of organic matter, derived allochthonously or autochthonously, results in specific biological strategies to handle and process the available resources within a temporal and spatial framework.

Net-spinning caddisfly larvae (Hydropsychoidea) often comprise a significant portion of zoobenthic biomass (Cushing, 1963; Ward and Short, 1979; Coulter, 1980) by utilization of drifting stream seston (Cummins, 1973; Wallace, 1975; Wallace, Webster, and Woodall, 1977). Stream size preference (Gordon and Wallace, 1975; Hauer, Zimmerman, and Stanford, 1979; Alstad, 1980) and the importance of various environmental parameters such as organic matter size and origin (Cummins, 1974, 1979; Sedell, Triska, and Triska, 1975) and temperature (Hynes, 1970; Cummins, 1975b; Gallepp, 1977; Stanford and Gaufin, in press) have been documented for certain species of aquatic insects.

Capture net mesh size, surface area, and position in the current are important factors in relationship to partitioning of particulate organic matter in stream seston by filter-feeding trichopterans (Wallace, Webster, and Woodall, 1977; Edington, 1968).

The ecological relationships of the Hydropsychidae were investigated in the various river segments, including the regulated portion below Hungry Horse Dam. Hydropsychid larvae were abundant in lotic erosional zones throughout the basin and frequently were a significant component of zoobenthic biomass. Hydropsychidae dominated the collector trophic functional group (see Cummins, 1973) and responded directly to gradation of environmental parameters.

During research to document life history dynamics, distribution and abundance of the Hydropsychidae, I observed what appeared to be displaced populations in regulated river sections. Similarities of species composition were observed among the Hydropsychidae in the river segment receiving hypolimnion discharge from the hydroelectric dam and populations in lower order streams. Parapsyche elsis dominated the net-spinning collector functional group in 1st and 2nd order streams.

Arctopsyche grandis replaced *P. elsis* as the dominant hydropsychid in 3rd and 4th order creeks. *Symphitopsyche cockerelli* and *S. oslari* were the most abundant net-spinning caddisflies in the large Flathead River prior to confluence of the regulated South Fork. Below the confluence of the South Fork, *A. grandis* became the dominant hydropsychid. To fully delineate the cause of the apparent anomoly in hydropsychid diversity and abundance, relationships of temperature (i.e. accumulation of degree-days), particulate organic matter in stream seston, and extent of spatial displacement with consideration to the River Continuum Concept were examined.

Life Cycle Dynamics

Four species of the Family Hydropsychidae commonly occured throughout the three major tributaries and Mainstream Flathead River: *Arctopsyche grandis* (Banks), *Symphitopsyche cockerelli* (Banks), *Symphitopsyche oslari* (Banks) (*Symphitopsyche* was changed from *Hydropsyche*, see Ross and Unzicker, 1977), and *Hydropsyche occidentalis* Banks. All four species coexist in similar microhabitats, frequently being found on the same small boulder. It was not uncommon for Hydropsychinae larvae to incorporate part of an *A. grandis* retreat into a side for their own retreat or an anchor for part of the filter net. This coexisting group of confamilial species displayed growth and emergence differences indicating refinement of species niche segregation.

A. grandis had a two year life cycle with a rapid fall growth period among 2nd year class larvae. Overwintering occured primarily in the 5th instar. Adult emergence began after the peak of the late spring runoff (ca. mid-Jun.) and continued to early Aug.. A detailed description of *A. grandis* life history was presented above.

S. oslari, *S. cockerelli*, and *H. occidentalis* had univoltine life cycles sequenced through five distinct instars (Fig. 20). *S. cockerelli* was the largest of the Hydropsychinae species with a mean interocular distance in terminal instar of 1.09 mm. *H. occidentalis* and *S. oslari* had similar mean interocular distances of 0.99 mm in final instar. An analysis of life cycle dynamics indicated a distinct segregation of specific growth and emergence patterns (Fig. 21). First instar larvae of *S. cockerelli* appeared within 4 to 6 weeks after the peak of adult activity. This species grew rapidly during the late summer and early autumn. By mid-Oct., in excess of 95 percent of the population had entered 5th instar. Most growth, therefore, occured while river temperature was above 7°C. Larvae remained active through the winter and spring and maintained retreats and filter nets. Pupation was initiated after the onset of spring runoff. Adult emergence and activity occured immediately after runoff maxima (Fig. 21). When compared to the other hydropsychids, *S. cockerelli* had a short adult activity period.

The life cycle of *H. occidentalis* was similar to that of *S. cockerelli* in that most of the larval growth occured during

Fig. 20. Instar discrimination of *Symphitopsyche cockerelli*, *Symphitopsyche oslari* and *Hydropsyche occidentalis* from the Flathead River, Montana, indicating mean, standard deviation, and range.

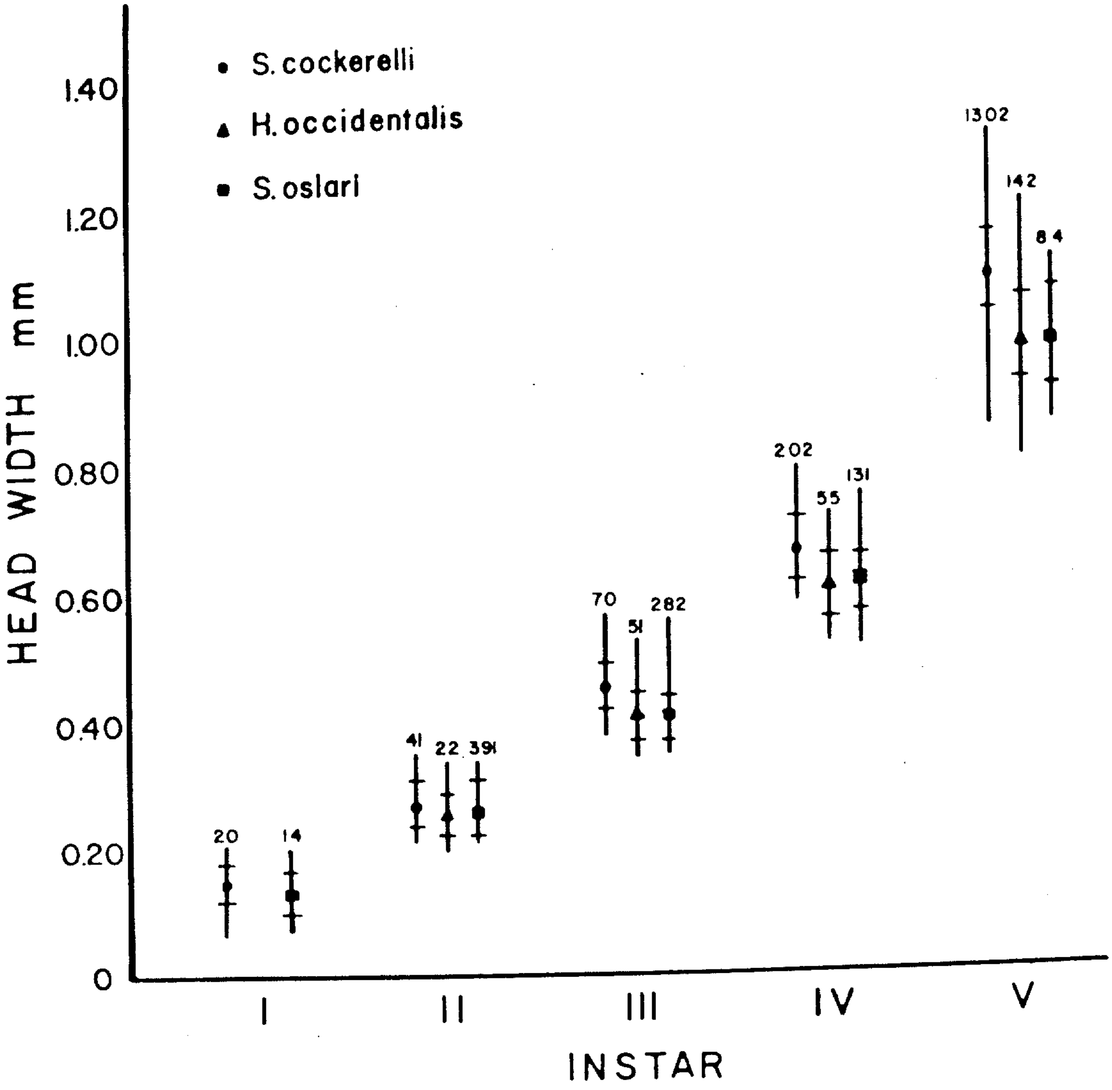
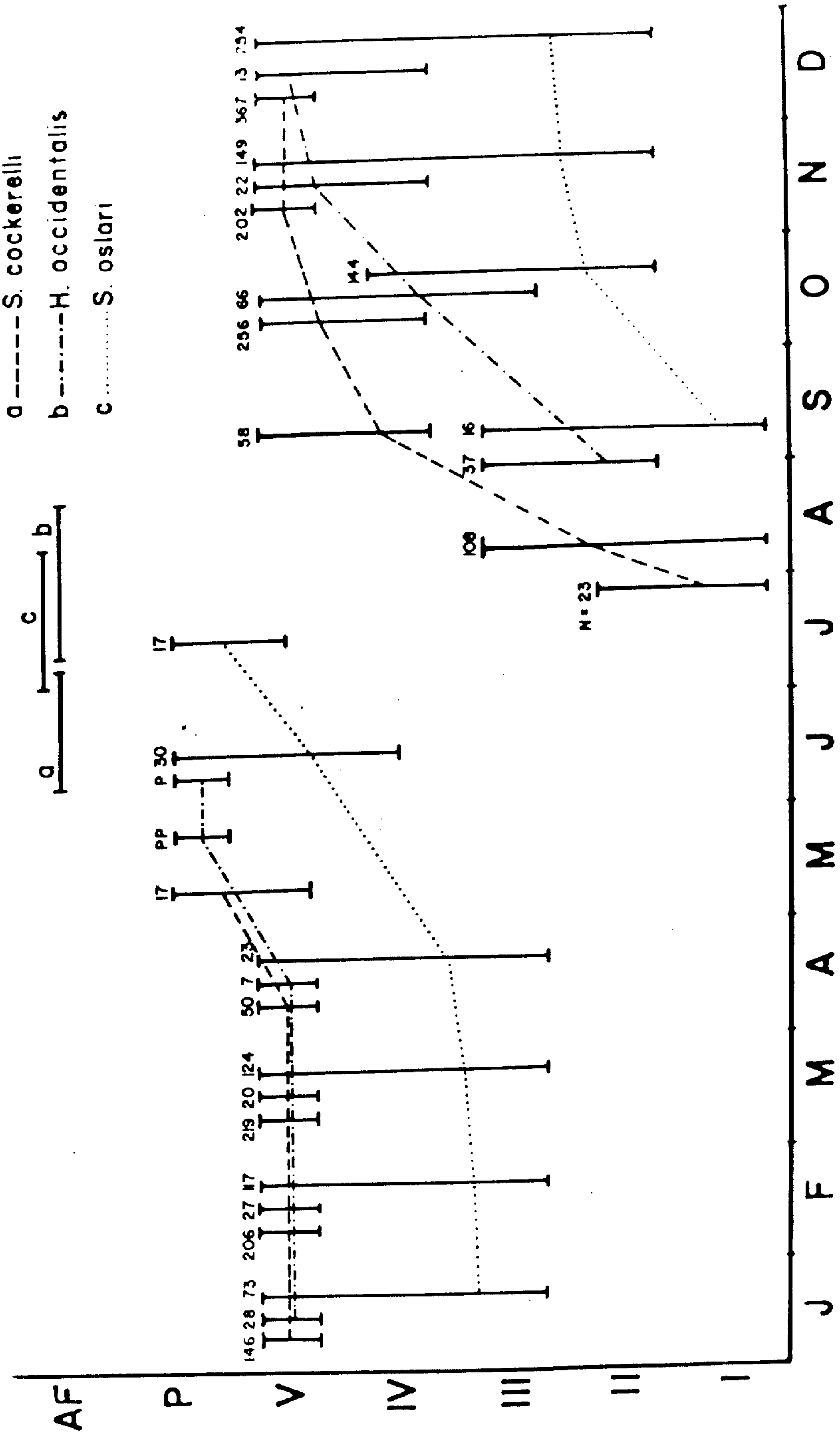

● S. cockerelli
▲ H. occidentalis
■ S. oslari
HEAD WIDTH mm
1.40
1.20
1.00
0.80
0.60
0.40
0.20
0
20
14
41
22
391
70
51
282
202
55
131
1302
142
84
I
II
III
IV
V
INSTAR

Fig. 21. Life cycles of *Symphitopsyche cockerelli*, *Symphitopsyche oslari*, and *Hydropsyche occidentalis* in the Flathead River, Montana. Larval instars (I-V), pupae (P), and adult flight period (AF) are indicated.

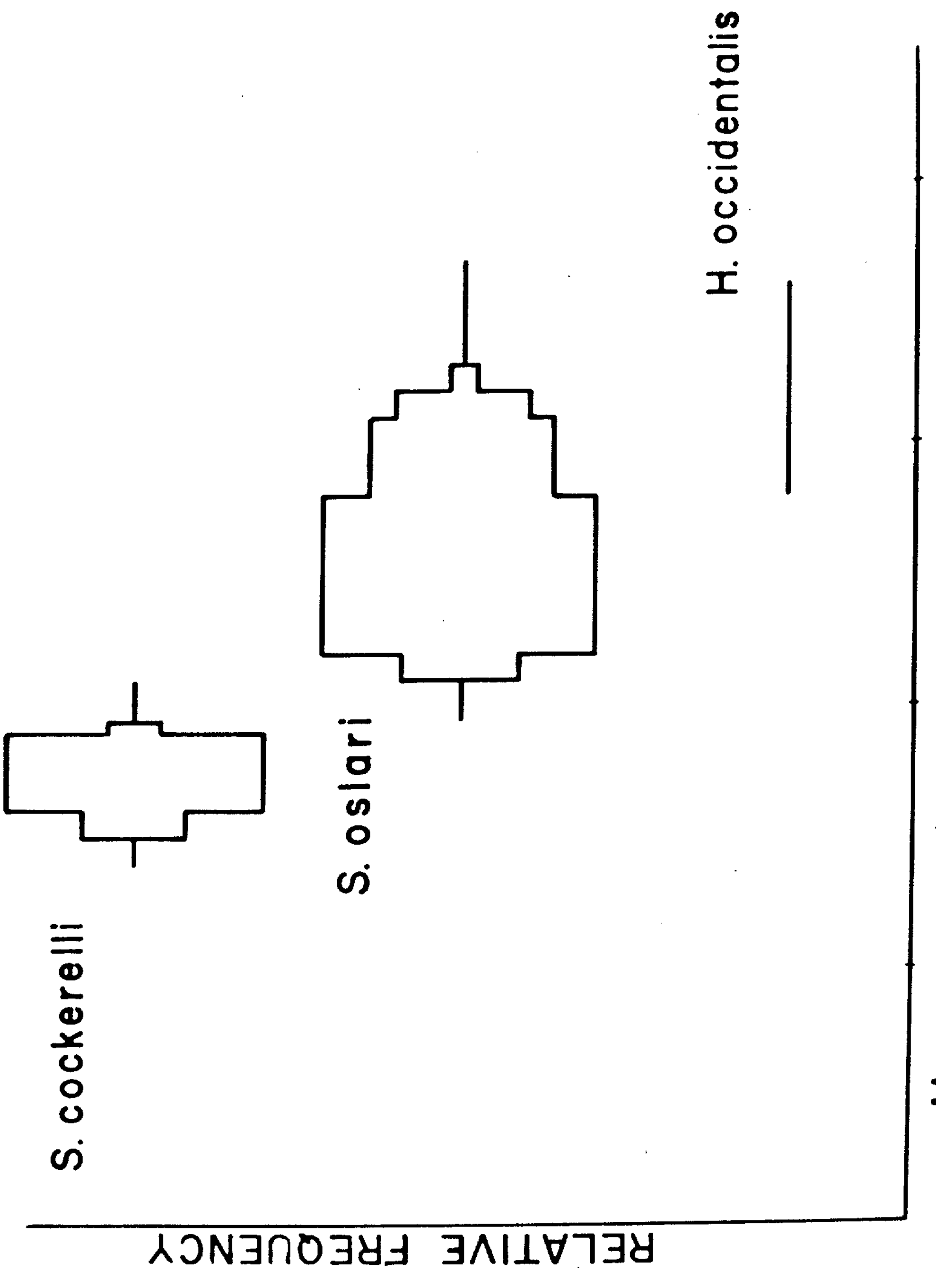

a ----- S. cockerelli
b -·-·-·- H. occidentalis
c .... S. oslari
a
c
b
AF
P
V
IV
III
II
I
J
F
M
A
M
J
J
A
S
O
N
D
146
28
73
206
27
117
219
20
124
50
7
23
17
PP
P
30
17
N = 23
108
37
16
58
256
66
144
202
22
149
367
13
254

the autumn. However, the life cycle was delayed approximately 4 to 8 weeks behind *S. cockerelli*. Larvae of *H. occidentalis* overwintered in 4th and 5th instar; all larvae had reached the final instar prior to spring runoff. Larval growth occured primarily within a temperature range below 5°C. Attempts to collect active *H. occidentalis* larvae after peak runoff in late Jun. were unsuccessful. Adult emergence and activity occured from mid-Jul. to mid-Aug. (Fig. 22). Since larvae were not collected after runoff and adults did not emerge until mid-summer, most likely larvae enclosed the pupal case during runoff and entered an approximately 6-week diapause prior to larval-pupal apolysis.

The life cycle of *S. oslari* was distinctly different from that of *S. cockerelli* or *H. occidentalis*. *S. oslari* larvae first appeared in mid-Aug. and Sep. samples. Although a few individuals, <1 percent of the population, grew during the autumn reaching 3rd or 4th instar prior to the winter months, most of the population remained in the first two instars through the fall and winter. Most growth of this species occured during spring and early summer when river temperatures were in excess of 5°C. A normal pupation period of a few weeks followed in Jun. and early Jul.. Adult emergence and activity occured from late Jun. to early Aug. (Fig. 22).

On Aug. 20, 1979, which was several weeks after the end of emergence and adult activity (Fig. 22), several last instar *S. oslari* larvae were collected from the Mainstream

Fig. 22. Adult flight period of *Symphitopsyche cockerelli*, *Symphitopsyche oslari*, and *Hydropsyche occidentalis*. Maximum width of bar graphs represents peak emergence.


S. cockerelli
S. oslari
H. occidentalis
RELATIVE FREQUENCY
M
J
J
A

sampling site. Collections from the North and Middle Forks during the same time period did not contain last instar *S. oslari* larvae. Apparent failure to complete life histories was most likely due to the suppressed thermal regime of the Mainstream River below the confluence of the South Fork. Absence of proper thermal cue (approx. 15°C), insufficient temperature summation, or inappropriate sequencing of environmental factor interaction may explain the failure of the larvae to pupate. Stanford and Gaufin (in press) reported that a sudden decrease in temperature due to discharge from Hungry Horse Reservoir in Aug. 1973, after a summer without discharge, effectively prevented *Classenia sabulosa* (Plecoptera) from emerging that year from the Mainstream River. The apparent failure to complete life cycle phenomena was attributed to an approximately 8°C suppression of the natural thermal regime by hypolimnion discharge from Hungry Horse Reservoir.

Abundance

Lotic macroinvertebrates are known to respond to an integration of chemical, physical, and biological parameters; producing observable patterns of distribution and abundance. Critical parameters, such as substrate size, current flow, or food availability, constitute the determining factors in distribution patterns (Cummins, 1975b). The three riverine sites were characterized by specific parameter differences. The North Fork had a large rubble-small boulder substrata and open interstitial space between the rocks. An analysis of A. grandis trophic dynamics indicated a considerable autotrophic contribution to the river seston. Conversely, the Middle Fork had a smaller rubble substrate than the North Fork with little open interstitial space and small gravel and coarse sand between the rubble. Food habits of A. grandis from the Middle Fork suggested a large component of detritus in the seston of this tributary river. The Mainstream was characterized by a substrate similar to that of the Middle Fork; however, periphytic growth in this river segment was extensive, particularly the green algae Ulothrix. The variance in discharge from Hungry Horse Reservoir resulted in current fluctuation and abrasion of periphyton and its subsequent suspension and transport downstream. Gut analysis from this river segment indicated green algae in the seston was a major food source for A. grandis. These differences in environmental factors were manifest in variance of species diversity and frequency. The four hydropsychid species were found throughout the North and Middle Forks and Mainstream River, but population abundance varied between sampling sites. S. cockerelli and S. oslari were abundant in the North Fork, annual mean abundance of 100.6 and 79.5 m^{-2}, respectively; but were conspicuously low in abundance at the Mainstream sampling site, 13.2 and 4.2 m^{-2}, respectively. Conversely, A. grandis was exceptionally abundant in the Mainstream River section, especially during winter and spring. Samples from the Mainstream site during spring yielded a frequency range of 598 to

268 m^{-2} compared to 50 to 0 m^{-2} in the North Fork samples and 86 to 6 m^{-2} in Middle Fork samples. *H. occidentalis* was infrequently collected at all sampling sites (Fig. 23).

Interval analysis (Scheffé's Interval; Scheffé, 1959), which is valid for comparisons of unequal replication and unequal variance, verified that *A. grandis* was significantly more abundant in the Mainstream River in comparison to the North and Middle Forks and dominated the net-spinning component of the zoobenthos in this river segment (Table IV). Conversely, *Symphitopsyche spp*. dominated the net-spinning component of the macroinvertebrate community of the Middle Fork. However, species dominance among the Hydropsychidae in the North Fork was indistinct. Based upon periodic quantitative and qualitative samples from Kintla Creek, Trail Creek, and several other tributaries of the North and Middle Forks, *A. grandis* appeared to dominate the collector group of Trichoptera in 3rd and 4th order streams. The differences in hydropsychid fauna are most likely attributable to thermal regime, quantity and size of particulate organic matter in the seston, and an interaction of substrate size, quantity of interstitial space, and current velocity.

The observed pattern of *A. grandis* and *Symphitopsyche spp*. distribution and level of abundance in the Mainstream River was a manifestation of river regulation. Cold water discharge and diurnal variability of discharge from Hungry Horse Reservoir have resulted in suppression of the Mainstream

Fig. 23. Relative abundance M^{-2} of larvae of *Arctopsyche grandis*, *Symphitopsyche cockerelli*, *Symphitopsyche oslari*, and *Hydropsyche occidentalis* in the North Fork, Middle Fork, and Mainstream Flathead River, Montana.

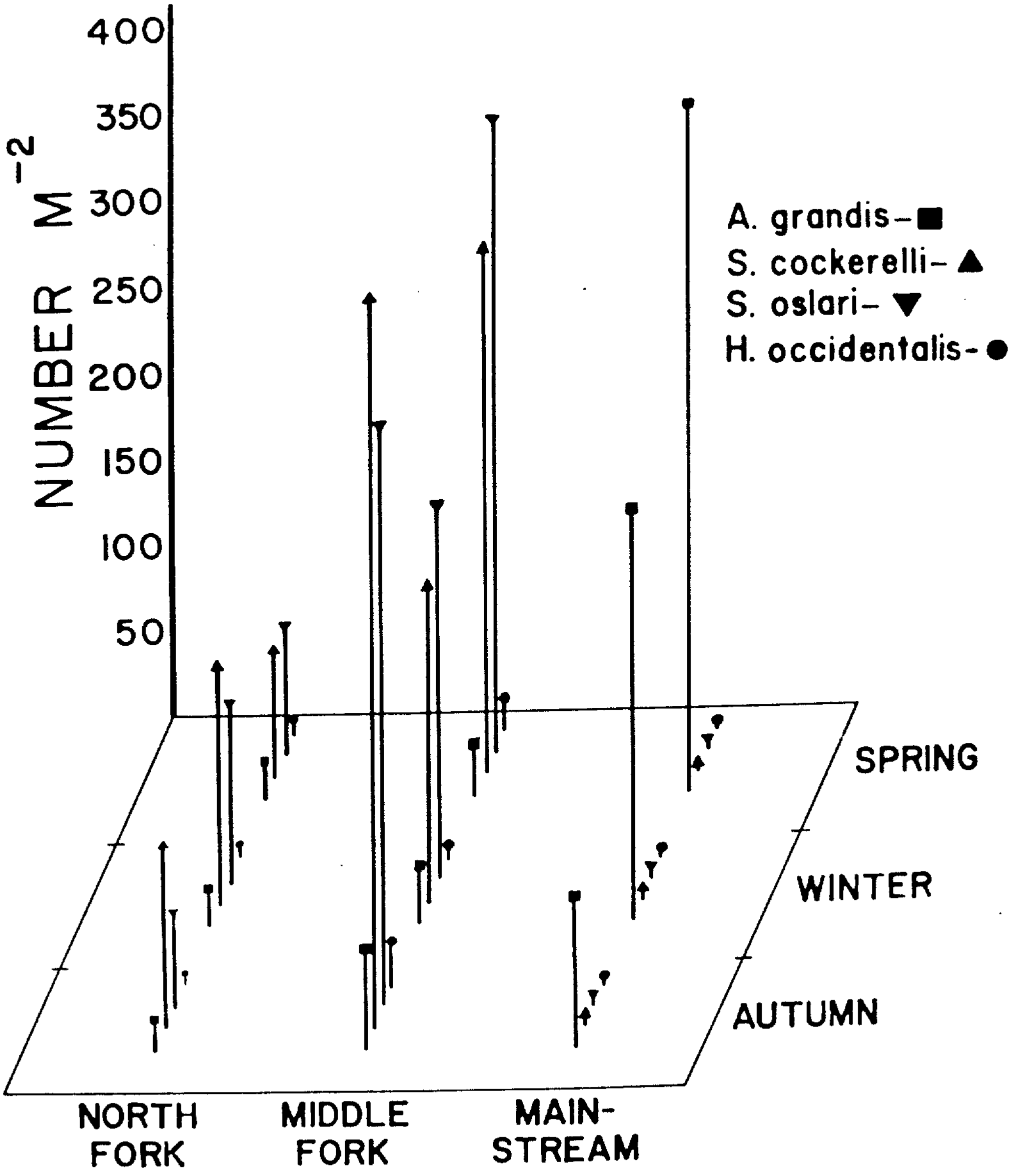

NUMBER M^{-2}
400
350
300
250
200
150
100
50
A. grandis-■
S. cockerelli-▲
S. oslari-▼
H. occidentalis-●
SPRING
WINTER
AUTUMN
NORTH FORK
MIDDLE FORK
MAIN-STREAM

Table IV. Interval analysis of seasonal mean abundance of the North Fork (Site A), the Middle Fork (Site B), and the Mainstream River (Site C).

	Site contrasts	A. grandis	S. cockerelli	H. occidentalis	S. oslari
Fall	A vs B	NSD	A B *	NSD	A B **
	A vs B	NSD	A C *	NSD	A C **
	B vs C	NSD	B C *	NSD	B C **
Winter	A vs B	NSD	NSD	NSD	A B *
	A vs C	A C **	A C *	NSD	A C **
	B vs C	B C **	B C *	NSD	B C **
Spring	A vs B	NSD	NSD	NSD	A B **
	A vs C	A C **	A C *	NSD	A C **
	B vs C	B C **	B C *	NSD	B C **

NSD - No significant difference.
* - Significantly different at 95 percent confidence level.
** - Significantly different at 99 percent confidence level.

thermal regime and alteration of seston dynamics. Data indicated similarity among these parameters between the Mainstream and lower order creeks, which may explain their resemblence in hydropsychid species composition and dominance.

Temperature

Aquatic insects frequently key behavior (Gallepp, 1977; Wojtalik and Waters, 1970) and life histories (Stanford and Gaufin, in press) on various thermal criteria. Macroinvertebrates may be restricted in distribution by narrowly defined environmental factors associated with temperature as well as other parameters such as trophic relationships and substrata (Cummins, 1975b; Sweeney and Vannote, 1978). Stanford (1975) demonstrated that the accumulation of a finite quantity of degree-days was necessary for maturation and emergence of *Pteronarcella badia* (Plecoptera).

Temperature plays a significant role in establishing faunal characteristics along a stream logitudinal profile. Hauer, Zimmerman, and Stanford (1979) have shown that in a North Fork tributary stream where other environmental parameters were typical of a 3rd order stream, the number of degree-days was typical of that found in the river due to a lake approximately 4 km upstream. The macroinvertebrate community in this stream was typical of that found in the main rivers.

Temperature data from Trail Creek and the North and Middle Forks revealed an expected increase in summer temperatures down the longitudinal gradient of the river basin (Fig. 24). Discharge of cold hypolimnion water from Hungry Horse Reservoir resulted in summer and early fall temperatures significantly decreased in the Mainstream River, thus causing a lower accumulation of degree-days from that expected if stream regulation were not present. The number of degree-days in the Mainstream River approached that found in Trail Creek, which may partially explain their similarity in hydropsychid community structure.

Particulate Organic Matter and Total Suspended Solids

The North and Middle Forks erode extensive deposits of glacial clays; however, the Middle Fork, which frequently courses through narrow canyon sections, carries a larger sediment load during spring runoff, does not clear as rapidly after runoff, and becomes turbid following occasional summer and fall rainstorms in the drainage basin. Fine particulate organic matter, composed of detritus from allochthonous and autochthonous sources, is closely associated with clay sediments in a colloidal floc. The organically rich sediments are deposited on and within the substrates of both rivers and are easily resuspended and transported downstream. Concentration values of particulate organic matter in the North Fork, Middle Fork, and Mainstream below the South Fork confluence exhibited substantial seasonal fluctuation (Fig. 25). POM was closely associated with total suspended solids. Both

Fig. 24. Thermal regima and temperature summation for Trail Creek, North Fork, Middle Fork, South Fork, and Mainstream Flathead River, Montana.

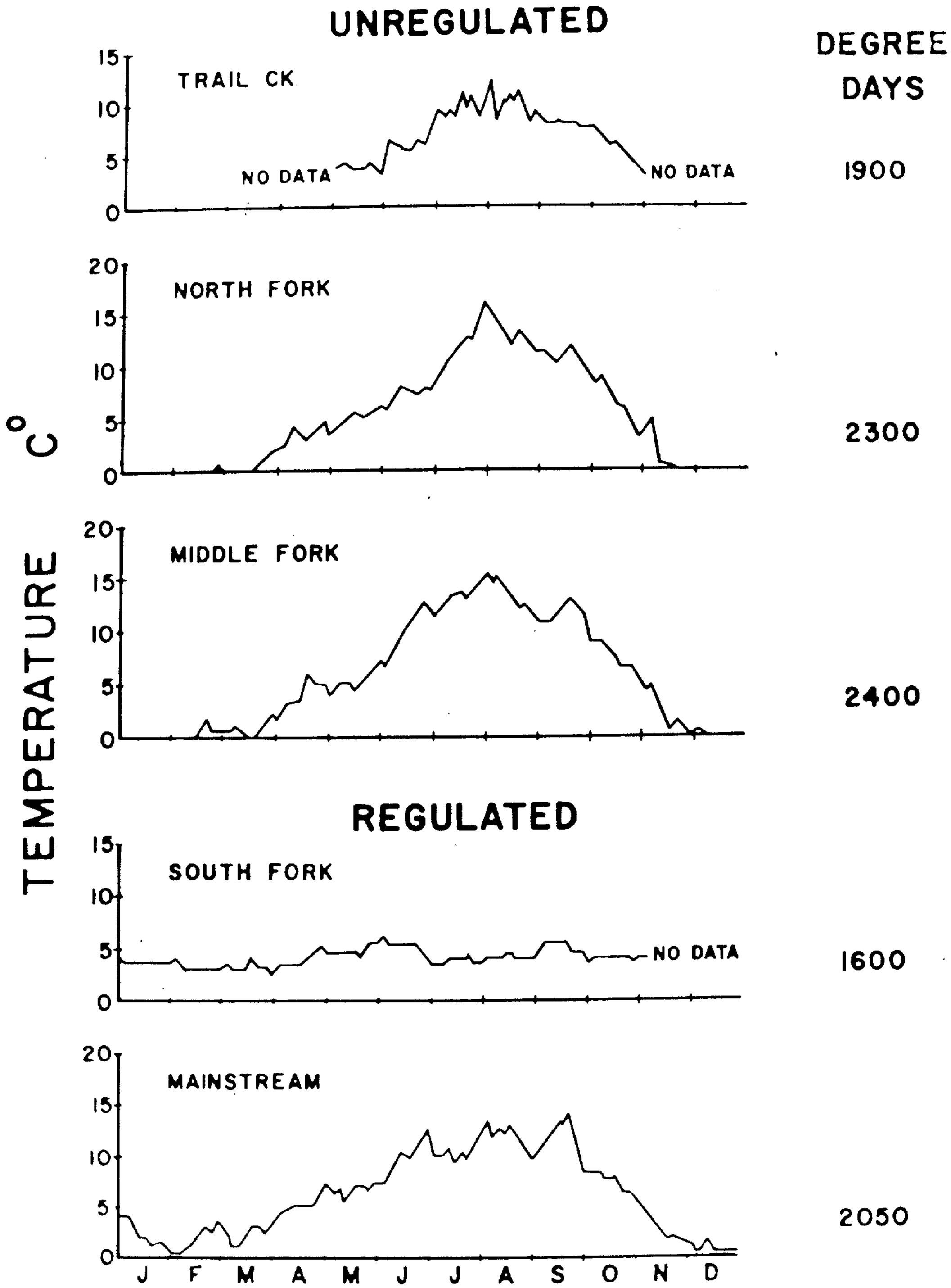
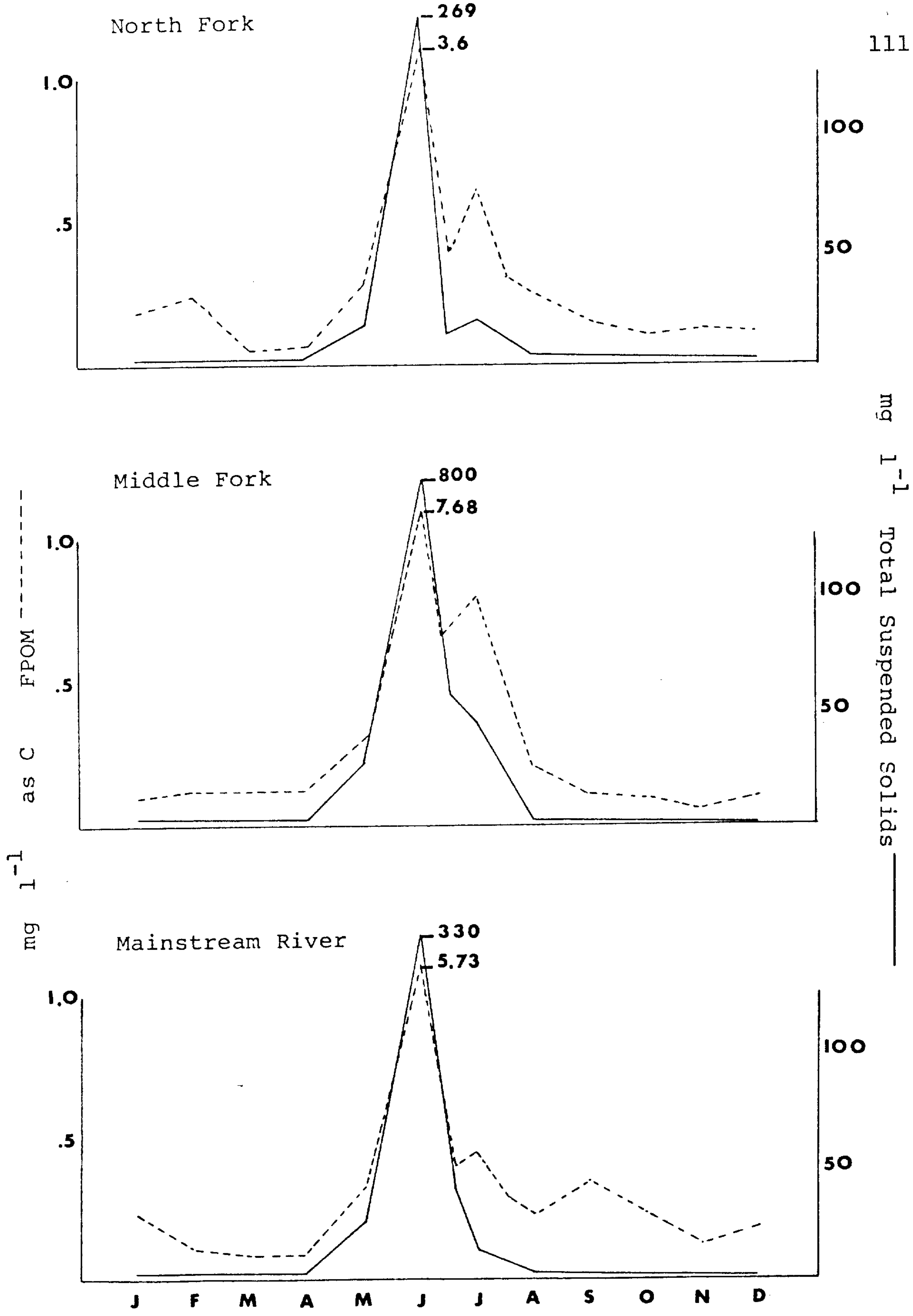

UNREGULATED
DEGREE DAYS
TRAIL CK
NO DATA
NO DATA
1900
NORTH FORK
2300
MIDDLE FORK
2400
REGULATED
SOUTH FORK
NO DATA
1600
MAINSTREAM
2050
TEMPERATURE C°
0
5
10
15
20
J
F
M
A
M
J
J
A
S
O
N
D

Fig. 25. Particulate organic carbon (POC) and total suspended solids (TSS) in the North Fork, Middle Fork, and Mainstream Flathead River, Montana.


North Fork
269
3.6
1.0
.5
100
50
Middle Fork
800
7.68
1.0
.5
100
50
Mainstream River
330
5.73
1.0
.5
100
50
J F M A M J J A S O N D
mg l^{-1} as C FPOM - - - -
mg l^{-1} Total Suspended Solids ——

parameters were closely correlated to the annual maxima of the runoff event, which reached maximum discharge in late May or early Jun. during the study period.

POM concentration was greater in the Mainstream River compared to the unregulated tributaries during late summer, fall, and winter. The Mainstream below the confluence of the regulated South Fork differed significantly from the unregulated tributaries in that substantial algal growth occured in the regulated segment. Algal filaments were abraided by the sluicing effect of the regulated discharges and were frequently observed heavily packed into Hydropsychidae filter nets. Green and diatomaceous algae contributed significantly to the trophic dynamics of *Arctopsyche grandis* in this river segment. The apparent abundance of large particle POM may partially explain the comparatively high density and dominance of *A. grandis* in the filter feeding component of the zoobenthos in the Mainstream River.

Stream Continuum and Stream Regulation

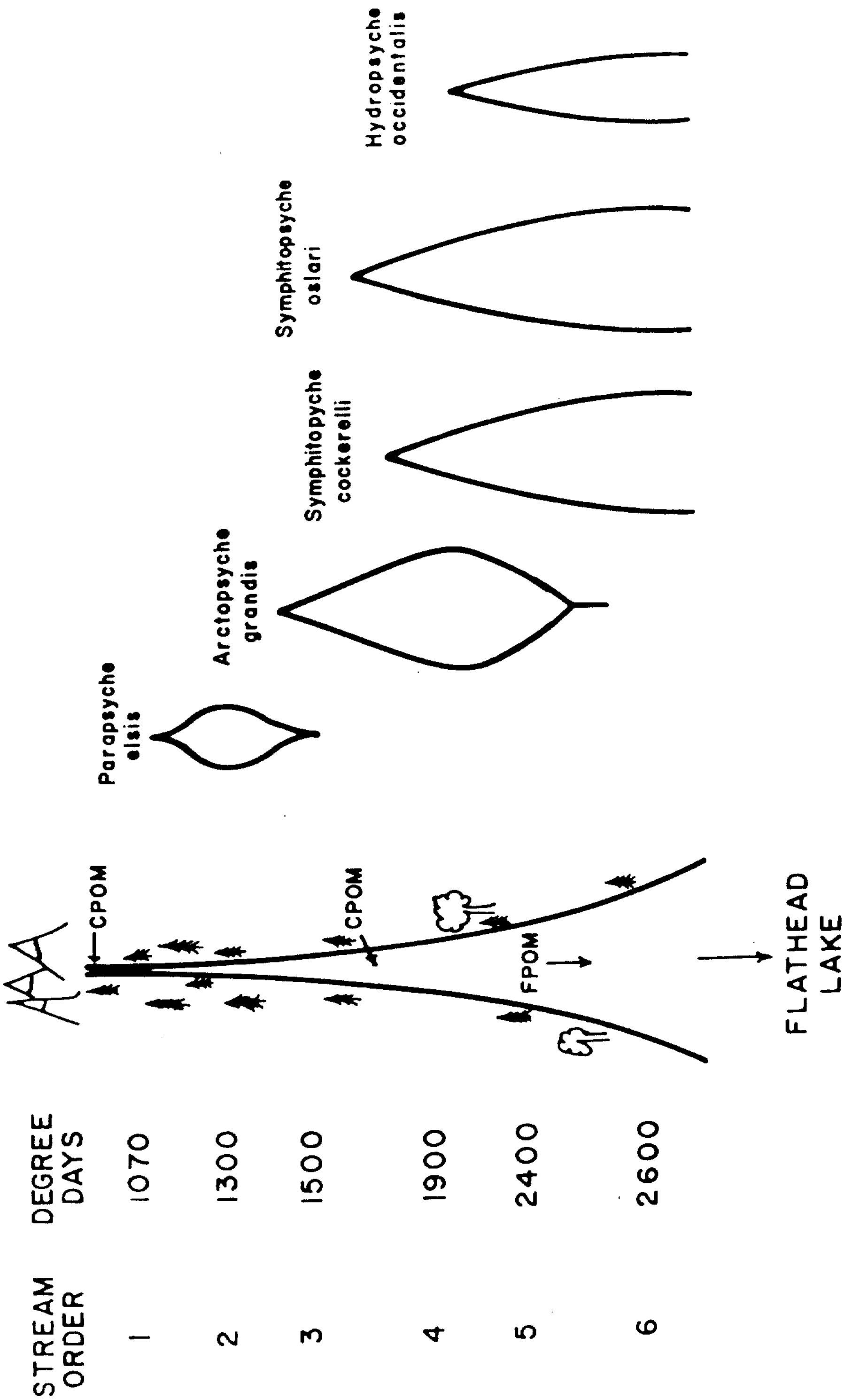
The Stream Continuum Concept (Cummins, 1975a; Vannote et al., 1979) predicts a changing relationship of the macroinvertebrate fauna that reflects the variation in availability of plant-derived energy sources. Small headwater streams are dominated by their terrestrial setting, depending upon the input of coarse particulate organic matter from allochthonous sources. Theoretically, canopy limits incident light and reduces temperature fluctuation. Medium-sized rivers are less dependent on terrestrial inputs with more autotrophy and greater temperature fluctuation. Western montane streams and medium-sized rivers are less dependent upon autumnal allochthonous detrital sources and autotrophy may be a significant contributing factor to the energy budget (Minshall, 1978). The different food sources of coniferous forest litter and greater autotrophy, in addition to other environmental factors such as temperature, substrate, and gradient, establish the basis for a typical montane fauna, which sequence in a finite distribution along the river continuum (Wiggins and Mackay, 1978).

The Flathead River system is within a predominantly coniferous forest. Small headwater streams originate as high mountain tributaries which are frequently derived from snow melt and glaciers. The very high streams often have an open canopy and may exhibit large diurnal temperature fluctuations. They also receive substantial quantities of light as well as a significant contribution of allochthonous organic matter from riparian vegetation. Upon entering the coniferous forest, the stream receives less light, and temperature fluctuation is reduced (Hauer, Zimmerman, and Stanford, 1979). The larger 5th order tributary rivers and the 6th order Mainstream River have open canopies; autotrophy is prevalent with substantial fall and spring periphytic growth.

Based upon distribution and abundance data, I have developed a conceptual model of the Flathead River system formulated upon the hypothesis of the stream continuum. Without Hungry Horse Dam on the South Fork, the hydropsychid community would integrate from P. elsis in the small streams to A. grandis, followed by the assimilation of the Hydropsychinae species into the community through a progression down the longitudinal gradient (Fig. 26). P. elsis is eliminated from the community in the 2nd or 3rd order streams. Loss of P. elsis from the community is most likely temperature related since larvae of this species have filter nets of similar mesh size to A. grandis larvae (Hauer, unpubl.). A. grandis, after considerable overlap with the Hydropsychinae, would be a minor component of the Mainstream River community as a result of a decrease in POM particle size and an increase in thermal regime. This model is consistent with the results of other studies (Alstad, 1980 ; Stanford and Ward, unpubl.; Wallace, Webster, and Woodall, 1977; Wiggins and Mackay, 1978).

The influence of Hungry Horse Dam on the Mainstream River has been substantial in terms of suppressed summer temperature, streambed fluctuation caused by changing discharge, and trophic dynamics as a result of periphyton abrasion and transport downstream. This has resulted in a deviation from the unaltered stream model (Fig. 26). The cold hypolimnion water entering the Mainstream from the South Fork has resulted in a decrease in the annual summation of degree-days. Also, discharge from Hungry Horse Reservoir was frequently increased during the day when river temperatures normally reach their maximum, thus

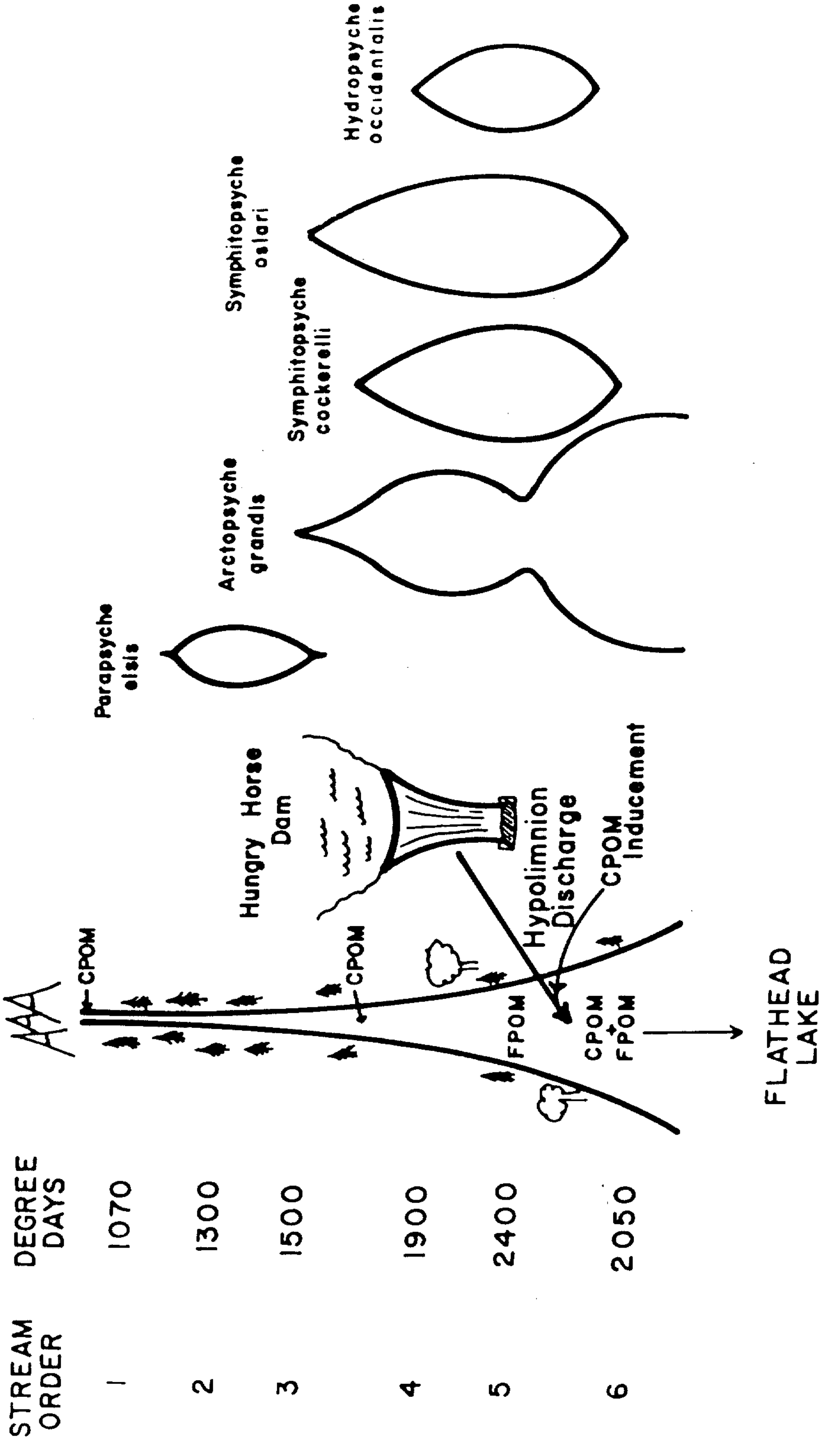
Fig. 26. Hypothetical distribution of selected parameters and the Hydropsychidae through the river continuum of the Flathead River Basin without Hungry Horse Dam on the South Fork.


STREAM ORDER
1
2
3
4
5
6
DEGREE DAYS
1070
1300
1500
1900
2400
2600
CPOM
CPOM
FPOM
FLATHEAD LAKE
Parapsyche elsis
Arctopsyche grandis
Symphitopsyche cockerelli
Symphitopsyche oslari
Hydropsyche occidentalis

increasing the effect of the discharge upon the macroinvertebrate fauna. *A. grandis*, which in the unaltered model declines in abundance because of an increase in temperature summation and a decrease in coarse grained POM, becomes very abundant in the regulated stream model (Fig. 27). The high *A. grandis* production is a consequence of a reduction of thermal criteria and the substantial amount of periphytic algae which is carried in the drift as a direct result of the fluctuating discharge. Hydropsychinae abundance was greatly reduced in the altered Mainstream River due, in part, to insufficient thermal criteria and possibly as a function of interspecific competition with *A. grandis*.

The presence of Hungry Horse Dam and the resultant hypolimnion discharge have culminated in a river continuum reset. The decrease in degree-days and increase in coarse grained POM, as direct consequences of the diurnal cold water discharges from the South Fork, have resulted in a definitive hydropsychid fauna response. In the partially regulated Mainstream, the Hydropsychidae community structure is similar to that of the lower order streams having a similar thermal regima; however, because of greater autotrophic production in the Mainstream, a higher level of secondary production has also resulted.

Fig. 27. Distribution of selected parameters and the Hydropsychidae through the river continuum of the Flathead River Basin as it exists with Hungry Horse Dam on the South Fork.


STREAM ORDER
1
2
3
4
5
6
DEGREE DAYS
1070
1300
1500
1900
2400
2050
CPOM
CPOM
FPOM
CPOM + FPOM
FLATHEAD LAKE
Hungry Horse Dam
Hypolimnion Discharge
CPOM Inducement
Parapsyche elsis
Arctopsyche grandis
Symphitopsyche cockerelli
Symphitopsyche oslari
Hydropsyche occidentalis

The Ecology of Brachycentrus americanus (Banks) (TRICHOPTERA: Brachycentridae)

Reports of caddisfly life cycles have usually cited five distinct larval instars sequenced within a univoltine, single cohort, growth and emergence pattern (Wiggins, 1977). Extremely harsh winter conditions, substantial environmental change between low flow and spring runoff, and the spatial heterogeneity of the substrate characterize many northern cordilleran streams and small rivers. Consequently, deviations from the generalized life cycle pattern should be expected from montane aquatic insects because of the heterogeneity of their environment.

Brachycentrus americanus (Banks), Brachycentridae, is widespread across the northern part of North America (Ross, 1944). Larvae are restricted to running water, although some inhabit slow currents. Some aspects of larval ecology have been reported including drift responses (Anderson, 1967), behavior (Gallepp, 1974, 1977), and food habits (Mecom, 1972; Mecom and Cummins, 1964; Shapas and Hilsenhoff, 1976). Detailed life cycle dynamics, particularly for populations residing in a moderately large cordilleran river, are unknown. Soon after the initiation of long-term research (Stanford and Gaufin, 1974; Potter and Stanford, 1975; Stanford and Hauer, 1978, Stanford, Hauer, and Stuart, 1979; Stanford and Gaufin, in press; Hauer, Zimmerman, and Stanford, 1979) it became apparent that B. americanus life history patterns in the Flathead Basin deviated from that of the typical trichopteran (see Wiggins, 1977). Two distinct size classes of larvae in the fall, winter, and spring were observed; and during the summer, there appeared to be an extended, yet disjunct, adult emergence and activity pattern. To clarify the life history pattern of this important component of the zoobenthos of the Flathead River, larval growth sequencing, adult emergence and activity patterns, and distribution and abundance of this species were investigated.

Life History

In the Flathead River Basin, *Brachycentrus americanus* life histories appeared to be closely associated with autotrophic periodicity. Although levels of autochthonous primary productivity are presently being quantified (Stanford, Hauer, and Stuart, 1979), general trends in annual periphyton biomass, primarily *Gomphonema*, *Navicula*, *Synedra*, and *Ulothrix*, appeared highest during the fall and again in the spring. Accelerated periphytic growth in spring, resulting in very evident accumulations of algae, was terminated by scouring action of spring runoff. During runoff, the river typically increases in discharge from 10 to 100 times mean fall-winter-early spring flow. Periphyton communities did not recover until late summer and fall. This latter period of growth was terminated by winter ice and shortened photoperiod.

Benthic invertebrate development and growth has been associated with a similar temporal periodicity (Hynes, 1970). Several investigators have documented high standing crops of periphyton in temperate streams during the same period (Cushing, 1967; Douglas, 1958; Gumtow, 1955). Based upon previous food habit studies (Mecom and Cummins, 1964; Mecom, 1972; Shapas and Hilsenhoff, 1976), which indicated diatoms and detritus were important components of *B. americanus* diet, I expected a close association between larval growth and autotrophic production.

Distribution of larval instars over the annual cycle revealed that *B. americanus* had five instars (Fig. 28), and the life cycle was completed in one year. However, larvae segregated into two distinct cohorts were also found (Fig. 29). The first cohort apparently originated from eggs deposited in Jun. just after peak runoff; first instar larvae were found in Jul. and Aug.. Growth of this cohort was rapid during autumn and larvae overwintered primarily in 4th instar. Larvae in the first cohort completed their growth during spring, attached cases to large stones and small boulders in the substrate, sealed the posterior and then anterior ends, and entered a resting condition. During this apparent diapause, larval-pupal apolysis was delayed until after the start of the runoff period, May - early Jun.. Adults emerged after the spring flood peaked, yet during the runoff event, usually mid-Jun. (Fig. 30).

The second cohort apparently originated from eggs deposited during the second adult flight period which occured during Aug. and early Sep.. First instar larvae appeared in

Fig. 28. Instar discrimination of *Brachycentrus americanus* from the Flathead River, Montana, indicating mean, standard deviation, and range.

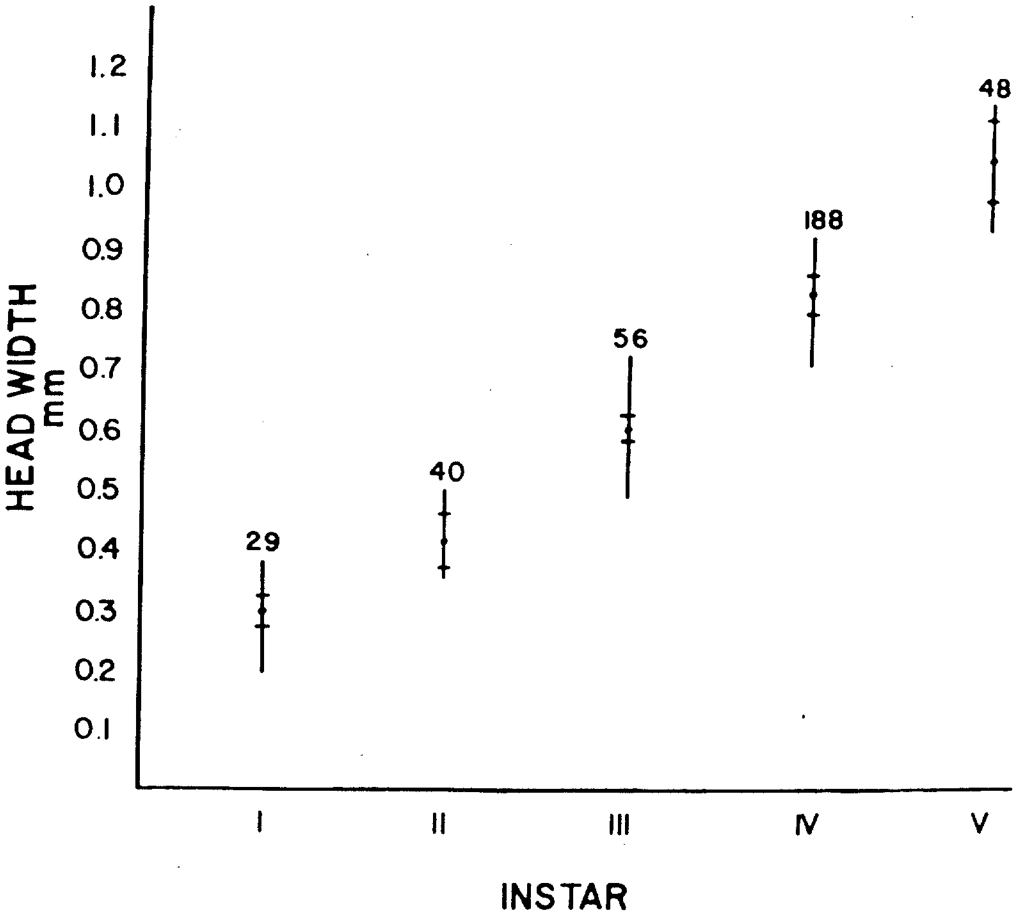

HEAD WIDTH
mm
1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
29
40
56
188
48
I
II
III
IV
V
INSTAR

Fig. 29. Life cycles of Brachycentrus americanus in the Flathead River, Montana. Larval instars (I-V), prepupae (PP), pupae (P), and adult flight period (AF) are indicated.

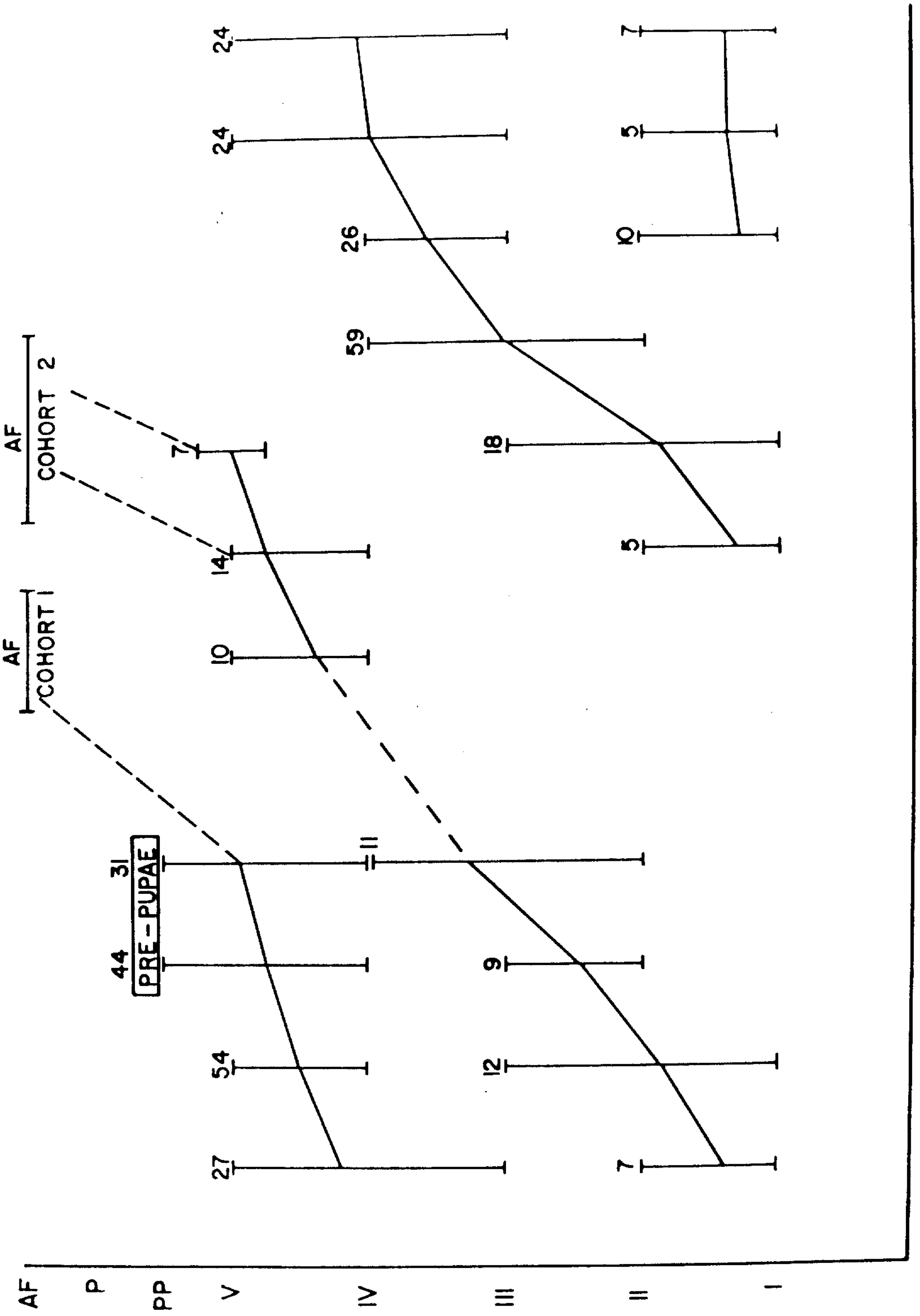
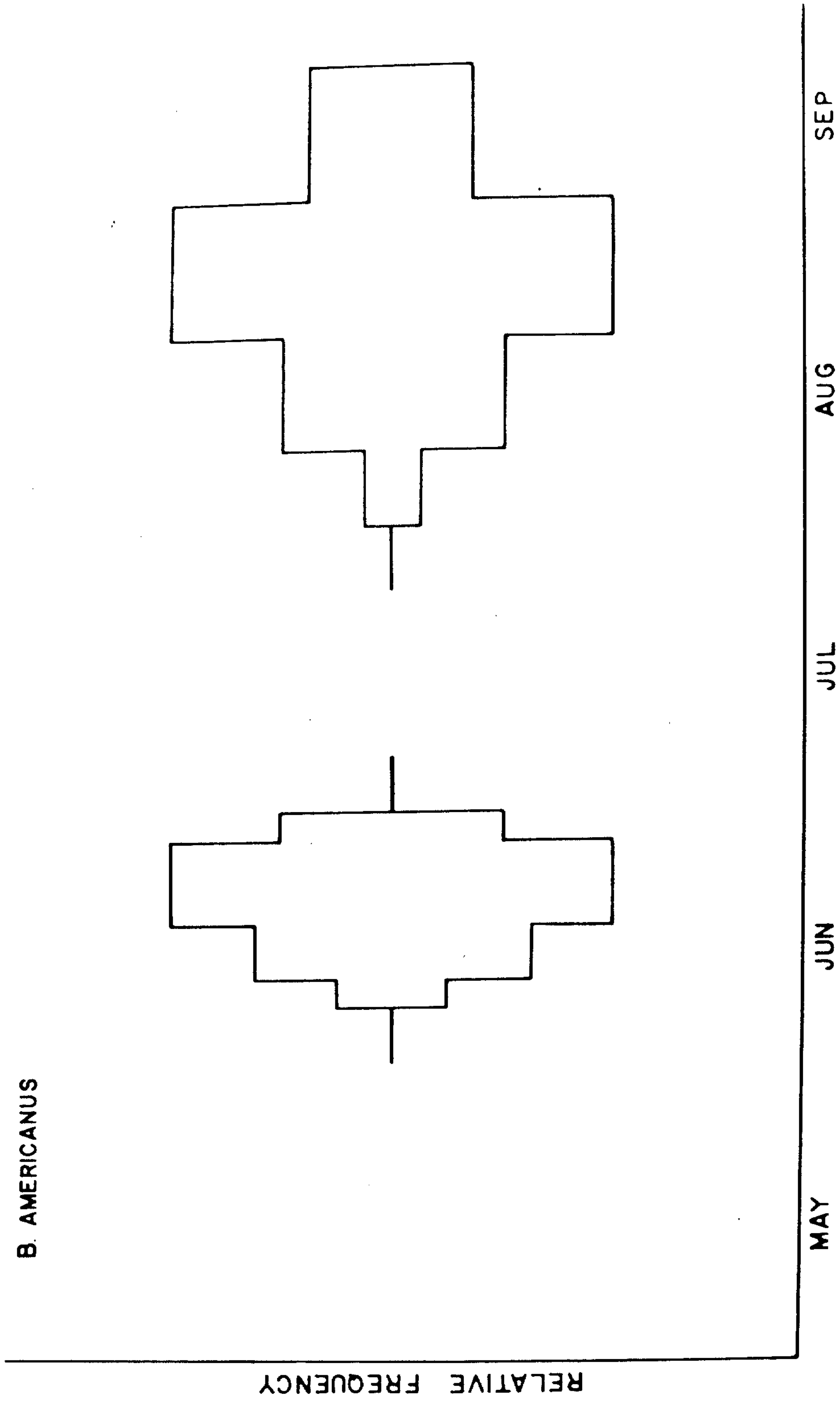

AF
P
PP
V
IV
III
II
I
J
F
M
A
M
J
J
A
S
O
N
D
27
54
44
31
PRE-PUPAE
AF
COHORT 1
AF
COHORT 2
7
12
9
11
10
14
7
5
18
59
26
24
24
10
5
7

Fig. 30. Adult flight periods of *Brachycentrus americanus* showing the distinctive cohort differentiation. Maximum width of bar graphs represents peak emergence.


B. AMERICANUS
MAY
JUN
JUL
AUG
SEP
RELATIVE FREQUENCY

Sep. and Oct., and individuals of this cohort remained in 1st and 2nd instar during autumn, overwintering as early instar larvae. Growth of second cohort larvae occured primarily during the spring and early summer (Fig. 29). Last instar larvae of the second cohort were still active after the emergence of first cohort adults. Second cohort individuals pupated in Jul., apparently did not enter a diapause, and emerged in Aug. and early Sep. (Fig. 30).

At the onset of pupation, larvae from both cohorts frequently moved to a location out of the current, fastened the leading edge of the case to the substrate with silk and closed off the posterior and anterior openings by spinning silk in a radial pattern with several holes in the end. Pharate adults, upon leaving the pupal case, swam to the surface and usually toward shoreline rubble or vegetation. Occasionally, individuals were observed floating on the surface attempting to disengage from the pupal cuticle. Adults were readily collected with aerial insect nets as they flew among the leaves of overhanging riparian vegetation during the day. At dusk and early evening, adults were attracted to the U.V. night light. Attempts at collecting adults just prior to dawn with the night light were unsuccessful. The sex ratio of adult B. americanus collected at light traps was 53.5 females:46.5 males. The sex ratio was 54 females:46 males for adults captured with the aerial net, thus indicating that neither sex is preferentially attracted to light.

Distribution and Abundance

B. americanus larvae were widely distributed throughout the 5th order tributaries and Mainstream Flathead River and occupied a wide variety of substrate types. *B. americanus* (Anderson, 1967), as well as *B. numerosus* (Lloyd, 1921), larvae have been reported to select sites in slow current and eddies during early instars, then migrate to midstream and other areas of swift current as late-instar larvae. I observed both early and late instar larve in areas of rapid, non-turbulent flow. Larvae attached the leading ventral edge of their case to the selected substrate, usually a stone or submerged log or tree branch, so that they faced the unbroken current. They filtered food particles carried in the current by positioning large mesothorasic and metathorasic legs radially in a perpendicular plane to the current. Occasionally individuals were collected from streams at the confluence with a main tributary river, but this usually occured in streams which drain the deep, glacial lakes on the west side of Glacier National Park.

The investigation of microdistributional patterns of larvae revealed a clumped distribution. Quantitative benthic collections yielded a range of 0 to 38 individuals m^{-2} for all riverine sites. A statistical analysis to test agreement with a Poisson series resulted in a rejection of the hypothesis of a random distribution ($P < 0.01$). The high value of chi-square ($x^2 = 654.69$) indicated that the larvae of *B. americanus* were contagiously distributed. As many as 100 larvae were often qualitatively collected from single sticks, ca. 0.5 m long, protruding from the substrate in areas with even, non-turbulent flow and a current speed of ca. 0.5 m^{-sec}. The high concentrations of larvae, usually in association with a protruding branch, tree root, or in selected areas of rubble substratum, were observed more frequently in the North and Middle Forks. These tributary rivers are not subject to diurnal changes in water elevation and current speed as is the partially regulated Mainstream River.

The clumped distribution of larvae among the rubble of individual riffles revealed a tendency of larvae to accumulate or select sites along the edge of bank seepage areas, where nutrients entering the river from low lying marshes tended to increase periphytic growth. Frequently, larvae selected positions along the perimeter of strong riffles orienting themselves on the tops of the rubble substrate in non-turbulent flow. Although larvae were occasionally found in strong riffle areas, current speed >1 m^{-sec}, positions within the interstitial space of the rubble were usually selected. Food habit studies of B. americanus indicated that the species is omnivorous (Gallepp, 1974; Mecom, 1972; Mecom and Cummins, 1964; Shapas and Hilsenhoff, 1976). Mecom and Cummins reported that diatoms constituted more than 95 percent of the diet while the other three studies found detritus to be an important component of the trophic dynamics. Gallepp also reported that larvae feed by grazing periphyton.

Significance of Cohort Segregation

In this and other studies, spatial and temporal segregation of congeneric or other closely related species (e.g. *Isocapnia* *spp*.; *Utacapnia* *spp*. (Stanford and Gaufin, in press); *Rhithrogena* *spp*. (Stanford and Hauer, unpubl.); *Symphitophsyche* *spp*.; *Rhyacophila* *spp*.; *Apatania* *spp*.) were observed. *B*. *americanus*, in this case, appears to be a single species operating as two independent functional units. Instead of there being two species keying on a temporally sequenced resource, such as food availability, a single species was segregated into two cohorts, which were temporally and, possibly, genetically independent. Although the adult flight patterns of the two cohorts are considerably different, I cannot discount the possibility of some gene flow. The life cycle of *B*. *americanus* in the Flathead Rivers is similar to that of *Ceraclea* *transversa* (Resh, 1976) which is greatly influenced by the gemmulation sequence in the annual cycle of the freshwater sponge.

Investigations of closely related stream species have revealed a multi-faceted integration of environmental parameters which establish ecological segregation (Cummins, 1964, 1973; Grant and Mackay, 1969; Wallace, Webster, and Woodall, 1977). *B*. *americanus* life history, reported here, was closely associated with the periodicity of autotrophic production. Intraspecific niche segregation has resulted in an atypical species differentiation. Occurrence of two cohorts certainly enhances fitness of the species in the Flathead Rivers. The apparent life cycle plasticity may explain the rather ubiquitous distribution of *B. americanus* in the Nearctic region.

Bionomics of Dicosmoecus gilvipes (Hagen) (TRICHOPTERA: Limnephilidae)

Dicosmoecus is a Holarctic genus restricted to western North America, Japan, and northeastern Asia (Wiggins, 1977). Although there is some taxonomic confusion regarding this genus, presently five species are recognized from North America (Flint, 1966; Nimmo, 1971), and the genus is presently under revision (Wiggins, per. comm.). The larvae are large and robust and, in final instar, have a correspondingly large case made of fine gravel. Larvae occured frequently in selected habitats corresponding to specific stages of their life history.

Although the genus is widely distributed, very little is known about its life history and ecology. Anderson (1976) reported D. gilvipes to be the most abundant Dicosmoecus species in Oregon. Larvae were found frequently in medium to fast streams, and aggregations of "aestivating" prepupae occured on the underside of stones during summer. Wiggins (1973) observed that D. atripes oviposited egg masses on objects along the waters edge, always partly or wholly submerged. Nimmo (1977) reported the geographical distribution of D. gilvipes from Alberta and British Columbia south to California and Colorado, however no Montana record was listed.

D. gilvipes was frequently collected in 5th and 6th order river segments and less frequently in lower order tributaries. Since the species appeared to be an important component of the diverse zoobenthic community in the rivers, the life history and ecology of the species was investigated.

Life History

In the Flathead River Basin, *D. gilvipes* deviated from the typical trichopteran life cycle of five larval instars sequenced within a univoltine emergence pattern (see Wiggins, 1977). Although individual larvae were observed and collected frequently, they were not abundant at any one time or place. Consequently, sample size for life history examination was small (202 specimens); however, because of the distinctiveness of successive larval instars, life history sequencing was very apparent. Larvae were sequenced within five discrete instars (Fig. 31), however the species did not follow a univoltine emergence pattern. First instar larvae appeared in the spring immediately after the beginning of spring runoff (Fig. 32). Second and third instar larvae were observed in Jun. and Jul.. Fourth instar larvae were most frequently encountered during Jul., Aug., and Sep.. Consequently, most of the growth for *D. gilvipes* in the Flathead Basin took place during the summer, after peak runoff, and among first-year class larvae. Larvae entered the fifth and final instar during the fall but remained active until Nov., when water temperatures varied diurnally between 0-2°C. Larvae entered an overwintering diapause during Nov. or Dec.. The anterior lip of the case was cemented to the underside of large rocks or small boulders in reaches of even, non-turbulent flow, usually two to five larvae aggregated together. This was probably not a simple quiescence which

Fig. 31. Instar discrimination of Dicosmoecus gilvipes from the Flathead River Basin, Montana, indicating mean, standard deviation, and range.

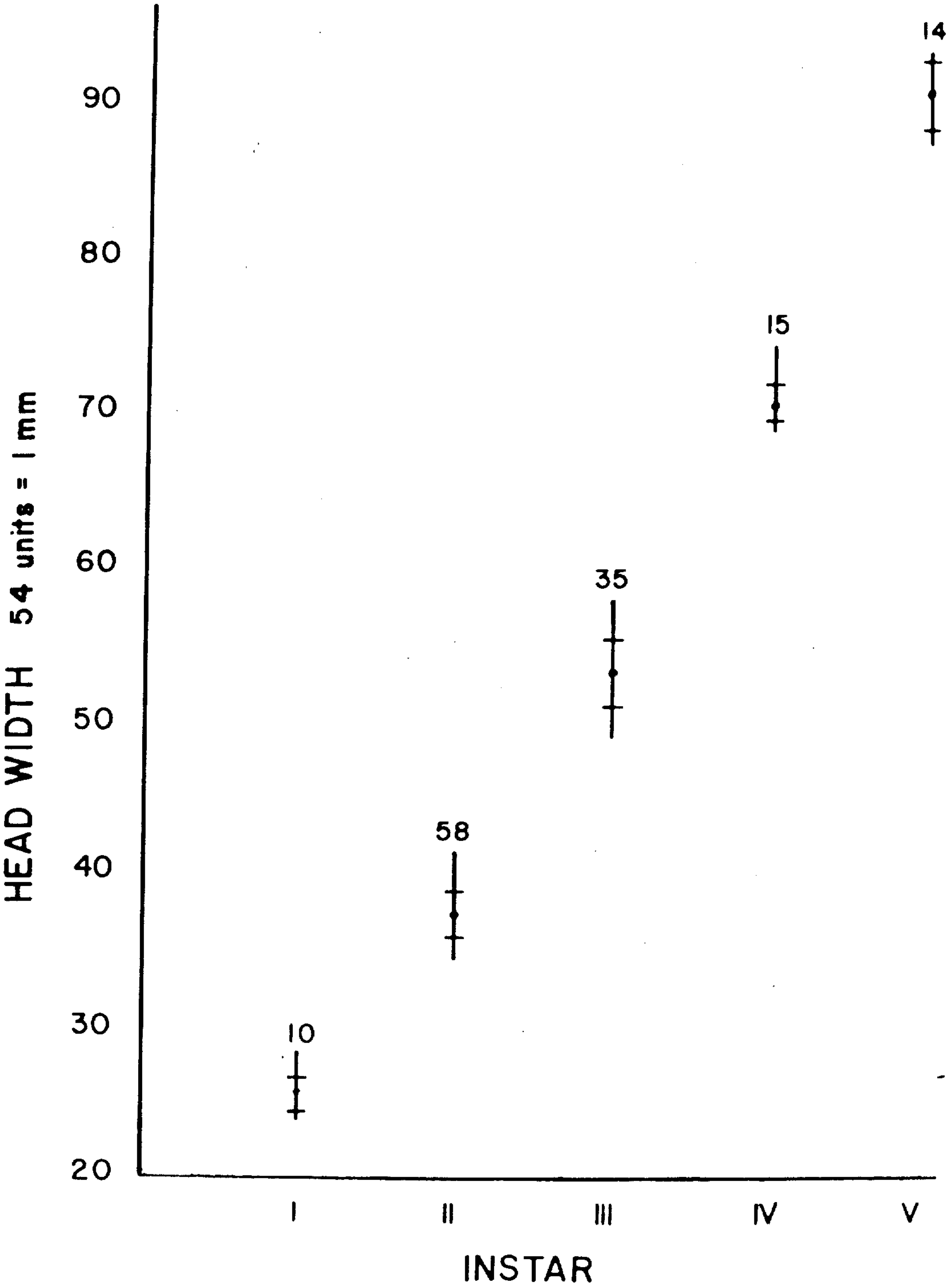
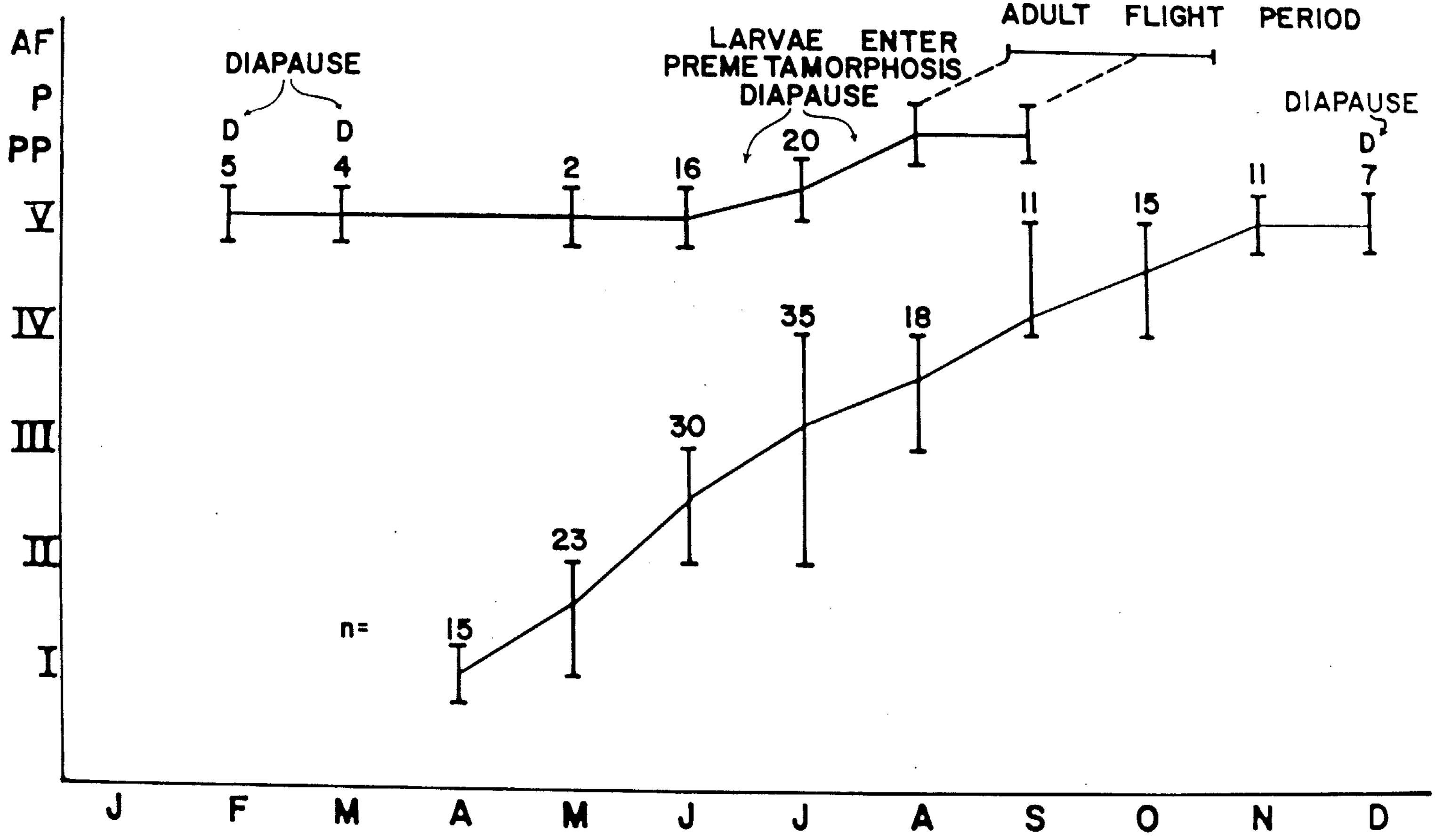

HEAD WIDTH 54 units = 1 mm
90
80
70
60
50
40
30
20
14
15
35
58
10
I
II
III
IV
V
INSTAR

Fig. 32. Life cycles of Dicosmoecus gilvipes in the Flathead River Basin, Montana. Larval instars (I-V), prepupal diapause (PPD), pupae (P), adult flight period (AF) and winter diapause (D) are indicated.


ADULT FLIGHT PERIOD
LARVAE ENTER
PREMETAMORPHOSIS
DIAPAUSE
DIAPAUSE
D
D
DIAPAUSE
D
AF
P
PP
V
IV
III
II
I
5
4
2
16
20
11
15
11
7
35
18
30
23
n=
15
J
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O
N
D

would have been characterized by inactivity, but without case attachment. Fifth instar larvae were again active during Jun. and Jul.. In Aug., last instar larvae attached their case a second time in similar location and aggregation as that of the winter diapause. Some attached final instar larvae were observed as early as mid Jul.. Larvae entered a prepupal diapause after attachment of the case which lasted from one to two months before larval-pupal apolysis. Case attachment during both diapauses generally occured several feet from shore, thus minimizing the chance of being frozen in winter ice or being exposed to desiccation by a drop in river volume during late summer and fall.

The overwinter diapause was probably temperature dependent, although photoperiod may also have been an important environmental factor. This diapause was probably in response to the extreme icing conditions which occur in the Flathead River, particularly along the edges and between riffles where active fifth instar larvae would otherwise be located.

Premetamorphosis diapause was also found to occur in the European species Anabolia furcata (Novak, 1960). Diapause was demonstrated to be terminated by a short-day photoperiod, but lowered temperature also played an important role in advancing termination. In this study, several fifth instar larvae returned to the laboratory during summer for rearing were placed in an experimental tank in which the temperature was maintained at $7^{\circ}C$. Photoperiod was maintained near natural conditions. The 3 individuals which emerged did so approximately 1 to 2 weeks earlier than those individuals maintained at near mean daily river temperature. Although not definitive, this suggests that D. gilvipes diapause is influenced by both photoperiod and temperature. This conclusion seems plausible because the reared larvae from both the experimental tank and the natural temperature tank required nearly 3 months from the time of collection to emergence. If temperature had been the only environmental cue, I would have anticipated a more rapid emergence by those larvae maintained at the lower temperature than occured.

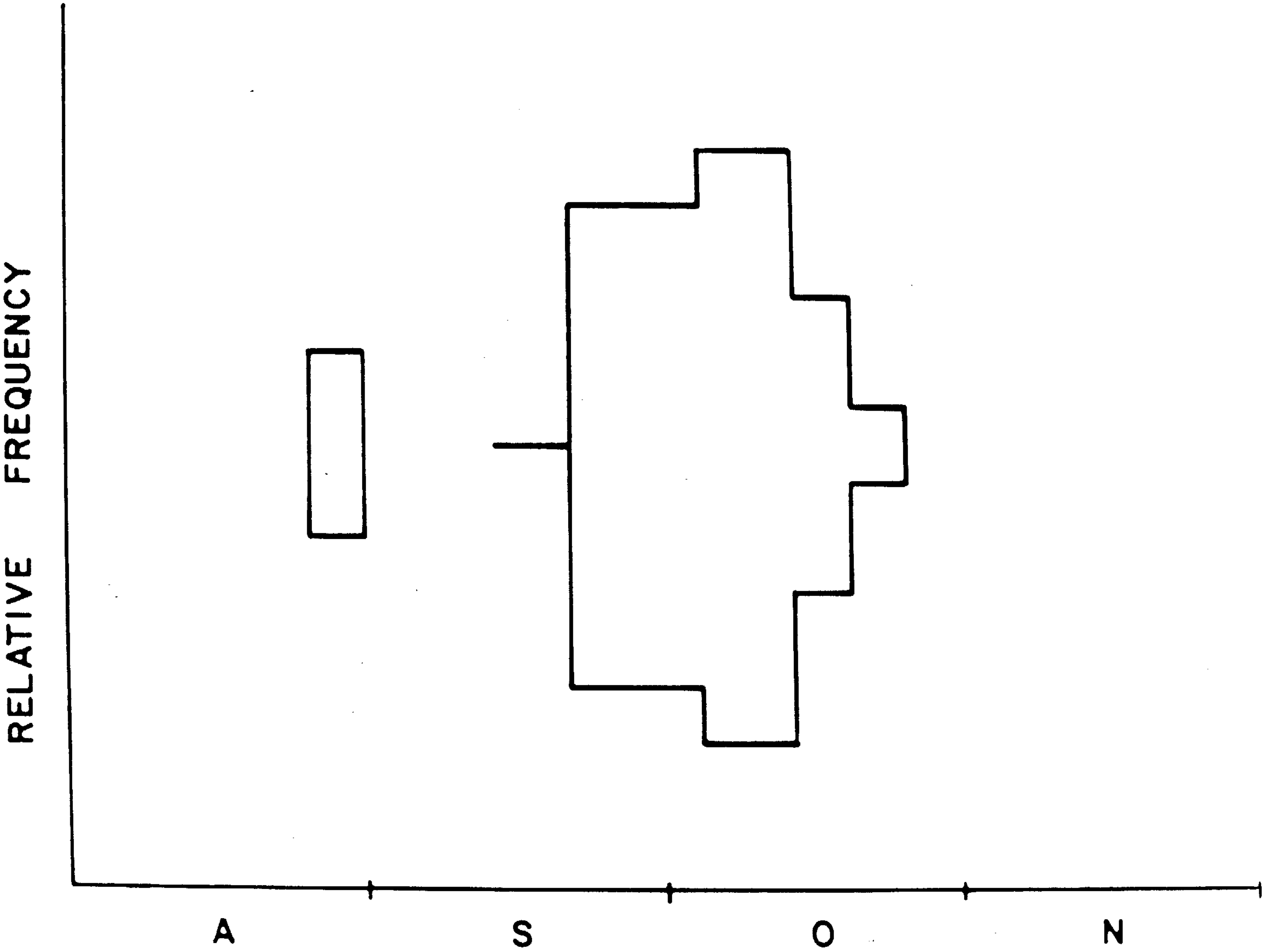
Successive larval instars constructed distinctive cases. First instar larval cases were constructed of 0.5 to 1 cm, fine twigs and needles arranged in an overlapping pattern with the outside end of the twigs pointing at a posterior angle, similar to the fletching of an arrow. Second instar larval cases were similar to those of first instar larvae, but larger, straight twigs and needles were used. Third instar larvae began incorporating coarse sand grains into the anterior end of the case, leaving the posterior end still largely composed of needles pointing at a posterior angle. Fourth instar cases were 70 to 80 percent mineral, with only the posterior end of the case remaining of plant material. The cases of fifth instar larvae were entirely composed of coarse sand grains with a slight dorso-ventral curve and usually a few larger pebbles on both sides of the anterior opening. Fifth instar larval cases ranged from 3 to 4 cm in length (Fig. 33).

In 1977 and 1978, a few individuals emerged during the last week in Aug.. Both years were markedly influenced during early Sep. by cold, wet weather. Adults were not active during this period, but reappeared after a return to sunny days and warm afternoons in late Sep. and Oct.. Peak adult emergence occured during the second week in Oct. of both years. No adults were collected after the third week of Oct. (Fig. 34). Adults were strong, steady fliers, frequently observed flying out over the river, and were collected most frequently with an aerial net. They were also collected under shoreline rubble and while resting on stems and twigs of riparian vegetation. Adults were also attracted to the U.V. night light.

Wiggins (1977) hypothesized synchronization of adult emergence by autumnally emerging species may be due to low night temperatures and consequent daytime activity by the adult. The daytime activity, which has been found in relatively few species of Trichoptera, portends a greater potential hazard to the adult. Consequently, synchronized emergence might compensate for these greater hazards. I offer an alternative hypothesis. With the onset of autumn, there was an accompanying decrease in the number of days climatically favorable to adult activity. In late Sep. and Oct., there were typically a few weeks of favorable weather,

Fig. 33. Picture of the cases of the five successive larval instars of *Dicosmoecus gilvipes*.

Fig. 34. Adult flight period of Dicosmoecus gilvipes. Maximum width of bar graph represents peak emergence.


RELATIVE FREQUENCY
A
S
O
N

during which peak emergence for D. gilvipes occured. Individuals which emerged after this relatively short period favorable to adult activity may have had a decreased opportunity for activity and reproduction. The consequence being a shortened emergence time and synchronization to specific environmental cues.

Distribution

D. gilvipes was collected throughout the Flathead drainage, in rivers and in tributary creeks. Larvae occured in a wide variety of habitats and on many different substrates. First instar larvae were observed post-inception of spring runoff, usually mid-Apr.. They were most frequently collected along the shoreline at the edge and just below riffles, where they were assisted in remaining out of the main current by small wave action caused by the riffles. Many first instar larvae were also observed crawling across the surface of fine organic matter in a seepage spring which drained a few meters into one of the tributary creeks of the North Fork. Later instar larvae were not observed in the seepage area. Second and third instar larvae were most frequently encountered in backwaters and large pools left on the flood plain after the receding of spring runoff high water. The backwaters and large pools were characterized by a silt and fine organic matter substrate and temperatures which are frequently different from the main rivers. These temperatures were warmer due to radiant exposure and a comparatively shallow depth or were colder due to cold spring waters entering the relatively small water volume. Infrequently, fourth and fifth instar larvae were also observed in these areas, but more frequently in the backwaters than the pools. Fourth and fifth instar larvae were most frequently observed in and on the rubble substrate along the edge of riffles or in the area of even flow and rubble bottom in the reaches between riffles. Although I did not investigate trophic relationships, the location of the late instar larvae indicated that rock surfaces were grazed for algae and fine organic particles. Larvae were also collected from tributary creeks (Hauer, Zimmerman, and Stanford, 1979), most notably from Howell Creek, a Canadian tributary of the North Fork, and Kintla Creek. Both creeks, at the location of larval collection, have thermal regimes similar to that of the North Fork. Howell Creek, unlike most of the North Fork tributaries, flows parallel to the river along the valley floor for approximately 5 km. Within this reach, there are several segments of low gradient and open canopy. Kintla Creek drains a large glacial lake located in Glacier National Park. Consequently, creek temperatures closely track that of the lake surface temperature.

Diapausing and active fifth instar larvae of *Dicosmoecus* were also collected from Yellow Bay Creek, an approximately 0.08 cms mean annual flow creek entering Flathead Lake at the edge of the University of Montana Biological Station. I do not know if these were *D. gilvipes*. This site differed considerably in thermal regime, canopy, and substrate from other locations in the drainage that *Dicosmoecus* was observed.

The apparently wide environmental parameters in which *D. gilvipes* larvae were found, first instar larvae in a seepage spring and along edges of riffles in the main rivers, second and third instar larvae in spring fed main river backwaters and warm flood plain pools, and fourth and fifth instar larvae in the mainstream river along the edge of riffles and in smaller creeks and even a first order stream, may explain the wide distribution of this species over the cordilleran western United States and Canada.

CHAPTER V

SUMMARY AND CONCLUSIONS

1. The primary purpose of this research was to document the structure of the Trichoptera community and describe the functional role they play in the riverine ecosystem. To fully understand the role of Trichoptera, it was necessary to investigate life histories, abundance, distribution, and microhabitat selection of dominant species. In selected habitats, particularly riffle areas, certain trichopteran species were the most prevalent taxa in the benthos. Differential response of Trichoptera to temporal, thermal, and trophic parameters manifest along altitudinal gradients and in regulated stream sections, provided considerable insight into the structure and function of the Flathead River macroinvertebrate community.

2. The Flathead Basin is dominated by several northwest-southeast longitudinally oriented mountain ranges separated by deep, broad valleys. High mountain spring snowmelt generally results in runoff discharge 10 to 100 times mean low flow, depending upon climatic variation. The annual flood excavates and redistributes sediments and detritus buried in the substrate. Organic carbon flux over the annual cycle maximized during the runoff period reaching a maximum of 7.68 mg l^{-1} of particulate organic matter, as C, in the seston,

During low flow, minute quantities of POM, as low as 0.033 mg l^{-1}, were recorded. Thermal criteria generally increased along the longitudinal gradient of the lotic environment. Trail Creek, a tributary of the North Fork, had an annual temperature summation of 1900 degree-days. The North and Middle Forks had 2300 and 2400 degree-days, respectively.

3. Stream regulation in the South Fork has resulted in profound environmental changes in downstream reaches. Significant alteration of the annual hydrographic pattern and concommittant redistribution of detritus and sediments were a direct result of impoundment. Hypolimnion release from Hungry Horse Dam flattened the annual temperature regime in the South Fork; annual temperature summation was 1600 degree-days. The Mainstream River, which receives the waters of the regulated South Fork, also has been significantly influenced by the hypolimnial discharge. Annual thermal regime was reduced to 2050 degree-days from an expected 2600 degree-days. The diurnal fluctuation in discharge caused downstream displacement of sloughed periphyton, thus increasing large particulate organic matter in the seston.

4. The Trichoptera community in the Flathead Rivers was composed of 36 species in 9 families. Larvae were consistently present on the river bottom, frequently more than 1000 individuals m^{-2}, at all sampling locations. Adults were occasionally abundant during emergence events. However, compared to results of studies from other rivers, standing

crops of caddisflies were comparatively low in the Flathead Rivers.

5. Life histories for 6 species and bionomic information for all but a few very infrequently collected species were documented. Major growth occured during fall and spring periods of maximum autochthonous productivity and less rigorous climatic and hydrographic stress.

6. Five species of hydropsychid larvae dominated the net-spinning collector trophic functional group in lotic environments. *Parapsyche elsis* was found only in low order streams. *Arctopsyche grandis* replaced *P. elsis* as the dominant hydropsychid in 3rd and 4th order tributary creeks. *Symphitopsyche cockerelli*, *S. oslari*, and *Hydropsyche occidentalis* became the most numerous hydropsychid larvae in the 5th order main tributary rivers, although *A. grandis* remained an important component in these segments. In the Mainstream River, below the confluence of the regulated South Fork, *A. grandis* larvae were unexpectedly numerous and dominated their trophic functional group. *S. cockerelli*, *S. oslari*, and *H. occidentalis* were infrequently collected. Hydropsychid community composition in the Mainstream was similar to that observed in 4th order tributary creeks. I concluded that decreased annual thermal regime and increased large particulate organic matter resulting from hypolimnion discharge acted as a reset mechanism of the River Continuum.

7. *A. grandis* was found in two distinct phenotypic populations at all stations sampled. Larvae with complete dark

head coloring were all females. Larve with a distinctly stripped head pattern were males and females. A correlation existed between relative abundance of each phenotype and availability of interstitial spaces within the rubble substrata. The all-female phenotype selected areas with large interstitial space. The male and female phenotype were more common in tightly compacted substrata. Food items selected varied both between larval phenotypes and between sites, indicating phenotypic differentiation in food habits as well as a natural variability of available food items in the environment. Presence of the all-female phenotype appeared to increase resource utilization and total species fecundity, thereby enhancing species fitness.

8. *Brachycentrus americanus* larvae, which filter large particulate organic matter from the river seston, occured primarily in the large main tributary and Mainstream rivers. Larvae preferred areas of nonturbulent flow and were contageously distributed. Large concentrations of larvae were occasionally observed along sticks or tree roots protruding from the substrata. *B. americanus* apparently had a univoltine life cycle, however two distinct cohorts were evident. Cohort 1 came from eggs deposited in Jun.. Larvae of this cohort grew during late summer and autumn. Larvae overwintered in late instars and emerged in Jun.. The second cohort came from eggs deposited in Aug. and Sep. and first appeared as early instar larvae in autumn. Larvae overwintered in early instar

and grew to later instar larvae during spring and early summer. Adults of Cohort 2 emerged during the late summer. The two cohorts operated as independent functional units; growth was closely associated with the biannual maxima of autotrophic production.

9. Dicosmoecus gilvipes was the largest caddisfly to occur in the Flathead Rivers. D. gilvipes had a two year life cycle; most growth occured during the summer of the first year. In late autumn, late instar larvae attached the anterior opening of their case to the underside of small boulders and entered an overwinter diapause. After the winter diapause, late instar larvae became active during late spring and early summer. In late summer, second year class larvae attached their case a second time to the underside of small boulders and entered a prepupa diapause. Diapause continued for four to six weeks prior to metamorphosis. Adults emerged during the fall with peak activity in Oct.. Other studies of D. gilvipes have reported a univoltine life cycle. Apparently the Flathead Rivers provide either insufficient annual temperature summation or food quantity for a univoltine life cycle.

10. Temperature, current/substrate factors, and food type, quantity, and quality directly control biota composition and processes in running water ecosystems. Many recent conceptualizations of stream systems have emphasized the types, sources, fates, and quality of organic substances (Cummins, 1974;

Wallace, Webster, and Woodall, 1977; McIntire and Colby, 1978; Minshall, 1978; Cummins and Klug, 1979). However, most of this work has involved unaltered, low order stream systems. Little is known of the autotrophy/heterotrophy balance (P/R) or organic quality/consumer relationships in mid-sized rivers. Even less is known of the influence stream regulation may have on primary producers, detritus, dissolved organics, and their nutritive content. This is particularly significant since the great majority of the major river systems throughout the world have been dammed (Ward and Stanford, 1979). Future research should continue to assess the functional relationship of the macroinvertebrate community. However, as life histories of dominant invertebrates are elucidated, emphasis should be directed toward analysis of the rates of gross primary production, community respiration, storage/processing, and export of organic matter, and the nutritive quality of organic matter, particularly as influenced by stream regulation.

LITERATURE CITED

Alstad, D. N. 1980. Comparative biology of the common Utah Hydropsychidae (Trichoptera). Amer. Midl. Nat. 103(1): 167-174.

Anderson, N. H. 1967. Biology and downstream drift of some Oregon Trichoptera. Can. Ent. 99: 507-521.

Anderson, N. H. 1976. The distribution and biology of the Oregon Trichoptera. Technical Bulletin No. 134, Agricultural Experimental Station, Oregon State University, Corvallis, Oregon.

Anderson, N. H. and J. R. Bourne. 1974. Bionomics of three species of glossosomatid caddis flies in Oregon (Trichoptera: Glossosomatidae). Can. J. Zool. 52: 405-411.

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

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

Anderson, N. H. and J. L. Wold. 1972. Emergence trap collections of Trichoptera from an Oregon stream. Can. Ent. 104: 189-201.

Banks, N. 1900. New genera and species of Nearctic neuropteroid insects. Trans. Amer. Ent. Soc. 26: 239-259.

Baumann, R. W., A. R. Gaufin and R. F. Surdick. 1977. The stoneflies (Plecoptera) of the Rocky Mountains. Mem. Am. Ent. Soc. 31. 208 pp.

Cloud, T. J. and K. W. Stewart. 1974. Seasonal fluctuations and periodicity in the drift of caddisfly larvae (Trichoptera) in the Brazos River, Texas. Ann. Entomol. Soc. Amer. 67: 805-811.

Coulter, J. D. 1980. Population dyanmics of macrobenthos in a regulated stream, 1970 and 1978. M. S. Thesis, North Texas State University, Denton, Texas.

Cummins, K. W. 1964. Factors limiting the microdistribution of larvae of the caddisflies Phycnopsyche lepida (Hagen) and Pycnopsyche guttifer (Walker) in a Michigan stream (Trichoptera: Limnephilidae). Ecol. Monogr. 34(3): 271-295.

Cummins, K. W. 1973. Trophic relations of aquatic insects. Annu. Rev. Entomol. 18: 183-206.

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

Cummins, K. W. 1975a. The ecology of running waters; theory and practice, pp. 227-293. IN: "Proc. Sandusky River Basin Symposium". D. B. Baker, W. B. Jackson and B. L. Prater, Eds., Int. Joint Comm., Int. Ref. Gp. Great Lakes Pollution from Land Use Activities, 1976: 653-346, U. S. Govt. Printing Office, Washington, D. C.

Cummins, K. W. 1975b. Macroinvertebrates, p. 170-198. IN: B. A. Whitton (Ed.) "River Ecology". University of California Press, Berkeley, California.

Cummins, K. W. 1979. The natural stream ecosystem, p. 7-24. IN: J. V. Ward and J. A. Stanford (Eds.) "The Ecology of Regulated Streams". Plenum Press, New York.

Cummins, K. W. and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Annu. Rev. Ecol. Syst. 10: in press.

Cushing, C. E. 1963. Filter-feeding insect distribution and planktonic food in the Montreal River. Trans. Amer. Fish. Soc. 92: 216-219.

Douglas, B. 1958. The ecology of the attached diatoms and other algae in a stony stream. Ecol. 46: 295-322.

Edington, J. M. 1968. Habitat preference in net-spinning caddis larvae with special reference to the influence of running water. Ecol. 37: 675-692.

Fisher, S. G. and G. B. Likens. 1973. Energy flow in Bear Brook, New Hampshire: An integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43: 421-439.

Flint, O. S. 1966. Notes on certain Nearctic Trichoptera in the Museum of Comparative Zoology. Proceedings of the United States Natural Museum 118(3530): 373-389.

Fraley, J. J. 1979. Effects of elevated stream temperatures below a shallow reservoir on a cold water macroinvertebrate fauna. p. 257-272. IN: J. V. Ward and J. A. Stanford (Eds), "The Ecology of Regulated Streams". Plenum Press, New York.

Gallepp, G. W. 1974. Diel periodicity in the behavior of the caddisfly, *Brachycentrus americanus* (Banks). Freshwat. Biol. 4: 193-204.

Gallepp, G. W. 1977. Responses of caddisfly larvae (Brachycentrus spp.) to temperature, food availability and current velocity. Amer. Midl. Nat. 98: 59-84.

Gaufin, A. R., W. E. Ricker, M. Miner, P. Milam and R. A. Hays. 1972. The stoneflies (Plecoptera) of Montana. Trans. Amer. Ent. Soc. 98: 1-161.

Gause, G. F. 1934. The struggle for existence. Williams & Wilkins. Baltimore, Maryland.

Givens, D. R. 1976. A synopsis of the western Arctopsychinae (Trichoptera: Hydropsychidae). M. S. Thesis. 117 pp. Central Washington State College.

Gordon, A. E. and J. B. Wallace. 1975. Distribution of the family Hydropsychidae (Trichoptera) in the Savannah River basin of North Carolina, South Carolina and Georgia. Hydrobiologia 46: 405-423.

Grafius, A. and N. H. Anderson. 1979. Population dynamics, bioenergetics, and role of Lepidostoma quercina Ross (Trichoptera: Depidostomatidae) in an Oregon Woodland Stream. Ecology 60: 433-441.

Grant, P. R. and R. J. Mackay. 1969. Ecological segregation of systematically related stream insects. Can. J. Zool. 47: 691-694.

Gumtow, R. B. 1955. An investigation of the periphyton in a riffle of the West Gallatin River, Montana. Trans. Amer. Microsc. Soc. 74: 278-292.

Haddock, J. D. 1977. The effects of stream current velocity on the habitat preference of a net-spinning caddisfly larvae, Hydropsyche oslari Banks. Pan Pac. Entomol. 53: 169-174.

Hauer, F. R., E. G. Zimmerman and J. A. Stanford. 1979. Preliminary investigation of distributional relationships of aquatic insects and genetic variation of a fish population in the Kintla drainage, Glacier National Park, Montana. IN: Proceedings of the Second Conference of Scientific Research in the National Parks; American Institute of Biological Sciences, Arlington, Virginia.

Huston, M. 1979. A general hypothesis of species diversity. Amer. Natur. 113: 81-101.

Hutchinson, G. E. 1961. The paradox of the plankton. Amer. Natur. 95: 137-145.

Hynes, H. B. N. 1970. The Ecology of Running Waters. Univ. of Toronto Press, Toronto, Ontario, Canada.

Lehmkuhl, D. M. 1970. A North American trichopteran larva which feeds on freshwater sponges (Trichoptera: Leptoceridae; Porifera: Spongillidae). Amer. Midl. Nat. 84: 278-280.

Lloyd, J. T. 1921. The biology of North American caddisfly larvae. Bulletin of the Lloyd Library No. 21, Entomological Services No. 1.

Mackay, R. J. 1978. Larval identification and instar association in some species of Hydropsyche and Cheumatopsyche (Trichoptera: Hydropsychidae). Ann. Entomol. Soc. Amer. 71: 499-509.

McIntire, C. D. and J. A. Colby. 1978. A hierarchical model of lotic ecosystems. Ecol. Monogr. 48: 167-190.

Mecom, J. O. 1972. Feeding habits of Trichoptera in a mountain stream. Oikos 23: 401-407.

Mecom, J. O. and K. W. Cummins. 1964. A preliminary study of the trophic relationships of the larvae of Brachycentrus americanus (Banks) (Trichoptera: Brachycentridae). Trans. Amer. Microsc. Soc. 83: 233-243.

Menzell, D. W. and F. R. Vaccaro. 1964. The measurements of dissolved and particulate carbon in sea water. Limnol. Oceanogr. 9: 138-142.

Merritt, R. W. and K. W. Cummins (EDS.). 1978. "An Introduction to the Aquatic Insects of North America". Kendall/Hunt, Dubuque, Iowa. 441 pp.

Milne, L. J. 1934-36. "Studies of North American Trichoptera." Pt. 1 1934: 1-19; Pt. 2 1935: 20-55; Pt. 3 1936: 56-128. Cambridge, Massachusetts.

Milne, M. J. 1938. The "metamorphotype method" in Trichoptera. J. New York Ent. Soc. 46: 435-437.

Minshall, G. W. 1968. Community structure in natural stream systems, p. 2-3. IN: The Stream Ecosystem, An American Association for the Advancement of Science Symposium. Boston, December 29, 1969. Technical Report No. 7, Institute of Water Research, Michigan State University, East Lansing, Michigan.

Minshall, G. W. 1978. Autotrophy in stream ecosystems. BioScience 28: 767-771.

Nielsen, A. 1948. Postembryonic development and biology of the Hydroptilidae. Kgl. Danske Vidensk. Selsk. Biol. Skr. 5(1):

Nimmo, A. P. 1971. The adult Rhycophilidae and Limnephilidae (Trichoptera) of Alberta and eastern British Columbia and their postglacial origin. Quaest. Ent. 7: 3-234.

Nimmo, A. P. 1977. The adult Trichoptera (Insecta) of Alberta and eastern British Columbia, and their postglacial origins. The familes Rhyacophilidae and Limnephilidae. Supplement 1. Quaest. Ent. 13: 25-67.

Novak, K. 1960. Entwicklung and diapause der Kocherfliegenlarven Anabolia furcata Br. (Trichoptera) Cas. Cs. Spol. Ent. 57(3): 207-212.

Odum, H. T. 1956. Primary production in flowing waters. Limnol. Oceanogr. 1: 102-117.

Olson, F. C. W. 1964. The survival value of fish schooling. Jour. Cons. Perm. Int. Explor. Mer. 29: 115-116.

Pearson, W. D. and R. H. Kramer. 1972. Drift and production of two aquatic insects in a mountain stream. Ecol. Monog. 42(3): 365-385.

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

Pianka, E. R. 1974. Niche overlap and diffuse competition. Proceedings of the National Academy of Science, U. S. A. 71: 2141-2145.

Pielou, E. C. 1975. Ecological Diversity. John Wiley and Sons, New York.

Potter, D. S. and J. A. Stanford. 1975. Influence on the plankton communities of oligotrophic Flathead Lake. Verh. Int. Verein. Limnol. 19: 1790-1797.

Powell, J. R. and C. E. Taylor. 1979. Genetic variations in ecologically diverse environments. Am. Sci. 67: 590-596.

Resh, V. H. 1976. Life histories of coexisting species of Ceraclea caddisflies (Trichoptera: Leptoceridae): the operation of independent functional units in a stream ecosystem. Can. Ent. 108: 1303-1318.

Ross, H. H. 1944. The caddis flies, or Trichoptera, of Illinois. Bull. Illinois Nat. History Surv., No. 23.

Ross, H. H. 1946. A review of the Nearctic Lepidostomatidae. Ann. Ent. Soc. Amer. 39: 265-291.

Ross, H. H. 1956. Evolution and Classification of the Mountain Caddisflies. University of Illinois Press, Urbana, Illinois.

Ross, H. H. and J. D. Unzicker. 1977. The relationships of the genera of American Hydropsychinae as indicated by phallic structures (Trichoptera, Hydropsychidae). J. Georgia Ent. Soc. 12(4):: 298-312.

Scheffé, H. 1959. The analysis of variance. John Wiley and Sons Inc., New York, New York.

Sedell, J. R., R. J. Triska, J. D. Hall, N. H. Anderson and J. H. Lyford. 1973. "Sources and Fates of Organic Inputs in Coniferous Forest Stream". Contribution Coniferous Forest Biome No. 66. IBP, Oregon State University, Corvallis, Oregon.

Sedell, J. R., F. J. Triska and N. S. Triska. 1975. The Proceeding of conifer and hard wood leaves in two coniferous forest streams. I. Weight loss and associated invertebrates. Verh. Int. Verein. Limnol. 19: 1617-1627.

Shapas, T. J. and W. L. Hilsenhoff. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera, and Trichoptera. Gr. Lakes Ent. 9: 175-188.

Smith, S. D. 1968a. The Arctopsychinae of Idaho (Trichoptera: Hydropsychidae). Pan Pac. Ent. 44: 102-112.

Smith, S. D. 1968b. The Rhyacophila of the Salmon River drainage of Idaho with special reference to larvae. Ann. Ent. Soc. Amer. 61(3): 655-674.

Stanford, J. A. 1975. Ecological studies of Plecoptera in the upper Flathead and Tobacco Rivers, Montana. Ph.D. thesis, University of Utah, Salt Lake City, Utah.

Stanford, J. A. and A. R. Gaufin. 1974. Hyporheic communities of two Montana rivers. Science 185: 700-702.

Stanford, J. A. and A. R. Gaufin. In press. Ecology and life histories of Plecoptera in the Flathead Rivers, Montana. Archiv fur Hydrobiol., Supplement.

Stanford, J. A. and F. R. Hauer. 1978. Preliminary observations on the ecological effect of flow regulation in the Flathead River, Montana. Report to U. S. Bureau Reclamation, Boise, Idaho.

Stanford, J. A., F. R. Hauer and T. J. Stuart. 1979. Annual report of work completed during 1978-1979 on limnology of Flathead Lake-River Ecosystem, Montana. p. 155. Annual Report, Flathead Basin Environmental Impact Study, Kalispell, Montana.

Stanford, J. A. and D. S. Potter. 1976. Limnology of the Flathead Lake-River ecosystem, Montana: a perspective. IN: "Proc. of the Symposium on Terrestrial and Aquatic Ecological Studies of the Northwest". R. Soltero, ed., Eastern Washington State College Press, Cheney.

Stanford, J. A. and J. V. Ward. 1979. Stream regulation in North America. p. 215-236. IN: "The Ecology of Regulated Streams". J. V. Ward and J. A. Stanford, eds., Plenum Press, New York.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell and C. E. Cushing. 1979. The river continuum concept. Can. Jour. Fish. Aq. Sci. 37: 130-137.

Vorhies, C. T. 1909. Studies of the Trichoptera of Wisconsin. Trans. Wisconsin Acad. Sci. 16: 647-738.

Wallace, J. B. 1975. Food partitioning in net-spinning Trichoptera larvae: Hydropsychidae venularis, Cheumatopsyche etrona, and Macronema zebratum (Hydropsychidae). Ann. Ent. Soc. Amer. 68: 463-472.

Walton, I. 1653. "The Complete Angler". London: printed by T. Maxey for R. Marriot.

Ward, J. V. and R. A. Short. 1978. Macroinvertebrate community structure of four special lotic habitats in Colorado, U. S. A. Verh. Int. Verein. Limnol. 20: 1382-1387.

Ward, J. V. and J. A. Stanford (Eds.). 1979. "The Ecology of Regulated Streams". Plenum Press, New York.

Webster, J. R. 1975. Analysis of Potassium and Calcium dynamics in stream ecosystems on three southern Appalachin watersheds of contrasting vegetation. Unpublished Ph.D. thesis, University of Georgia, Athens.

Whitton, B. A. 1975. River Ecology. University of California Press. Berkeley, California.

Wiens, J. A. 1977. On competition and variable environments. Am. Sci. 65: 592-597.

Wiggins, G. B. 1973. A contribution to the biology of caddisflies (Trichoptera) in temporary pools. Life Sciences Contribution, Royal Ontario Museum. 88 pages.

Wiggins, G. B. 1977. Larvae of the North American Caddisfly Genera (Trichoptera). University of Toronto Press, Toronto, Ontario, Canada.

Wiggins, G. B. and R. J. Mackay. 1978. Some relationships between systematics and trophic ecology in nearactic aquatic insects, with special reference to Trichoptera. Ecology 59(6): 1211-1220.

Wojtalik, T. A. and T. F. Waters. 1970. Some effects of heated water on the drift of two species of stream invertebrates. Trans. Am. Fish. Soc. 99: 782-788.