Ecology of aquatic insects in the Gallatin River drainage
by Daniel L Gustafson

A thesis submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biological Sciences
Montana State University

Abstract:

The aquatic insect fauna of the Gallatin River drainage in southwest Montana, USA includes 58 species of Ephemeroptera, 67 species of Plecoptera and 97 species of Trichoptera. These species, as well as few species of Coleoptera and Diptera, were characterized with respect to their longitudinal pattern of abundance, type of life cycle, habitat preferences, general habits, trophic preferences, seasonal abundance and body growth..

Insect life history patterns generally follow taxonomic lines, but are not fully predictable based on taxonomic affinities alone. Closely related species usually have an obvious difference in one aspect of their life history.

Spatial, longitudinal and temporal patterns of community organization were examined using a variety of multivariate statistical techniques. Dominant patterns were discussed in terms of the species involved and pertinent environmental variables.

The spatial structure of the benthic community in the lower parts of the river is temporally variable and most strongly determined by current velocity. The community during the summer has more species occurring in shallow, slow water than during the remainder of the year. During mid-summer the community occurring on individual boulders in swift current is dependent upon the degree of cluttering on the rock, while by early spring these rocks have very similar communities. Spring flooding serves as an important reset mechanism by cleaning the boulders of accumulated debris.

Community organization along the course of the mainstem indicated three distinct faunal regions corresponding to the lower valley, middle canyon and upper meadow areas of the river. Community organization within the tributary streams revealed several sets of replicated faunas, which are determined primarily by stream size and elevation, but influenced also by the openness of the drainage. Taylor Creek has more influence on the lower river than does the upper mainstem.

Patterns of temporal community organization in the lower parts of the Gallatin River are largely determined by the life cycles of the insects. Temporary migration from shallow water during the winter, and responsiveness to annual variation in flow and temperature, are also involved.

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IN THE GALLATIN RIVER DRAINAGE

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APPROVAL

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Daniel L. Gustafson

This thesis has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the College of Graduate Studies.

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TABLE OF CONTENTS

TABLE OF CONTENTS-*Continued*

Page

LIST OF TABLES

LIST OF TABLES-*Continued*

LIST OF TABLES-*Continued*

LIST OF FIGURES

LIST OF FIGURES-*Continued*

LIST OF FIGURES-*Continued*

ABSTRACT

The aquatic insect fauna of the Gallatin River drainage in southwest Montana, USA includes 58 species of Ephemeroptera, 67 species of Plecoptera and 97 species of Trichoptera. These species, as well as few species of Coleoptera and Diptera, were characterized with respect to their longitudinal pattern of abundance, type of life cycle, habitat preferences, general habits, trophic preferences, seasonal abundance and body growth..

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INTRODUCTION

Most aquatic insect species are very poorly known taxonomically and biologically. The majority of species records are either purely taxonomic or are useful only for describing the geographic range of the species, which is itself very incompletely known for most species. The lack of basic life history data for aquatic insects is due in part to gaps in taxonomic information, but many taxa, which have been taxonomically well known for some time, still have little life history information available. The large number of species, relative to the number of researchers is an important factor.

Aquatic insect communities in river systems are usually characterized by relatively stable assemblages of many species that are strongly organized along the course of the river from the headwaters to the mouth. Stream communities at any longitudinal site along the river show further structure that is both temporal and spatial, especially in terms of water depth, current velocity and substrate size. The sequence of species that is encountered when proceeding from the headwaters to the mouth has been described for a few streams, as has the seasonality of adult emergence at some sites. These studies are usually based only on the adults and consider only a narrow taxonomic group and they are, to that extent, limited in the information they provide on the dynamics or structure of invertebrate communities.

The present investigation is a study in breadth of the species of Ephemeroptera, Plecoptera and Trichoptera and their community structure within the Gallatin River drainage in southwest Montana, USA. A few species of Diptera and Coleoptera are also included because of their occurrence in the quantitative data sets. The seasonality of occurrence of the various life history stages, longitudinal zonation, spatial population structure, longitudinal population structure and seasonal population dynamics were investigated simultaneously with body growth, feeding habits and microhabitat preference. Data collected from June 1981 through August 1990 are included. The core of the quantitative sampling was done during 1984 and 1985. By that time, many of the common species in the drainage were already well known.

A very large amount of observational data is presented, analyzed and discussed. The primary purpose is to find and describe regularities in the various aspects of species life histories and in the patterns of species abundances. The approach is descriptive and statistical as opposed to experimental or model-based. It is intended to generate hypotheses more than to test them. It is also intended to lay a foundation for future hypothesis testing. Hypothesis testing in ecology generally requires experimentally controlled conditions. It is about such experiments that Pielou (1977) writes:

> *But it is impossible to duplicate, in the laboratory, communities whose member species vary enormously in respect of such characteristics as size, longevity, phenotypic plasticity, generation time, fertility, morbidity, mortality, and motility. It is communities such as these, which constitute most of the biosphere, that should engage the lion's share of ecologists' collective attention.*

Answering narrowly focused questions concerning communities in a laboratory system is very much easier than applying the answers, so obtained, back to the natural community. Many modern ecologists are unaware of the enormous number of invertebrate species present in most communities and of the great plasticity or specificity that the individuals, and that the species themselves, sometimes exhibit. Experimental studies conducted without sufficient knowledge of the taxonomy and natural history of the organisms are often a waste of time.

The data base provided by this study is sufficiently large and diverse that many hypotheses may be supported or refuted by selective use of the data. That is, with enough sites and enough species, many patterns, which might be postulated based on some hypothesis, will be found, as will exceptions. For this reason, truly testable ecological hypotheses must be so specific that they may be of little general interest.

This thesis is organized as a single study. A multi-part report may have served better to bring related material closer, but would have hindered comparisons and integration of the various topics. The Methods section is divided into a number of small parts, thus allowing easy access to information, as needed, for interpreting any of the results. Results and Discussion are combined into a single section to avoid excessive separation of the presentation of data and its interpretation. This large section is organized into two major divisions, species ecology and community ecology.

Species ecology is organized taxonomically by order and family and summarizes much of the information available about many of the species of aquatic insects known from the Gallatin drainage. Community ecology is organized into three parts, spatial structure, longitudinal structure and temporal structure. Spatial community structure contains two data sets from the same site; the first addressing mid-summer spatial organization and the second addressing early-spring spatial organization. Spatial community structure is used here to refer to the organization of species across the expanse of a pool riffle sequence in response to variation in substrate size and water depth and velocity. Longitudinal community organization likewise contains two data sets; the first addressing community organization along the mainstem of the river and the second addressing community organization in the tributary streams as well as the mainstem of the river. Longitudinal structure is here distinguished from spatial structure. Temporal community organization is examined at a single site with a single large data set. The Conclusions and Perspectives For Further Work sections are based on all aspects of this study.

Species Ecology

A few species of aquatic insects have been studied in detail, usually only at a single site within a drainage and not in the context of the community within which they occur. Many studies which involve the aquatic stages of insects do not achieve identification to the species level and are therefore of limited comparative value. Aquatic insects are very rarely identified to species in the field. The ecology of the species will remain poorly known until this is rectified. Well over half of the total efforts in this study were purely taxonomic, yet this is not a taxonomic study.

Taxonomic revisions usually reveal the presence of previously undescribed species, synonymous names and inaccuracies in the morphological characters previously used to recognize the species. Unfortunately, previous ecological work cannot be readily interpreted unless the identity of the species can be verified. Misidentifications, of course, have the same effect even with a stable taxonomy. Undoubtedly, due to misapplied names, many species appear more widespread and variable in the literature than they actually are.

The analysis of species communities is highly dependent upon the species being taxonomically well known. However, synonymous names, undescribed species, even cryptic ones, can be detected in detailed ecological studies. Behavior, seasonality, longitudinal zonation and habitat utilization provide many easily recognized and important characters not available in museum-based studies. Recognition of the conspecificity, or lack of it, with populations outside the study area is unlikely to be achieved in ecological studies. These are more easily amended later, but make the literature more difficult to interpret.

Community Ecology

When the interactions between species are complex, numerous and strong, communities are expected to respond to environmental gradients many species at a time.

These species assemblages may be more obvious than the underlying environmental gradient itself. It is for this reason that terrestrial habitats are more frequently characterized by the occurrence of plant species, than by environmental measures such as elevation, rainfall and temperature. The most obvious patterns in stream communities include spatial organization at a site, temporal organization at a site and longitudinal organization along the course of the stream.

The spatial structuring of lotic insect communities is usually studied in terms of various substrate relationships, and is less frequently studied than either longitudinal or temporal community structure. The most common variables examined in these studies, include the amount of aquatic plants, organic debris and silt, substrate composition, size, heterogeneity, texture, pore space, stability, depth and current velocity. The usual data set includes measures of these variables as well as counts of invertebrate species obtained from the area enclosed by some sampling device. Interpretation may be difficult because of the pooled nature of these area-wide samples.

Recent studies of the longitudinal structuring of lotic communities are heavily influenced by the river continuum concept (Vannote *et al.*, 1980). This concept provides a theoretical framework against which field data can be compared. In brief, the river continuum concept recognizes several distinctive ecological features of streams: lack of nutrient cycling, lack of biological succession, ancient origins and continuous heritage which differentiate streams from terrestrial and lentic, freshwater environments. The river continuum concept proposes that stream communities are organized in a way that makes maximal and continuous use of the available resources; and that these resources, in terms of availability and variability, as well as temperature, discharge and substrate characteristics, are strongly organized and predictable along the length of a stream. Downstream communities are thought to adjust to take maximal advantage of the leakage from upstream communities. The river continuum concept predicts patterns in species diversity and trophic structure of the aquatic communities along river courses.

Temporal organization of insect communities in streams is usually based on the seasonality of adults. Adults are frequently the most readily obtainable of the various life history stages, and are by far the most readily identified. However, many species are very secretive as adults. Simultaneous coverage of both adults and larvae is obviously preferable. The seasonality of larval growth and population densities is more ecologically important than is the adult emergence owing to the trophic role of the larvae.

A quantitative description of the variation in spatial, longitudinal and temporal community organization, each as a function of the others, would require a very large sample size. In this study, only a single site was included in all five of the community ecology data sets. At that site, these interactions can be described to some extent by interpolation of the existing data.

METHODS

Study Area

The Gallatin River drainage consists of 3480 km^2 and occupies much of Gallatin county as well as small portions of Madison and Park counties in Montana, and has its headwaters in Yellowstone National Park, Wyoming. The north-flowing drainage spans latitudes 44° 52' to 45° 55' and is centered approximately on longitude 110° 15'. The mainstem of the river begins at Gallatin Lake in Yellowstone National Park and runs 150 km before emptying into the Missouri river just downstream of its source at the junction of the Madison and Jefferson rivers. Elevation within the drainage ranges from 1225 m at its mouth to 3440 m in the Taylor Peaks of the Madison mountain range. The perimeter of the drainage is 380 km long and contains many peaks over 3000 m. The Gallatin drainage is bordered to the west and to the south by the Madison mountain range and the Madison River drainage and to the east by the Gallatin mountain range and the Yellowstone River drainage. The river is briefly characterized as a cold, high-gradient, unregulated Rocky Mountain stream. Dominant substrates are boulders and cobble. Compared to its two neighbors, the Madison and Yellowstone Rivers, it is considerably colder and less productive.

The average discharge from the Gallatin drainage over 71 years is 30.4 m^3/sec (U.S. Geological Survey, 1987). During the first four years of this study, discharge averaged from 121 to 145% of normal. The 1985 water year (October 1, 1984 through September 30, 1985) was only 82% of normal, 1986 was 107% of normal, 1987 was only 71% of normal, and 1988 was 75% of normal. Peak flows normally occur in early June due to snow melt (Figure 1). In the lower parts of the mainstem, high flow during normal years is of sufficient

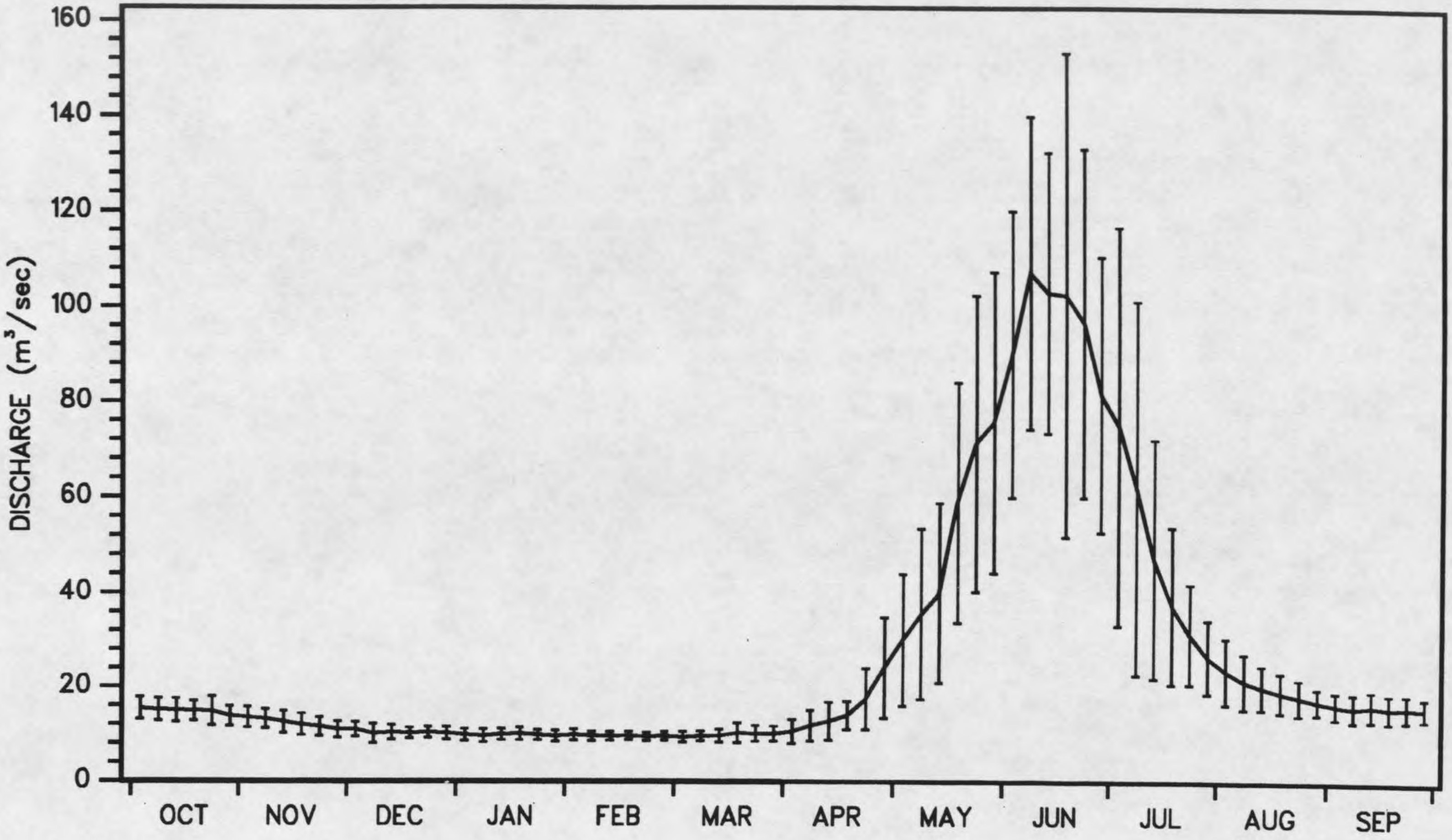

Figure 1. Average discharge of the mainstem of the Gallatin River near the forest boundary based on ten years beginning October 1971, based on U.S. Geological Survey water resources data. Error bars are standard deviations at five day intervals.

magnitude and duration to sort much of the bed material. The substrate left within the stream when high water subsides is made up almost entirely of boulders. The boulders themselves are worn smooth and are generally spherical to ellipsoid in shape. Those portions of the bed sorted to gravel or sand are largely left out of the water during most of the year. During low flow, the depositional areas of the river accumulate silt, sand and organic material only until the next flood and are poorly populated with insects because of their ephemeral nature.

Upstream of Bozeman, the Gallatin River lies very close to US highway 191 and is at many places narrowed or armored to protect the road. Hyalite dam is the only flow-regulation structure within the drainage. Hyalite reservoir is a small mountain reservoir which drains into the East Gallatin River. It has a negligible effect on the lowermost station on the mainstem of the river and has no effect on any of the remaining stations used in the quantitative data sets.

The river upstream of Bozeman is subject to only minor inputs of human contaminants. Irrigation withdrawals, likewise, become significant only downstream of Bozeman. Upstream of Bozeman, annual low flows occur in mid February due to freeze up. Between Bozeman and the confluence of the mainstem with the East Gallatin River, much of the river experiences lowest flow during the summer and is sometimes dewatered entirely due to irrigation withdrawals.

The mainstem of the river and its flood plain are sufficiently wide to allow direct solar irradiation of the stream bed for much of each day. The rocks support abundant diatoms and scattered tufts of the green alga *Cladophora*. Vascular plants and bryophytes are normally absent in the lower parts of the mainstem because of bedload movement and physical scouring. Bryophytes are sometimes abundant in higher parts of the mainstem, where the substrate is more stable. Bryophytes are also common in many of the mountain tributary streams. Aquatic vascular plants occur in some protected springs throughout the drainage and are abundant in spring creeks and ponds across the Gallatin Valley. The dominant elements of the coniferous forest which covers most of the Gallatin drainage include lodgepole pine *Pinus contorta* Dougl. ex Loud., whitebark pine *P. albicaulis* Engelm., Douglas fir *Pseudotsuga menziesii* (Mirb.) Franco, Engelmann spruce *Picea englemannii* Parry ex Engelm. and subalpine fir *Abies lasiocarpa* (Hook.) Nutt.

The present fishes of the Gallatin drainage include as native species: mottled sculpin *Cottus bairdi* Girard, white sucker *Catostomus commersoni* (Lacepede), longnose sucker *C. catostomus* (Forster), mountain sucker *C. platyrhynchus* (Cope), longnose dace *Rhinichthys cataractae* (Valenciennes), mountain whitefish *Prosopium williamsoni* (Girard), arctic grayling *Thymallus arcticus* (Pallas), and cutthroat trout *Oncorhynchus clarki* (Richardson). Arctic grayling and cutthroat trout, however, are now largely absent from the running waters of the drainage and are represented primarily by exotic strains introduced into mountain lakes. Introduced species, which occur in the drainage, include brown trout *Salmo trutta* Linnaeus, rainbow trout *Oncorhynchus mykiss* (Walbaum), golden trout *O. aguabonita* (Jordan) and brook trout *Salvelinus fontinalis* (Mitchill). The extent to which these recent changes in fish species composition have affected the distribution and abundance of invertebrate species is not known.

A few stream names within the drainage require clarification. The Gallatin River itself is sometimes referred to as the West Gallatin River presumably to better distinguish it from the East Gallatin River. This usage may be confused with the West Fork of the Gallatin River and has apparently been so-confused in some published locality data. Here, the West Fork of the Gallatin River is called West Fork Creek. This should not be confused with West Creek in the Squaw Creek drainage. Taylor Fork of the Gallatin River is sometimes used for what is referred to here as Taylor Creek. Hyalite Creek in the Gallatin valley is sometimes called Middle Creek and the lower part of Bozeman Creek is sometimes referred to as Sourdough Creek. Two streams, apparently unnamed are referred to here by the nearest named landmark. Beehive Creek thus drains Beehive basin and Andesite Creek is adjacent to Andesite Peak, both in the Middle Fork of West Fork Creek drainage. All other stream names are as used on 1:62500 scale U.S. Geological Survey maps. Stream order, link magnitude and elevation were also obtained from those maps as was drainage area and stream lengths after the maps were digitized. A first order stream has no tributaries. A second order stream begins at the confluence of two first order streams, a third order stream begins at the confluence of two second order streams, and so on. Stream order changes only when streams of equal order merge together. For example, additional first order streams entering a second order stream have no effect on the order of that stream. Link magnitude is the number of first order streams that occur in a drainage upstream of a site.

Taxonomy

No single reference can provide the taxonomic coverage needed here. Merritt and Cummins (1984) provide an excellent starting point at the genus level, except for adult Trichoptera. Baumann *et al.* (1977) provide very complete coverage of the Plecoptera species within the drainage. For other taxa, the primary literature was intensively used. Over 30,000 pages of taxonomic literature relevant to nearctic Ephemeroptera, Plecoptera, Trichoptera, as well as certain Coleoptera, Diptera, Crustacea and Mollusca, were assembled and indexed by species during this study. This included original species descriptions, reviews, revisions, monographs, regional faunas and reference books. Recent taxonomic revisions, when available, proved to be the most reliable aids in species identification. Use of a number of keys, while consulting the available descriptions, proved far superior to reliance on any single key. In many cases the process of elimination using the original species descriptions was necessary.

Species determinations were predominantly based on the reproductive structures of adult males. Specimens were cleared in hot 10% Potassium hydroxide and slide mounted, when necessary, for identification. The experts listed in the acknowledgments were consulted for confirmation of most of the important identifications which were uncertain. Mistakes that undoubtedly remain are of course my own. Voucher specimens for all species are in my collection, which numbers over 3000 vials and 5000 pinned specimens. Specimens of many species have also been deposited at Montana State University and with the consulted experts.

Qualitative Collecting

Both adults and immatures were sought out using many methods. Many adults were easily obtained with aerial nets or sweep nets, especially near dawn and dusk. Hand picking or aspirating from among shoreline rocks and bridges yielded others. Ultraviolet light traps, funnel traps, and a variety of emergence traps and shoreline pitfall traps were also used. Many shoreline inhabitants were obtained by flooding the shoreline by bailing water onshore with a bucket, netting up the floating debris and extracting it through a Berlese funnel. The use of Berlese funnels also helped obtain some inconspicuous inhabitants of dense aquatic debris. Adult insects were preserved and stored in 70-80 percent ethanol. Mayflies were separately placed into many small vials to help keep specimens more nearly intact, or at least to keep the parts associated.

The core of qualitative aquatic sampling consisted of disturbing the substrate upstream of various aquatic nets. All available substrate types and sizes in all depths and current velocities were sought out. In areas with little or no current, the aquatic net was swept back and forth across the area disturbed. Rapid deployment of the net in such areas is most efficient, as some of the species which occur there rapidly retreat or take refuge deep within the substrate when disturbed.

Gently sieving aquatic samples through a 12 mm sieve, submerged in a bucket, frequently helped reduce the bulk of these samples. Extraction of the rocks, gravel and sand by sedimentation in the same bucket also helped reduce the volume of material, and maintained the specimens in better condition. The extracted gravel was retained because it often contained concentrated Trichoptera larvae with heavy cases, as well as mollusks.

Hand picking from individual rocks, that were removed from the stream, yielded specimens not easily dislodged otherwise. Submerged wood frequently contained many individuals of species rarely encountered otherwise so it was frequently removed from the stream and examined by hand. Many invertebrates were obtained from submerged wood and other dense debris by drying it above a white sheet, forcing some of the hidden occupants from their retreats. Some species of aquatic insects that are rarely encountered during the day, may be found in large numbers at night by using artificial lights. Drift nets set overnight frequently took many specimens of species rarely encountered otherwise.

Immature insects and bulk aquatic samples were preserved with Kahle's fluid and later placed in 70-80 percent ethanol. Bulk aquatic samples were gently sieved underwater through 8.00, 2.36 and 0.417 mm sieves to facilitate laboratory sorting.

Association of Larvae and Adults

The larvae and adults of caddisflies are sometimes easily associated because the adults of most species develop with the larval exuvia remaining in the pupal cocoon. These metamorphotype associations can be obtained directly in the field, frequently in routine collections. Holding the pupae in a damp, cool container until the wings of the pharate adult darken assures that it will be sufficiently mature to be identified. Attempts at rearing Trichoptera starting with the free larvae were seldom successful. The association of known exuvia from metamorphotypes with intact larvae is usually not difficult. The larval case, if present, is very helpful in this regard as it is retained by the pupae.

Stoneflies with dark wing pads collected near shore, are usually easily reared, if kept cool in a Styrofoam cup containing some damp paper or moss. Mayflies could sometimes be reared in the field in half submerged containers, especially during periods of decreasing flows. Rearing in a refrigerated aquarium in the lab yielded many more associations for mayflies, as the subimagoes could be promptly removed to a dry Styrofoam cup so as to prevent their accidental drowning before the final molt. Stoneflies were very easily reared in refrigerated aquaria. Mayfly nymphs are frequently found in the process of molting to the subimago in the field. In this situation the association can be made by rearing the subimago as above while retaining the cast skin of the nymph. Extreme care in handling live subimagoes is necessary, especially during hot weather. Circumstantial association of emerging subimagoes with drifting exuviae or those found on nearby shoreline rocks frequently proved erroneous, unless the fauna at the site was already very well accounted for.

Life History Determination

Many populations of immature insects were sampled repeatedly over time, sorted as well as possible, and retained. Most of these were eventually reared to adults. Once reared, the series of samples were resorted, starting from the exuviae of the reared larvae and working backwards. Several years were sometimes required to obtain adequate knowledge of a particular species to allow its collection in sufficient numbers and to associate the immature stages with the adults. Some of these life history studies are not yet completed. Life histories constructed from this type of data may well miss details involving delayed or variable egg hatching, but contain the important aspects of the life cycle with regard to community interactions that might occur.

The serial association of life history stages identified many errors in the original sorting and helped achieve recognition of the species at early instars. Microscopic examination of the shed or cleared exuviae frequently provided many characters useful in species recognition. Field identification of many species was achieved by sorting the species in the field and checking them later in the lab.

Head capsule widths were measured using an ocular micrometer in a dissecting microscope, with magnification appropriate to the size of the specimen. The larval instars of Trichoptera, Diptera and Coleoptera are generally easily recognized when all instars are simultaneously available for study. The instar number of individual Ephemeroptera and Plecoptera nymphs cannot be precisely determined unless the individuals are reared from eggs. The final instar is, however, always recognizable when compared to mature final instars.

Material for the life history analyses was obtained primarily from the 13 sites located on Figure 2 and described in Table 1. These were selected from the much larger number of sites visited, because they contain most of the species known from the drainage, span the longitudinal range of most of these species, and are easily accessible.

Table 1. Frequently visited sampling stations used for determining life histories, field rearing and adult trapping listed by station number and giving for each station the stream order (SO), distance from the headwater (km), link magnitude (LM), elevation (m) and drainage area (km^2).

#	Name and description	SO	Dist.	LM	Elev.	Area
1	Gallatin R. below Logan	6	149.7	578	1244	4649.0
2	Gallatin R. west of Bozeman	6	113.5	461	1439	2498.8
3	Gallatin R. above Spanish Creek	6	91.7	394	1585	1922.0
4	Gallatin R. below Yellowstone Park	5	37.8	72	2024	467.5
5	East Gallatin River	4	32.9	104	1433	439.8
6	Bridger Creek	4	24.3	33	1494	163.0
7	Bozeman Creek (lower)	3	16.0	18	1646	73.4
8	Bozeman Creek (upper)	3	8.4	13	1829	42.7
9	Hyalite Creek (lower)	3	24.2	22	1707	126.0
10	Hyalite Creek (upper)	3	15.3	18	1930	93.4
11	East Hyalite Creek	3	10.2	6	2043	26.0
12	West Hyalite Creek	2	8.5	7	2073	29.1
13	Blackmore Creek	1	3.6	1	2134	7.2

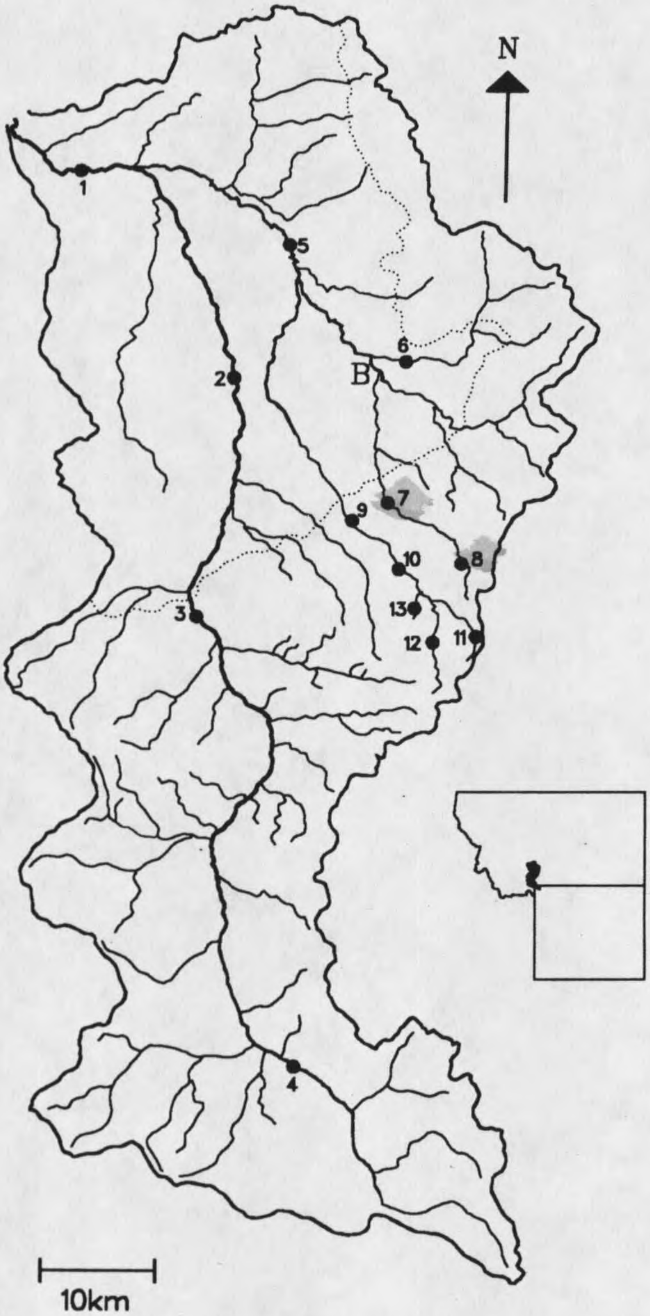

Figure 2. The Gallatin River drainage showing the locations of the 13 most important stations used in species life history studies. These are coded by the station number identified in Table 1. The dotted line indicates the approximate downstream limit of the forest. The letter "B" marks the location of the city of Bozeman.

Food Habits

Foregut contents of representatives of most of the species that were taken as larvae were examined under a compound microscope. Only specimens killed and preserved with Kahle's solution immediately upon removal from the stream were used for this purpose. For most species, specimens spanning the longitudinal range of the species and from several collection dates were used. The percentage of the gut contents consisting of diatoms, filamentous algae, bryophytes, vascular plant fragments, animal parts and fine detritus was roughly estimated by volume for each of the individuals dissected. The goal was to classify the species into major trophic categories. Many species were observed while alive, either in the field or in the lab, either in simple holding trays or in a more naturally arranged, refrigerated aquarium, to further substantiate food preferences.

Spatial Data Sets

Spatial community structure was examined quantitatively with two data sets collected at a single site on the mainstem of the river directly west of Bozeman. The primary goals were to identify patterns of species abundances related to position within a pool-riffle sequence, and to relate these patterns to spatially variable physical variables, primarily water depth, current velocity, and substrate size.

The nature of the substrate in the mainstem of the Gallatin River immediately suggested sampling from individual rocks. Single-rock samples are attractive to community ecologists, as the individuals on a single rock are subject to more direct interactions with each another than are those on different rocks. If only the surface layer of rocks is considered, any individual organism is associated with a single rock at a time. The individual rock thus constitutes the habitat while positions on the rock constitute microhabitat. The attractiveness of a rock to the individuals of the various species is undoubtedly a complex function of the physical conditions prevailing at the site of the rock, primarily water depth and velocity, the size and texture of the rock as well as the biological assemblage already present there.

Single-rock sampling provides no straightforward method for calculation of total, area-wide densities; but, then, area-wide samples seldom provide that information with any degree of reliability, based on comparisons with adult emergence.

The details of sampling a single rock necessarily vary somewhat with the circumstances of the rock. The intent was always to obtain all of the invertebrates associated with the rock, while avoiding those around the rock, but in fact, oriented toward other rocks. In shallow water with moderate to fast current, rocks were simply approached from downstream and lifted gently into a plastic bucket, while yielding to the current to minimize turbulence. Underwater observation of the procedure and the use of variously positioned back-up nets indicated this method was very efficient at capturing the insects living on the rock, and that it dislodged mostly those living on the upper surface of the rocks below. Those species which are in part lost from the rock, tend either to be small in size and both very abundant and variable or rather large sized, but very rare. In either case the loss is not very important to the aims of this study. Many species are taken exactly as they occur with these samples and are usually under-represented in samples that do not include such a thorough treatment of the individual rocks.

The use of a downstream net to hold the rock as it was lifted from the water proved unsatisfactory for two reasons. The net captured many organisms living around the rock, but not on it. The net also actually captured fewer of the individuals living on the rock than did the net-free method because of the loss of many small individuals who were prone to burrow through the net while alive. Finer nets performed even more poorly because of the great turbulence and backwash created by a fine net in swift current.

The individuals living on rocks in areas of little or no current were much less inclined to remain on a rock while it was lifted from the water. Some individuals of actively swimming species abandoned their positions on a rock when approached within a distance of several meters. In these areas, net backwash was no problem so a fine net (0.30 mm) was used to immediately encircle the rock as it was lifted from the bottom.

Once confined in the bucket, the rock was thoroughly rinsed clean of all invertebrates and closely inspected. Excess water was removed from the bucket through a 0.30 mm mesh as needed. The contents of the bucket retained on a 0.30 mm sieve were preserved with Kahle's fluid.

Rocks were sampled from all accessible areas of the river over a single pool-riffle sequence, spanning a distance of about 200 m. Only rocks which were not strongly cemented into the substrate were sampled. The sampled area centered on a large stable pool. Sample locations were measured from transect markers and the markers mapped by triangulation to give a map of the spatial arrangement of all samples. Two sets of samples were taken, the first on August 19-22, 1984, and the second on April 26-29, 1985. These two periods represent periods of relatively stable flow, and approximate the peak development of the summer and winter communities. The relative positions of the individual rocks for the August and April spatial samples are indicated in Figure 3.

The depth of water to the bottom of the rock, the overlying water velocity and the weight of the rock were recorded with each sample after the rock was removed from the stream. Additional notes were taken on any characteristics of the rock or sample that would not be apparent when processing the invertebrate sample. Point measures of velocity using electronic and mechanical current meters proved unsatisfactory due to the highly turbulent nature of flow around and over large rocks. The method finally adopted consisted of drifting a 125 ml Nalgene sample bottle filled with water on a string 2.0 m in length over the sample site and recording the time required to complete the distance. If the 2.0 m length was clearly too long to give a measure characteristic of the sample site it was

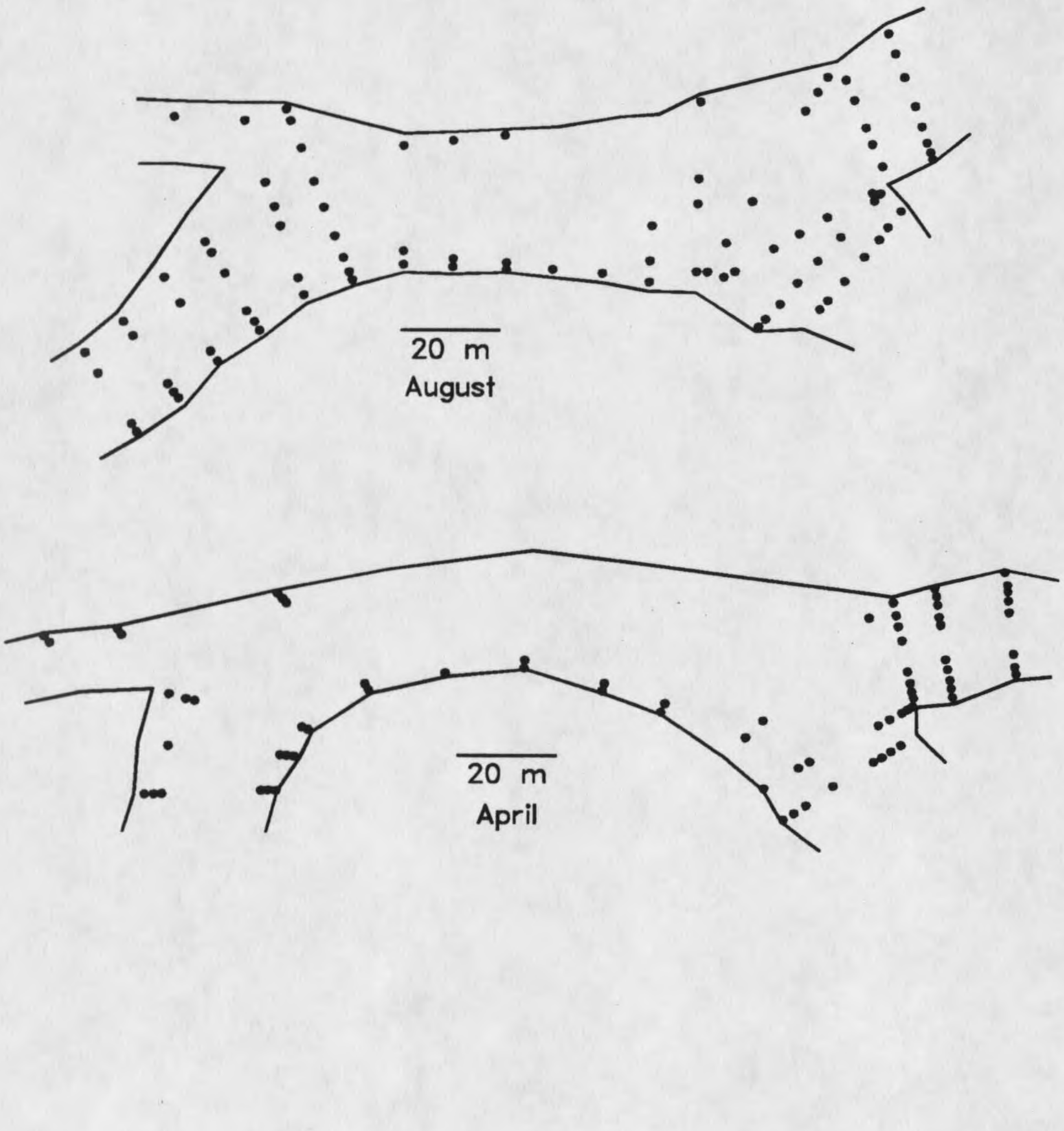

Figure 3. Relative positions of the individual rocks in the August (N = 93) and in the April (N = 76) spatial studies. The outline represent the stream edge at those two times. Gaps in the transects occur where water velocity or depth prevented sampling and where rocks were buried in fine sediment.

reduced 1.0 m. This unsophisticated method gave results that were highly repeatable and generally indicative of the current velocity at the site of the rock.

In the laboratory, the samples were processed through 8.000, 2.360 and 0.417 mm sieves as described for qualitative aquatic sampling. Those organisms passing dead through the 0.417 mm sieve were sometimes examined but these were always found to be primarily early instars of chironomids and baetids, or unidentifiable, and were not counted. All organisms retained on the larger two sieves were picked and counted. The finest sieve usually contained a few species in huge numbers relative to the rest. The entirety of this material was processed in fractions and picked so as to entirely remove as many species as possible while largely ignoring the few very abundant species. After this initial processing, the sample was again pooled and divided by bulk into quarters and one randomly chosen quarter was processed for all remaining invertebrates. The final counts for all species were corrected for those individuals found in the subsample. This sub-sampling procedure provided exact or nearly exact counts for all but a few species and saved considerable time. The taxa most often substantially affected by subsampling were in order, chironomids, simulids, *Baetis tricaudatus*, *Lepidostoma pluviale* and hydropsychid species with first instar larvae present. All field work and laboratory processing of the samples were conducted personally by myself.

Rock size is an interesting variable only if independent of simple area effects. Consequently, the counts on all rocks were transformed to correspond to the area of the average rock in each data set based on rock weight and assuming equal density and spherical shape of all rocks. These assumptions are reasonably consistent with the range of rock sizes and shapes used in the samples. Counts from single rocks are sometimes expressed as number per unit surface area of the rock. Results here are expressed simply as number per rock as this is more readily interpretable. No species occurs on all surfaces of a rock in equal density and the total surface area of the rocks occurring at a site, and represented by any particular sample is unknown.

Mainstem Longitudinal Data Set

The first of the two data sets addressing patterns of longitudinal community structure focused on the undisturbed portions of the mainstem, upstream of Bozeman. Sixteen stations were used in this reach of the river, as indicated in Figure 4 and described in Table 2. The selection of these stations was based largely on ease of access while avoiding areas disturbed by recreational users, and attempting to obtain relatively equal spacing along the length of the river. Areas immediately downstream of tributaries were avoided because of possible tail-water effects of the tributary.

Table 2. Sampling stations used for the mainstem longitudinal study listed by station number and giving for each station the stream order (SO), distance from the headwater (km), link magnitude (LM), elevation (m) and drainage area (km^2).

#	Name and description	SO	Dist.	LM	Elev.	Area
1	Gallatin R. west of Bozeman	6	113.5	461	1439	2498.8
2	Gallatin R. above Axtel Bridge	6	107.8	461	1475	2436.7
3	Gallatin R. above Gallatin Gateway	6	104.6	450	1500	2301.5
4	Gallatin R. above William's Bridge	6	98.2	436	1548	2179.2
5	Gallatin R. above Spanish Creek	6	91.7	394	1585	1922.0
6	Gallatin R. above Hellroaring Creek	6	87.7	390	1609	1903.4
7	Gallatin R. above Cascade Creek	6	82.1	343	1713	1690.7
8	Gallatin R. above Swan Creek	6	76.4	303	1731	1553.7
9	Gallatin R. above Portal Creek	6	69.2	270	1780	1448.8
10	Gallatin R. above Jack Smith Bridge	6	64.4	258	1814	1404.0
11	Gallatin R. above Porcupine Creek	6	57.9	187	1878	1030.6
12	Gallatin R. above Buck Creek	6	51.5	183	1902	1003.1
13	Gallatin R. above Buffalo Horn Creek	6	43.5	147	1975	843.0
14	Gallatin R. below Yellowstone Park	5	37.8	72	2024	467.5
15	Gallatin R. above Specimen Creek	5	28.2	41	2097	293.4
16	Gallatin R. above Fan Creek	3	20.1	7	2170	91.9

The sampling units were again loosely arranged, individual boulders from the surface layer of rocks as described above. Here however, rock size, water depth and water velocity

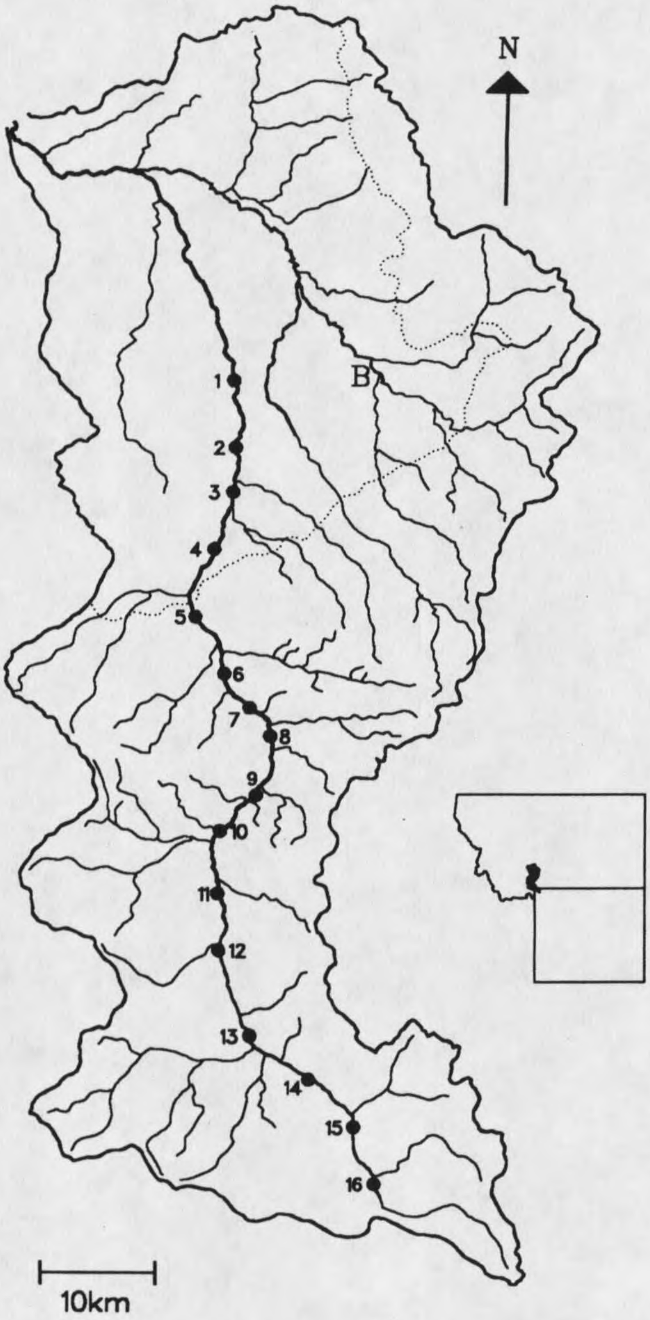

Figure 4. The Gallatin River drainage showing the locations of the 16 stations used in the mainstem longitudinal study. These are coded by the station number identified in Table 2. The dotted line indicates the approximate downstream limit of the forest. The letter "B" marks the location of the city of Bozeman.

were held to within relatively narrow limits. Rock weight was held to 10 to 14 kg, water velocity was held to 1.2 to 1.8 m/sec and the rocks were submerged by 6 to 12 cm of water. This set of circumstances is readily recognized in the field and is representative of much of the river. Rocks selected for sampling had shape and texture not deviating substantially from the typical spherical to ellipsoid, finely worn, igneous rocks that compose the majority of the stream bed. Otherwise, rocks were sampled and processed as described for the spatial data sets. Algae and bryophyte presence were not considered in sample selection. Any vegetation that was present on a rock was removed and preserved with the sample.

Tributary Longitudinal Data Set

The second data set addressing longitudinal community organization, was intended to reduce the very high correlations among the various measures of stream size that necessarily occur for sites along a single river, and to provide quantitative information on smaller streams than can be reached on the mainstem of the Gallatin River. The uppermost section of the Gallatin River, besides being rather inaccessible is closed to use for much of the year to minimize human contacts with grizzly bears *Ursus arctos* Linnaeus. Forty-five stations from throughout the drainage were included in the tributary data set. These are shown on Figure 5 and named and described in Table 3.

Table 3. Sampling stations used for the tributary longitudinal study listed by station number giving for each station the stream order (SO), distance from the headwater (km), link magnitude (LM), elevation (m) and drainage area (km^2).

#	Name and description	SO	Dist.	LM	Elev.	Area
1	Gallatin R. below Logan	6	149.7	578	1244	4649.0
2	Gallatin R. above Central Park	6	131.2	464	1311	2820.5
3	Gallatin R. west of Bozeman	6	113.5	461	1439	2498.8
4	Gallatin R. above Spanish Creek	6	91.7	394	1585	1922.0
5	Gallatin R. above Portal Creek	6	69.2	270	1780	1448.8
6	Gallatin R. below Yellowstone Park	5	37.8	72	2024	467.5
7	Gallatin R. in Wyoming	2	13.7	4	2243	51.8
8	Cottonwood Creek	3	16.1	9	1744	58.5

Table 3. *Continued.*

#	Name and description	SO	Dist.	LM	Elev.	Area
9	Bear Creek	3	13.7	5	1634	37.0
10	Spanish Creek	4	21.7	40	1597	227.1
11	North Spanish Creek	3	16.1	8	1707	67.6
12	South Spanish Creek	4	11.3	21	1853	77.7
13	Hellroaring Creek	3	15.3	12	1902	78.5
14	Squaw Creek (lower)	3	19.3	32	1683	104.4
15	Squaw Creek (mid)	3	12.1	20	1853	47.1
16	Squaw Creek (upper)	3	4.8	8	2170	13.3
17	Mica Creek	2	4.8	3	1804	8.8
18	West Creek	1	4.0	1	1853	2.8
19	Smith Creek	2	4.8	2	1878	7.0
20	Orchid Creek	2	2.4	2	1951	4.4
21	Spring Creek	1	2.4	1	1975	1.8
22	Butte Creek	1	1.6	1	2219	1.5
23	Cascade Creek	3	8.1	8	1780	27.2
24	Swan Creek	4	15.3	27	1963	74.3
25	Moose Creek	2	8.1	9	1823	31.1
26	Portal Creek (lower)	3	11.3	20	1829	50.0
27	Portal Creek (upper)	3	4.8	11	2317	22.0
28	Hidden Creek	2	3.2	4	2249	6.2
29	Deer Creek	2	7.2	5	1829	16.3
30	Goose Creek	2	3.2	2	1853	5.4
31	Dudley Creek	1	8.1	1	1841	19.7
32	West Fork Creek	4	19.3	29	1841	209.3
33	Middle West Fork Creek (lower)	3	8.9	9	1975	41.7
34	Middle West Fork Creek (upper)	1	1.6	1	2304	2.3
35	North West Fork Creek	2	10.5	4	1987	25.4
36	Andesite Creek	1	7.2	1	2134	1.6
37	Beehive Creek	2	2.4	3	2256	8.8
38	Porcupine Creek	4	11.3	28	1896	64.7
39	Buck Creek	3	13.7	12	1926	56.2
40	Buffalo Horn Creek	3	11.3	15	2024	48.4
41	Taylor Creek (lower)	5	22.5	59	2024	256.7
42	Taylor Creek (mid)	4	16.1	29	2121	136.5
43	Wapiti Creek	4	11.3	20	2097	67.6
44	Tepee Creek	2	4.8	3	2048	10.1
45	Specimen Creek	4	12.9	20	2121	78.5

The great variety of physical conditions encountered at these sites made sampling individual rocks impractical. Instead, four $0.5 m^2$ area-wide samples were taken using a 1.0 m wide net with 1.0 mm mesh size from each site. All substrate falling within the triangle formed by the front of the net and extending 1.0 m upstream of the net's center was

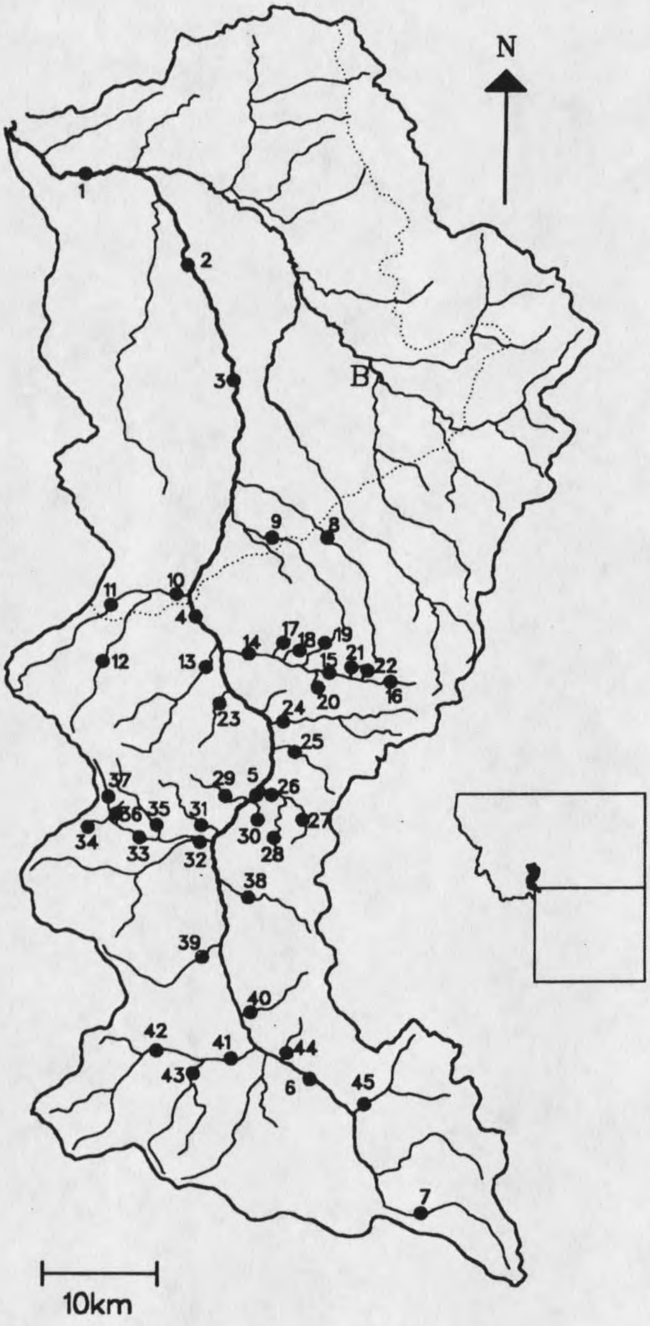

Figure 5. The Gallatin River drainage showing the locations of the 45 stations used in the tributary longitudinal study. These are coded by the station number identified in Table 3. The dotted line indicates the approximate downstream limit of the forest. The letter "B" marks the location of the city of Bozeman.

thoroughly worked by hand and foot to dislodge the invertebrates, which were swept into the net by the current. The four areas were chosen to best fit the following four respective descriptions; very fast current with large boulders, shallow water with gravel substrate, moderate current in deep water, and shoreline areas with organic substrates. These were pooled in the field. By the time these samples were taken, April and May 1985, most of the more common species in the drainage were already fairly well known with regard to the simple habitat preferences that the four areas represented. Potential sites were carefully examined over some distance to ensure the areas sampled fit the above four descriptions as well as that stream section could provide. The intent was to obtain a good species list for each site with less emphasis on detailed replicated enumeration. These samples were processed as before, but more species counts were estimated using sub-samples.

Temporal Data Set

The temporal data set was collected using the same methods as described for the mainstem longitudinal data set. A single station, near the area used for the two spatial data sets was sampled on 19 dates over the course of a year beginning in July 1984. Sample size ranged from 8 to 12 rocks at each date. The sampling area necessarily migrated slowly over the course of the year as water level rose and fell. Samples were not taken during or after times of rapid or major changes in water level.

During the course of collecting the temporal data, some of the sampled rocks were returned to the stream, after being sufficiently mapped and described to allow positive recognition later. These were sampled again at various times ranging from later the same day to many months later, but these counts were not included in the temporal data set. They were intended to provide information on the colonization rates of the various species.

Statistical Analysis

Much of this study is largely descriptive, so many of the statistical analyses are very straight forward and frequently employ graphical presentation. This is particularly true of the species ecology section. Means, standard errors, fraction present or constancy and correlation analysis require no special discussion here. The community ecology section employs a number of multivariate statistical techniques. Mardia *et al.* (1979) provide a concise, mathematical summary of these techniques. An ecologically oriented summary of each of the analyses used, is provided below.

Principal components analysis was used with each of the five community data sets to identify the presence and nature of assemblage behavior; that is to reveal sets of species behaving in similar fashions. This analysis finds linear combinations of the original variables that have maximal variance, subject to the constraint that the linear combinations are orthogonal and uncorrelated with one-another. Two or three of these linear combinations often account for much of the total variation in a large data set, and thus represent a concise summary of the pattern in the data. This is very much more concise than presenting the raw covariance matrix or similarity matrix based on all the species. The lack of correlation in principal components greatly simplifies interpretation. Principal components analysis can be useful in transforming the data before subjecting it to further analysis. This removes the unique or individual characteristics of the observations and can greatly simplify interpretation of subsequent results.

For each of the species community data sets, the covariance matrix is used rather than the correlation matrix, as it provides more natural weights to the strengths of relationships between variables which are already expressed in comparable units. To further facilitate interpretation of the principal components, only taxa that are identified to species were used in the analyses.

To reduce over-fitting, and to simplify interpretation, the number of taxa was reduced for each analysis. As each data set was specifically designed to address one aspect of community organization, the species in that data set with greatest variance were selected for primary analysis. Those are the species that vary most with regard to the structure of the sampling. The principal components analysis in all these cases was totally blind to the fact the samples came from a structured design. The conclusion that the structure of the samples drives the species assemblages is in no way circular or artifactual.

In order to determine the extent to which other taxa participate with the assemblages identified by the principal component analyses, many more species are summarized in terms of their correlations with the principal components, as well as with other pertinent biological and physical measures. This also provides a quantitative summary of species that is of interest in its own right. The principal component scores, when examined in the context of these environmental or biological measures, either graphically or by way of correlation analysis, provide better insight as to the relationship of those measures to the dominant patterns of species abundances.

Canonical correlation analysis was used to provide further insight as to the relationships between sets of species and sets of physical measures. This analysis finds linear combinations of the variables, in each of two sets of variables, so as to maximize the correlation. Subsequent pairs of linear combinations are formed which also have maximal correlation, but subject to the constraint that they be uncorrelated with all previously formed combinations. Unlike principal components analysis, this analysis is unaffected by the scale of the variables.

Discrimination analysis finds linear combinations of the original variables which can most effectively differentiate between previously identified sets of observations. Fisherian discrimination is a discrimination method which makes no assumptions about the distribution of the data. This procedure finds a set of axes where the ratio of the between-groups variance to the within-groups variance is maximal. The groups should be most easily identified in the space of these axes. Discrimination analysis is of value when looking for sets of indicator species for any specific need. Fisherian discrimination analysis is unaffected by scale, but most easily interpreted when the variables are standardized. Discrimination analysis is very closely related to canonical correlation.

Cluster analysis is intended to summarize the distances between the observations in a multidimensional space. This analysis, unlike the ones discussed before, does not have a unique, optimal solution. The analysis, however, provides an easy method for labeling the observations and classifying them into categories based on any number of dimensions.

The clustering procedure used here was hierarchical agglomeration using Euclidean distance and defining group location as half-way between the two groups joined to form it. The observations themselves represent groups of one with their own location. This algorithm avoids both over-dispersal and under-dispersal, but is not necessarily monotonic unless the groups are mostly spherical.

A jackknife validation can be used to test any statistical analysis of a data set for over-fitting and to identify heavily weighted or outlier observations in that analysis. Over-fitting can occur when the number of variables is not dwarfed by the number of observations. Over-fitting can be a serious problem in studies of invertebrates because of the very great number of species that are normally encountered and the great amount of work involved with processing each sample. A jackknife validation repeats the entirety of the original statistical analysis after removing each observation one at a time. The performance of the analysis each time is evaluated using the observation that was excluded. For example, when used with regression or discrimination analysis, the jackknife validation provides an estimate of the true predictive ability of the function.

Bootstrap sampling is a technique to assess the role of sampling variance on a statistical result. This procedure repeats a statistical analysis many times, each time using a data set which was created by re-sampling the original data set randomly and with replacement. It can be used to test the sensitivity of an analysis to sample size. Bootstrap sampling is free of any particular assumptions as to the shape of the underlying distribution of the data, and should correctly characterize the population which is represented by the sample.

Monte Carlo simulation is a procedure which repeats a statistical analysis many times using randomly constructed data. The random data are usually constructed so as to represent a null-model for the analysis in question. This procedure allows accessing the probability of obtaining an observed statistical result, given that the null model is true. Monte Carlo simulations are naturally most useful where statistical theory has not already provided a more direct answer.

All of the above statistical methods were normally employed in a number of combinations with various subsets and transformations of the data. Results that did not seem robust or that did not preform well under jackknife validation or that were insignificant, based on Monte Carlo simulation, were quickly dismissed without formal presentation. More specific aspects of each of these analyses are discussed with the applications. All statistical analyses were programed and verified personally using Microsoft FORTRAN 4.01 on an IBM PC AT. Several routines were adapted from Press *et al.* (1986). All graphics were likewise generated using FORTRAN programs written to address the Hewlett-Packard Graphics Language, HP-GL directly. Two persons assisted greatly with this effort as already acknowledged.

RESULTS AND DISCUSSION

The separation of species ecology and community ecology in this study is a matter of convenience, which is sometimes difficult to maintain. Species ecology is presented first, as community ecology makes much better sense when the individual species are ecologically characterized. This is especially true for invertebrate species, which are mostly very poorly known.

Readers interested in a particular taxon can quickly locate pertinent information in the taxonomically organized section on species ecology. They should also consult the tables and figures of each major part of the community ecology section for additional information. The quantitative results from the community ecology section are only rarely included in the species ecology section, except that all available data were used in constructing the tabular summaries. Readers interested primarily in spatial, longitudinal or temporal patterns of species abundances may turn directly to those parts of the community ecology section. These persons may want to use the species ecology section to provide information about the species as needed in interpreting the patterns of species abundances.

Over half of the species discussed in the species ecology section did not occur in any of the data sets that are presented in the community ecology section. Many of the species which did occur in the those data sets, occurred there in such small numbers that no statements were made pertaining to them in that section. The rare occurrence of a species in the quantitative data sets should not be interpreted as the species being rare in the natural environment. The habits and habitats of many species can easily render them less liable to being captured by the particular quantitative collection techniques employed. Qualitative and quantitative techniques together, for both the aquatic and terrestrial stages provide a much clearer picture of the community than does any subset of collection methods.

Results presented in the species ecology section are relatively free of sampling problems, and appear to be generally portable to different drainages throughout the northern Rocky mountain region. Results presented in the community ecology section are, of course, highly dependent upon the sampling design. Comparisons with other data sets are not made, in this discussion, and should be entertained only with great caution.

Species Ecology

A great deal of new ecological and taxonomic information on a large number of species was acquired during the course of this study. Only the ecological information is presented here. Taxonomic gaps, which were partially filled during this study would be better discussed in a context broader than a single river drainage. For many of the species, this represents the first contribution to their known ecology. All species of Ephemeroptera, Plecoptera and Trichoptera known from the drainage are included. Diptera and Coleoptera that were identified to species, and which also occurred in the quantitative data sets are also included. In all, 241 species are discussed. A few additional species from outside the Gallatin drainage are discussed when it helps to further characterize the Gallatin drainage fauna or when the species are expected to be eventually found in the Gallatin drainage. The summary presented here is necessarily highly condensed because of the number of species involved. It emphases comparative statements about the species as these are more portable and also more useful in interpreting patterns in community structure. Individual collection records including frequencies of instars or sexes are too numerous to be listed and do not add substantially to understanding the ecology of the species.

Life History Terminology

Much of the ecological data is summarized in tabular form arranged by family. The genera and species within a family are arranged either alphabetically, or according to one of the tabular entries, to facilitate comparisons. Species of a genus are, however, always placed together in these tables. Tables 4 and 5 provide brief descriptions for the codes and abbreviations, which are used in those tables. These are discussed further below. For all entries in all tables, a question mark by itself indicates that information is not available to address that particular item. Most of these instances involve species known only from adults or which were very rarely collected. Question marks which follow a table entry indicate that the entry is based on inconclusive evidence or was inferred using data from closely related species or from the literature. Use of two codes indicates a status intermediate or variable between the two.

Table 4. Descriptions of the seven longitudinal zones and abundance codes used in the tables summarizing species ecology and distributions within the Gallatin River drainage.

Longitudinal zones	
a	The main-stem, East Gallatin River and spring creeks in the Gallatin valley downstream of Bozeman.
b	The main-stem from Bozeman upstream to the forest boundary.
c	The main-stem from the forest boundary upstream to Specimen Creek.
d	The lower reaches of Spanish Creek and Taylor Creek.
e	The main-stem from Specimen Creek upstream to Fawn Pass and warmer, more productive mountain streams such as the lower parts of Bear Creek, Buffalo Horn Creek, Cottonwood Creek, Porcupine Creek, Squaw Creek, Wapiti Creek and West Creek.
f	Colder, less productive mountain streams such as Cascade Creek, Moose Creek, Portal Creek, Specimen Creek and Swan Creek.
g	Coldest, high mountain streams such as Beehive Creek, Butte Creek, Goose Creek, Orchid Creek, Smith Creek, Tepee Creek, West Creek and the upper sections of larger streams such as Portal Creek and Squaw Creek.
Abundance codes	
0	Absent, never collected.
1	Sporadic, not consistently collected.
2	Rare, consistently collected but only in small numbers.
3	Common, easily collected in numbers of 25 or more.
4	Abundant, collected in excess with little effort.

Table 5. Definitions for the abbreviations used in the tables summarizing species ecology and distributions within the Gallatin River drainage.

Life cycle types

U	Univoltine, completing one generation per year.
S	Semivoltine, requiring more than one year to complete a generation.
A	Asynchronous, univoltine with individuals growing much out of phase or multivoltine with overlapping generations.
w	winter, larvae present over the winter months.
s	summer, larvae present only over the summer months.

Habitats

G	General, living in moderate currents in the open channel.
T	Torrential, restricted to areas of extreme current velocities.
M	Marginal, restricted to shoreline areas including islands.
L	Lentic, restricted to standing water.
S	Springs, restricted to areas with pronounced ground water influence.
H	Hyporheic, normally occurring only very deep in the substrate.

Habits

Sw	Swimmers, highly mobile between different substrate objects of diverse types where they attach only temporarily.
Cg	Clingers, largely restricted to a single substrate object where they attach strongly to smooth surfaces.
Cb	Climbers, slowly mobile between different substrate objects where they attach strongly to rough surfaces.
Sp	Sprawlers, slowly mobile over soft or silty substrates where they attach only loosely.

Trophic groups

SH	Shredder-herbivore, feeding on living plant material by tearing away small pieces of the whole,
SD	Shredder-detritivore, feeding on dead plant material by tearing away small pieces of the whole.
CF	Collector-filterer, feeding on organic particles obtained from the water column.
CG	Collector-gatherer, feeding on organic particles obtained from the sediment or from loosely attached materials.
Sc	Scraper, feeding on tightly attached organic material, mainly diatoms.
Pr	Predator, feeding on living animals.

Longitudinal Zones: Longitudinal zonation is easily described when confined to a single waterway. Linear distance, elevation, stream order, link magnitude, and drainage area are all monotonic functions. No single measure seems adequate when working on many different streams of a large drainage. For describing the zonation of the individual species here, seven zones were constructed based primarily on the fauna observed with the longitudinal community data (presented later). These zones correspond reasonably well to measures of stream size when accounting also for elevation. The inferred abundance of each species in each zone represents a consensus of its abundance at all of the sites of that zone.

The abundance designations assume that sampling was done in the proper habitat and at the appropriate season. Therefore, abundance designation necessarily reflects the state of knowledge about the species as well as the commonness of the species itself. Most newly discovered species in this study tended to be quickly promoted in their designated abundance as their zonation, seasonality and habitats became better known. Some species remained rare or sporadic in the collections after several years of work and may be truly rare within the drainage. Abundance designation was based on aquatic stages, cast exuviae and terrestrial stages, except that adult Trichoptera records at a site were not counted when the larvae were not known from the site, and were known from a nearby site. Adult Trichoptera are much more mobile than Ephemeroptera or Plecoptera. They may be taken at distances as great as the width of the drainage from the stream of their origin. Adult records for species unknown as larvae were taken at face value.

The designation "Absent" is self explanatory, but was easily subject to being promoted to the "Sporadic" designation with the capture of a single individual. "Sporadic" implies unpredictable, more than rare. Sporadic species are usually out of their normal range: For example, rare downstream individuals of a more headwater species. Sporadic species are sometimes opportunistic species colonizing microhabitats that are themselves unpredictable. "Sporadic" species are not expected to be present even in large samples. The designation "Rare" implies that the species could be predictably taken, but usually only in numbers considerably less than 25 individuals, even with considerable effort. "Rare" species are often near the edge of their normal range. The designation "Common" refers to species which were taken in numbers exceeding 25 individuals with reasonable effort. This number provided the minimum number used in measuring head capsule widths.

"Abundant" species are those which were taken in very large numbers incidental to collecting 25 individuals of "Common" species. Most specimens of "Abundant" species were discarded after examination or measurement to conserve specimen storage space.

Life Cycle Types: Life cycle terminology and notation are adapted from Clifford (1982). A very great majority of the species in the cold, highly seasonal Gallatin River are univoltine and well-synchronized in both growth and emergence. The usual division of univoltine life cycles into winter and summer cycles is useful, but somewhat arbitrary. The species listed here as having winter cycles had the majority of the new generation of larvae appear in the benthos before January 1. Species with the majority of the new generation of larvae appearing after January 1 are designated as having summer life cycles. A few species of large Plecoptera and Trichoptera are semivoltine, that is they require more than a year to complete larval growth. The designation "asynchronous" is used here for life cycles which could not be reliably determined from field collections alone. These species may be univoltine with greatly staggered egg hatching, growth and emergence, or they may be multivoltine with overlapping generations. This group was mostly made up of small mayflies, spring-inhabiting caddisflies, and beetles, with both adults and larvae present throughout the year. Some of the spring-inhabiting caddisflies are truly non-seasonal, with adults and all larval instars present every month of the year. Variable life cycles are very rare in the Gallatin drainage. A few species are univoltine in the lower parts of their range and semivoltine in the upper parts. A few species with winter cycles in the lower parts of the river have summer cycles in the upper parts. Complex life cycles are not known for any of the Gallatin drainage species.

Habitats: Six types of aquatic habitats are designated for the Gallatin River drainage. These are self-explanatory. They are sufficiently broad that species from different habitats are unlikely to interact substantially. Vascular plants and soft sediments are both limited and ephemeral in the running waters of the upper parts of the Gallatin drainage. Species limited to these are either absent or sporadic in occurrence in this area.

Habits: Insect habits describe the use of the habitat or mode of existence. Four categories, adapted from Cummins and Merritt (1984) are used. Swimmers are usually substrate generalists. They frequently change their location and quickly colonize new substrates. They need not swim in any particular manner. Clingers, on the other hand are highly dependent on specific substrate, and are usually limited by its availability. These species normally shift to new substrate objects only through drifting. This is especially true in clean-boulder riffles where the individual rocks have very limited contacts with one-another. Clingers obviously prevent others from inhabiting the area they directly occupy. Most species of clingers exclude competitors from a much larger area through aggressive behavior. Clingers which build fixed retreats cemented to rocks easily interfere with, or even displace, species that require clean surfaces for attachment and movement. Rocks cluttered with these retreats become more available for climbers. Climbers are normally characteristic of organic substrates, but occur also on rocks with rough surfaces or those with filamentous algae or bryophytes attached. Sprawlers are rather limited in the Gallatin drainage. They are specialized for very silty substrates, which neither clingers nor climbers utilize.

Trophic Groups: Trophic group is intended to describe the feeding mechanism more than the specific type of food ingested, and is also adapted from Cummins and Merritt (1984). Most closely-related species are of the same trophic group. The six trophic groups used are sufficiently broad that species from different trophic groups are unlikely to be competing for the same food resources. The designation "Collector-gatherer" was used when a species did not show a clear specialization toward either a shredder or a scraper mode. Many species are so unspecialized as feeders that there is as much variability between the individuals of a species as there is between different species. Nearly all species will readily take easily handled living animals for food, yet it is clear that most species are not primarily predatory in their natural environment. The collector-gatherers primarily consume the fine detritus that surrounds them in abundance, and are unlikely to be limited by food. Most predator species consume mainly chironomids and simulids. Shredders are frequently highly congregated in areas of accumulated detritus or patches of bryophytes and are likely limited by food availability. They are frequently of sporadic occurrence and exhibit unusually large annual fluctuations in densities. Scrapers require clean substrates and are rather easily displaced by siltation or by the cluttering of rocks by filamentous algae, bryophytes or collector species with fixed retreats. They are frequently highly aggregated in areas with their preferred substrate.

Ephemeroptera

Seven families, 23 genera and 58 species of Ephemeroptera are known from the Gallatin River drainage. Based on the rate of discovery of species new to the drainage and on the number of collections of each species, mayflies are the best known of the three orders treated here in full. There is unlikely to be more than a couple of species present in the upper parts of the drainage which are not reported here. The mayflies of Montana are, however, much more poorly known than either the Plecoptera or Trichoptera. State records are currently based on so few publications, that the new Montana records are not yet very meaningful.

Two nominal species that were recognized from adults, *Baetis persecutus* McDunnough and *Cinygmula mimus* (Eaton) are excluded from this discussion as they do not appear to represent distinct species within the Gallatin drainage. They are included with *Baetis tricaudatus* and *Cinygmula reticulata* respectively.

Contrary to the situation with both the Plecoptera and the Trichoptera, Ephemeroptera species are better inventoried by collecting the nymphs than by collecting the adults. The adults can usually be reared when necessary for identification. Only 61% of the species known from the drainage were taken as swarming adults and several of these were only very rarely encountered. The mayflies of lower elevation streams are more frequently encountered as swarming adults than are those of cold, mountain streams.

Compared with Plecoptera and Trichoptera, Ephemeroptera are represented by few species. Mayfly species tend, however, to be represented by more abundant individuals. Over half (53%) of all the mayfly species known from the drainage are given the highest abundance designation somewhere in the drainage. Only three of the species have maximal abundance designation less than common. None of the Ephemeroptera species known from the drainage is known only from a single site. Only four mayfly species are known from only one of the longitudinal zones and two of these extend far downstream of the study area. The general absence of rare and locally distributed species of Ephemeroptera in the drainage may be partially due to the short and fragile adult phase of the mayfly life cycle. Small, local populations of mayflies would most likely be of short persistence in physical environments as extreme as southwest Montana.

All but six of the 58 species of mayflies known from the Gallatin drainage are best categorized with regard to trophic relations as general collector-gatherers. Four of the mayfly species are shredders, one is a scrapper and one is largely predatory. This relative lack of trophic specialization may also be partially responsible for the limited number of species in the drainage and for the relatively large populations of most of the species. Gilpin and Brusven (1970) summarize food habits and ecology for 28 mayfly species from the St. Maries River in Idaho. Twenty-five of these species occur in the Gallatin drainage and generally correspond well to their descriptions.

While mayflies, when compared to stoneflies or caddisflies, are uniform with regards to trophic function, their habitats and habits are relatively diverse. Well over half of all the species of Plecoptera and Trichoptera were given the most general of the habitat designations. That is they occur on rocks in the open channel exposed to moderate current. Only 28% of the Ephemeroptera species receive this designation. Over half (52%) of the mayfly species in the Gallatin drainage occupy rather specialized habitats along the shorelines of streams in reduced current, 17% prefer very rapid current velocities, the remaining 3% of the species are entirely lentic. Some mayfly species, within the drainage, occur abundantly in springs, but unlike stoneflies and caddisflies, none of mayfly species from the Gallatin drainage are restricted to springs. The habits of swimming and sprawling are well represented in the Ephemeroptera, but entirely absent from the Plecoptera and Trichoptera species known from the Gallatin drainage.

Ephemeroptera life cycles within the Gallatin drainage are also more diverse than seen in either the Plecoptera or Trichoptera. For the latter two orders, over 70% of all the life cycles are of the univoltine-winter type. Less than half (41-48%) of the Gallatin drainage mayfly species have this type of life cycle. Most of the remaining species (34-41% of the total) have the univoltine-summer life cycle, and show great variation in the timing and duration of the various stages. Fifteen percent of the mayfly life cycles seen in the drainage are so asynchronous that their exact nature cannot be determined in the field. Most of these asynchronous life cycles are limited to the summer season, while two occur throughout the year. One *Ameletus* species in the drainage may require 2 years to complete its growth.

Longitudinally, mayflies are most diverse in the lowest parts of the drainage. Thirty-seven species occur in the two longitudinal zones below the forest boundary. Most of these species occur also downstream of the Gallatin drainage. Several additional species that are known from just below the drainage may eventually be found within the Gallatin drainage. Two of these are the burrowing mayflies *Ephemera simulans* Walker (Ephemeridae) and *Ephoron album* (Say) (Polymitarcyidae), which have no relatives in the Gallatin drainage. The remaining species from outside the drainage are discussed below, in comparison with taxonomically related species that do occur within the drainage. Only 20 mayfly species occur in the streams from the highest of the seven longitudinal zones. The absence of species with summer life cycles from the higher sites is largely responsible for the reduced number of mayfly species in headwater streams.

About 64% of the Ephemeroptera species known from the entire Gallatin drainage occur in the mainstem of the river directly west of Bozeman. Many of these species are at the edge of their longitudinal distribution and are very rare at that site. The phenologies of the 29 species which are dominant elements of the community at this site are presented in Figure 6. Two species, *Heptagenia adequata* and *Rhithrogena morrisoni*, while commonly taken as adults swarming over the river at this site, occur in the benthos in significant numbers only in lower parts of the drainage. Two very small species, *Acentrella insignificans* and *Tricorythodes minutus* are not taken in the benthos until some of the individuals are nearly mature. Gray (1981) reared members of both of these genera from egg to adult in about 10 days in the Sonoran Desert. Most mayfly species emerge during July and August at this site. Ten species overwinter as growing nymphs. The remaining species have rather varied lengths of nymphal growth. Two species of *Ameletus* may have a summer egg diapause.

Family Baetidae: The family Baetidae with 9 species (Table 6) contains some of the most abundant species of mayflies within the drainage, but also some of the most poorly known. The lotic species are small, difficult to handle and to recognize, especially in the field.

All but three of the asynchronous life cycles among the mayflies studied are found in the Baetidae, as is the most ecologically and morphologically variable of the mayflies studied, *Baetis tricaudatus*. This species exhibits great morphological variation as both nymphs and adults, and exhibits greater life history flexibility and wider distribution within the drainage than any other mayfly species. It is also the most widely distributed Nearctic

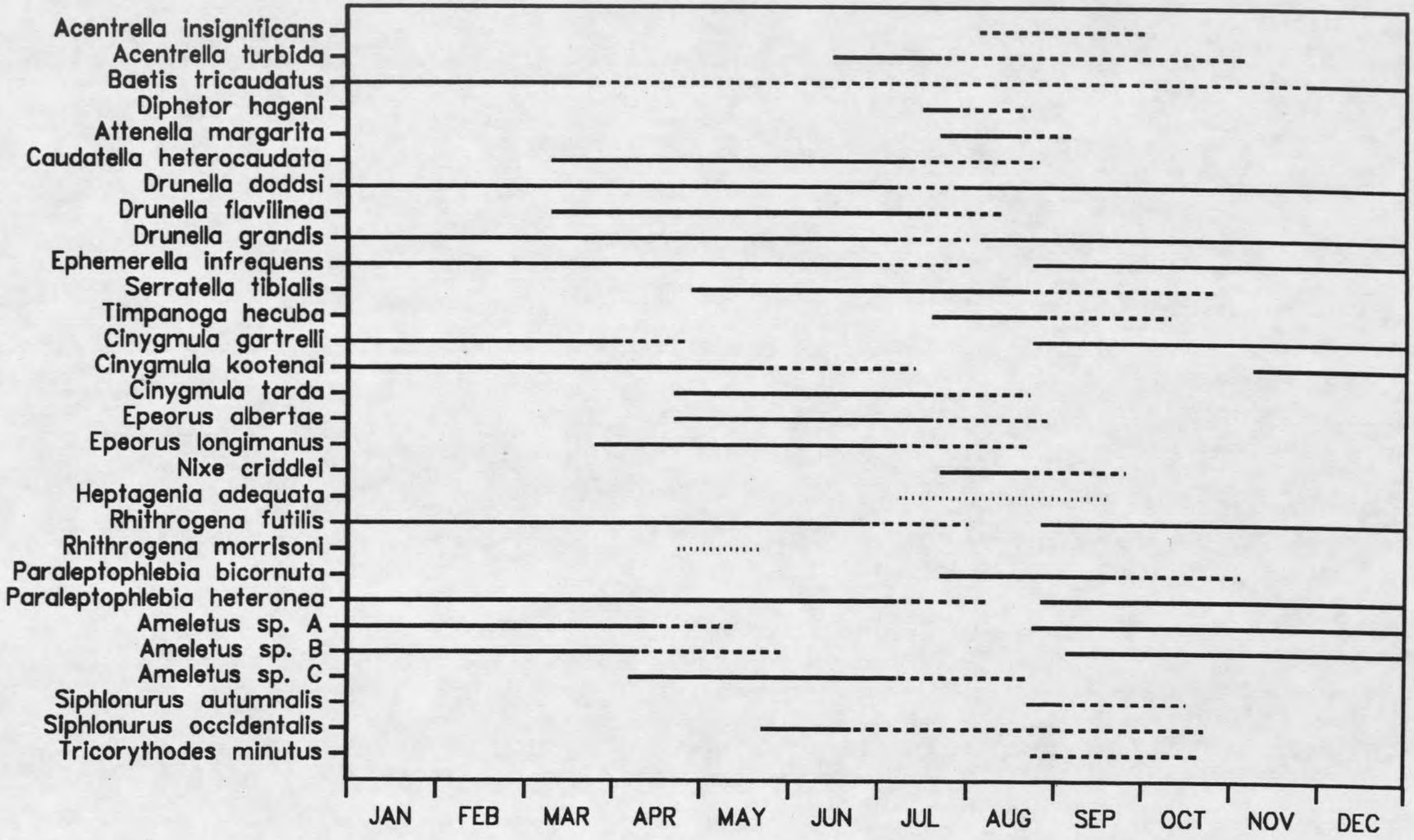

Figure 6. Phenology of 29 Ephemeroptera species that were common in the Gallatin River near Bozeman during 1984. Solid line represents the occurrence of nymphs only, dotted line of adults only and dashed line the occurrence of both.

species of *Baetis* (Morihara and McCafferty, 1979). The nymphs are so small that the methods used were inadequate to obtain a random sample of all sizes, but the results presented in Figure 7 should be relatively unaffected by sampling inefficiencies. The presence of three major generations may be indicated, but the amount of overlap is great. Laboratory study is required to determine the timing of egg hatching.

Table 6. Baetidae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Acentrella insignificans (McDunnough)	3200000	Us	G	Sw	CG
A. turbida (McDunnough)	4433300	As	G	Sw	CG
Baetis bicaudatus Dodds	0000344	Aws	G	Sw	CG
B. tricaudatus Dodds	4444320	Aws	G	Sw	CG
Callibaetis nigritus Dodds	3300000	As	L	Sw	CG
C. coloradensis Banks	0000032	As	L	Sw	CG
Centroptilum bifurcatum McDunnough	2100000	Us	GM	Sw	CG
Diphetor hageni (Eaton)	3320000	Us	G	Sw	CG
Pseudocloeon edmundsi Jensen	3200000	As	G	Sw	CG

Baetis bicaudatus, like *B. tricaudatus*, has an asynchronous life cycle with nymphs present throughout the year and adults emerging from June through September from high mountain streams. It likewise exhibits substantial variation in the appearance and size of the individuals. Individuals emerging late in the season may be taken substantially further downstream than can those which overwinter and emerge early in the summer. A multivoltine life cycle seems unexpected in highly seasonal and predictable headwater streams. Two or more species should be able to achieve better physiological adaptation than a single, flexible species. *Baetis bicaudatus* is the only alpine, lotic species, within the drainage, which is not both univoltine and highly synchronized.

Most nymphal collections of *B. bicaudatus* in this study contain few males and sometimes no males. The species has been hypothesized to be sometimes parthenogenetic,

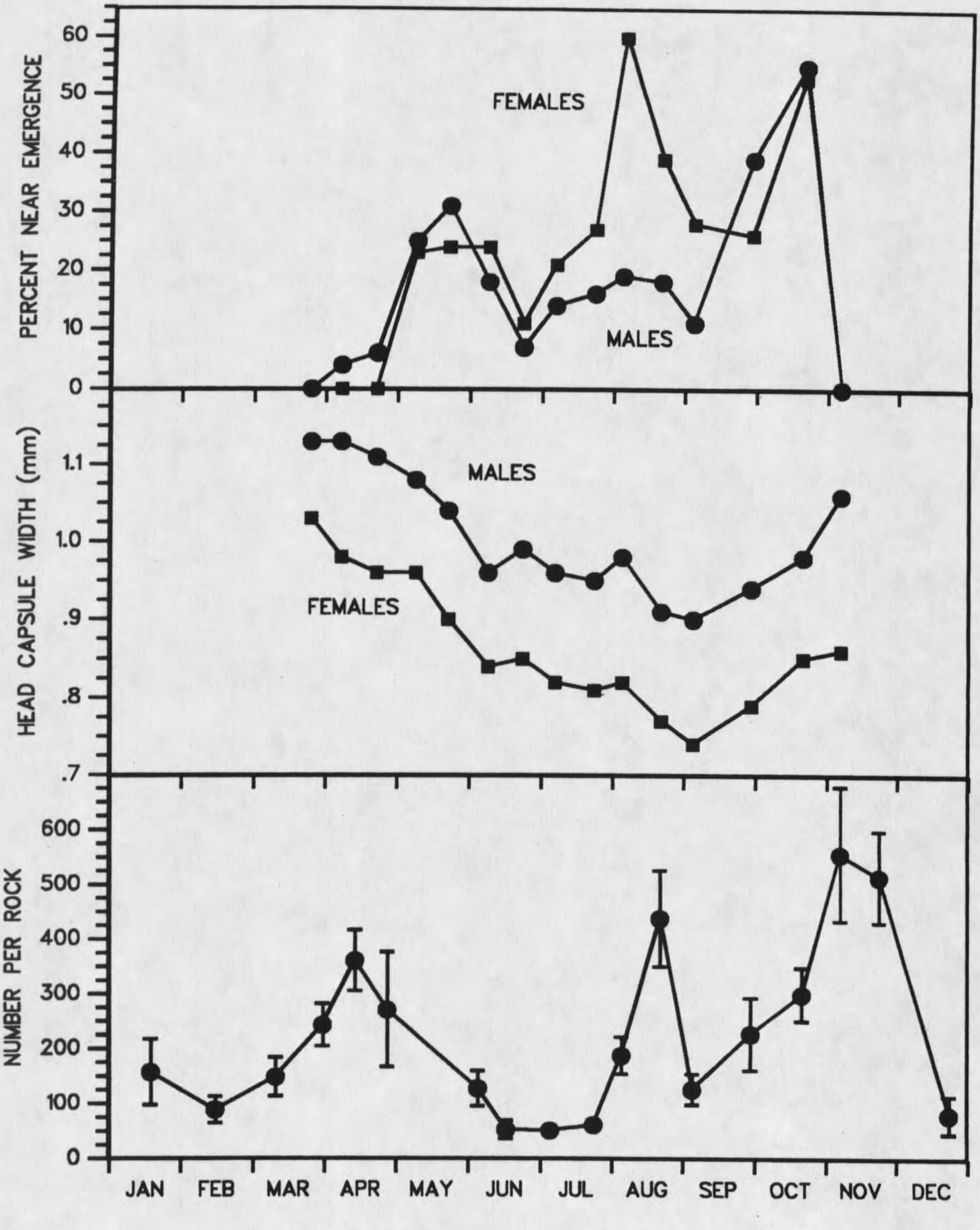

Figure 7. Percent of final instar *Baetis tricaudatus* nymphs with black wing pads, mean head capsule width of final instar nymphs and mean density on average sized boulders in swift current in the Gallatin River west of Bozeman during 1984. Error bars represent standard error for the mean of 8 to 12 samples.

especially in cold sites (McCafferty and Morihara, 1979). Males are, however, frequently encountered swarming from high elevation sites throughout the drainage and throughout the emergence period. *Baetis bicaudatus* and *B. tricaudatus* are morphologically very similar as both nymphs and adults, except for the median terminal filament of the nymphs. All nymphs seem clearly referable to one species or the other using that character alone. Most sites have only one species with *B. bicaudatus* always occurring further upstream than *B. tricaudatus*. Where both occur, one species always greatly predominates numerically.

Acentrella turbida is abundant in the lower parts of river, and its appearance is restricted to the summer season. Its small size and rapid growth make it very difficult to study. It favors much larger substrates and faster waters than the other baetids that occur in the drainage. Growth and emergence are highly asynchronous, but confined to the summer. *Acentrella insignificans* is also confined to the lower river and to the summer, but is seldom common. It is apparently univoltine, but with very rapid growth.

Pseudocloeon edmundsi occurs only in the lowest parts of the Gallatin drainage and is most common in vegetated spring creeks. It is also confined to the summer season and not very abundant within the drainage. This species is more abundant in nearby warmer or more heavily vegetated rivers.

Diphetor hageni is an easily recognized species having a single apparent generation each year. It is restricted to the summer season and to the lower parts of the drainage. This species also has rapid growth and is first encountered as nymphs only shortly before its emergence begins. In the Gallatin drainage, it is present in the benthos for a very short time each year.

Centroptilum bifurcatum is another baetid species that enters only the very lowest parts of the Gallatin drainage. It becomes much more common in the warmer streams downstream of and adjacent to the Gallatin drainage. It is restricted to the summer season and has very rapid body growth.

Two nominal species of *Callibaetis* are known from the drainage. Both species are entirely restricted to lentic habitats and thus are not associated with any of the lotic species. Neither species is represented in any of the quantitative data sets. *Callibaetis nigritus* occurs in floodplain ponds across the Gallatin Valley and *C. coloradensis* occurs in similar habitats in high mountain meadows. There is little suitable habitat between these two areas. The characters used to distinguish these species were consistently encountered with specimens from the Gallatin drainage, but this may prove to be environmentally induced. The genus is in need of a critical revision.

Both nominal species of *Callibaetis* may be very abundant with several apparent generations during the summer. The nymphs do not appear to overwinter in the shallow ponds in this drainage, which either go completely dry before winter or freeze solid. This observation conflicts with the claim that the genus is universally ovoviviparous (Berner and Pescador, 1988) and indicates further study is needed. Either very small nymphs do survive in these ponds, or the ponds are recolonized each year from more permanent water bodies, or a resistant egg is present. During the summer, the various isolated populations in different ponds are often more asynchronous than are the nymphs of a single pond. The life cycles of these two species cannot be determined without experimentally controlled conditions. The abundance of these species is a function of the availability of suitable lentic waters and this is strongly determined by the dynamics of the flooding river and by summer weather. *Callibaetis nigritus* exhibits enormous fluctuations in its abundance from year to year. Such large fluctuations are very rare for the lotic mayfly species in the drainage.

Family Ephemerellidae: The ephemerellids, or spiny-crawlers, in the Gallatin River drainage constitute an interesting assemblage of 15 species placed in six genera (Table 7). Only two species of this family are known to occur in Montana, but have not been found in the Gallatin drainage; *Serratella micheneri* (Traver) in south-central Montana and *Drunella pelosa* (Mayo) in northwest Montana. Neither of these species are expected to be found in the Gallatin drainage. The elevation of the former *Ephemerella* subgenera to full genera (Allen, 1980) makes the ecological diversity within each genus more similar to that encountered in other mayfly genera.

Table 7. Ephemerellidae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Attenella margarita (Needham)	4430000	Us	M	Sp	CG
Caudatella edmundsi Allen	0130000	Uw	GT	Cb	SH
C. heterocaudata (McDunnough)	2342000	Us	GT	Cg	SH
C. hystrix (Traver)	0013342	Uw	GT	Cb	SH
Drunella coloradensis (Dodds)	0002343	Uw	G	Cg	CG
D. doddsi (Needham)	3444443	Uw	GT	Cg	Sc
D. flavilinea (McDunnough)	4443300	Us	G	Cg	CG
D. grandis ingens (McDunnough)	4443320	Uw	G	Cb	CG
D. spinifera (Needham)	0000233	Uw	G	Cb	Pr
Ephemerella alleni Jensen & Edmunds	0000023	Uw	GM	Cb	SD
E. aurivillii (Bengtsson)	0112330	Uw	M	Cb	CG
E. inermis Eaton	4000000	Uw	G	Cg	CG
E. infrequens McDunnough	4444430	Uw	G	Cg	CG
Serratella tibialis (McDunnough)	3444330	Us	G	Cg	CG
Timpanoga hecuba (Eaton)	3320000	Us	M	Sp	CG

Ephemerellid species take advantage of a great many microhabitats and food sources. Many species may be found occurring together spatially and temporally. As many as seven species were taken at one time from a single rock during this study. The morphological diversity of the nymphs is great, though the adults are often difficult to distinguish. Species taxonomy within this family, has traditionally been based on the nymphs. Many species were described based on nymphs alone. Several species were reared during this study, not for the usual purpose of establishing nymphal identification, but rather to establish or verify adult identification, especially for females.

The family Ephemerellidae contains all of the mayfly species known from the Gallatin drainage, which are not best-categorized as collector-gatherers. *Drunella doddsi* is best-categorized as a scraper. It feeds almost entirely on diatoms, often with minimal included detritus. Occasionally, an individual was found which contained a large amount of insect exoskeleton in its gut. This material may be the softer parts of their own cast exuviae. *Drunella spinifera* is highly carnivorous. It feeds on a variety of insects, especially other mayflies. All three species of *Caudatella* function primarily as shredders. *Caudatella edmundsi* feeds almost exclusively of living bryophytes. *Caudatella hystrix* and *C. heterocaudata* likewise feed on bryophytes, but also include coarse filamentous algae. *Ephemerella alleni* consumes considerable amounts of shredded detritus in addition to collected detritus, and is only found in abundance where coarse organic debris has accumulated. The same habitat is occupied by *E. aurivillii*, though further downstream, but that species feeds almost exclusively on fine collected detritus, as do all remaining species of the family occurring in the Gallatin drainage.

All ephemerellid species are univoltine and well synchronized in both growth and emergence within the Gallatin drainage. The eight species, which are dominant elements of the community in the river near Bozeman, exhibit three types of life cycles (Figure 8). Three species take almost a full year to complete nymphal growth. Young of the year of *Drunella doddsi* were frequently found in the benthos before all of the last generation of nymphs had emerged. The same situation sometimes occurs for *D. grandis*. These species exhibit typical univoltine, winter life cycles. Three other species do not appear in benthic samples until early in the spring before the summer where they emerge. Body growth is completed in 5 or 6 months. These species have typical univoltine, summer life cycles.

Two species, *Timpanoga hecuba* and *Attenella margarita* have life cycles which do not fit either of the above patterns. Body growth was so rapid, that the date of egg hatching was difficult to approximate. Even with the habitat of each species fully identified, the nymphs go from absent to rather large in a few days. Some individuals emerged only one month after first being detected. All individuals of these species emerged after just two or three

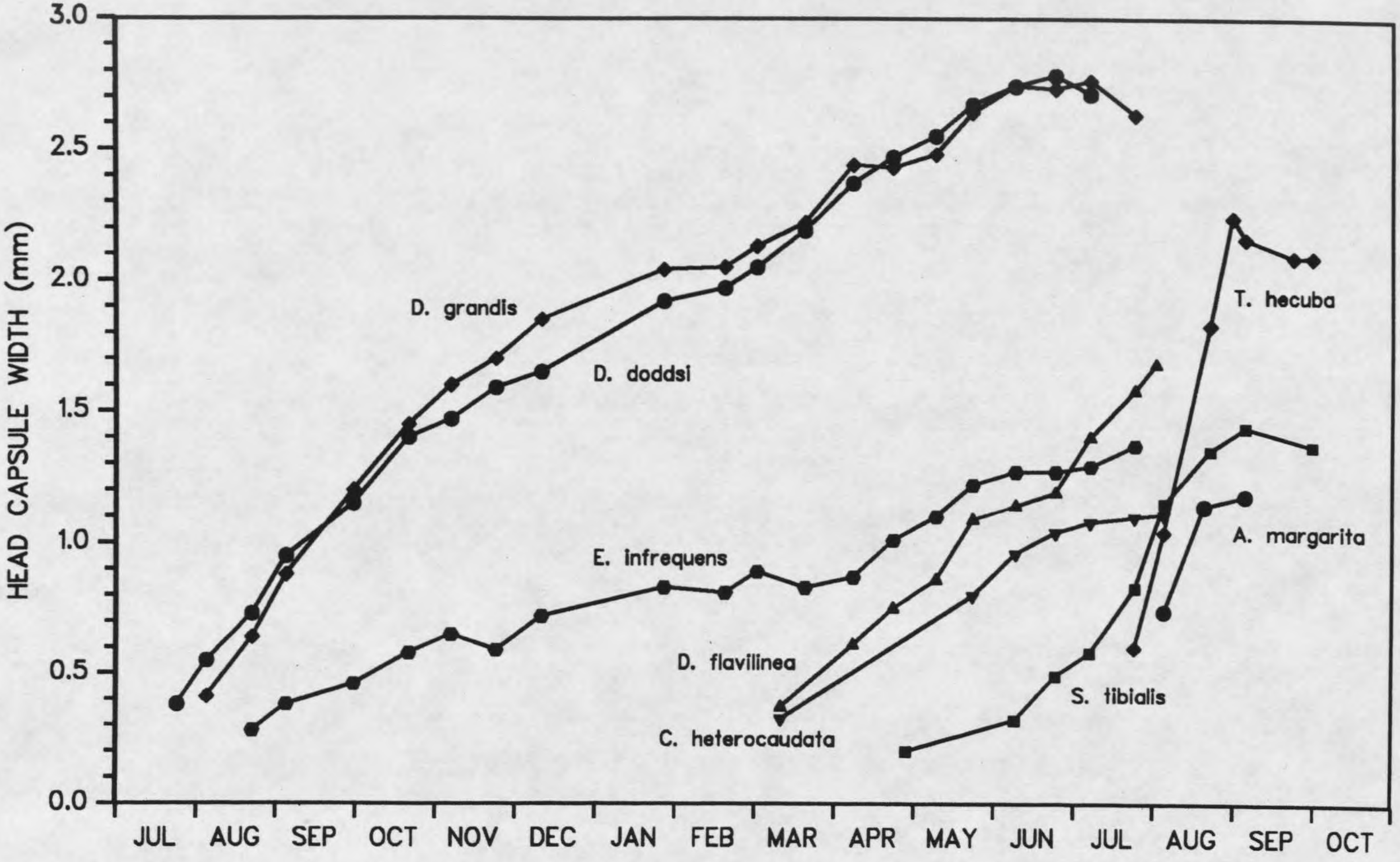

Figure 8. Mean head capsule width of 8 species of Ephemerellidae occurring in the Gallatin River near Bozeman. Only nymphs derived from eggs laid in 1984 are shown.

months in the river. These species do not exhibit this rapid growth in all streams where they occur. They have apparently adapted their life cycle in the lower Gallatin drainage to take advantage of the short period of warm temperatures, high food availability and reduced competition by other species. Allen and Edmunds (1959) described a coastal subspecies, *Timpanoga hecuba pacifica*, and reported that the nymphs require about 11 months to complete their body growth. This is very different from observations in Montana for the typical subspecies. Both *T. hecuba* and *A. margarita* occur on silt covered shoreline rocks or large woody debris. Neither species tolerates much current. They appear to be ecologically identical, but differ greatly in size and morphology.

A few species of this family were frequently encountered as swarming adults, while others, though very abundant in the benthos, were not seen swarming. Female swarms were especially frequent in this family. The species not encountered swarming probably swarm after darkness, far from water or very high. Adults of all species were reared, yielding both imagoes and subimagoes for both sexes, except for *Ephemerella alleni* where only females were obtained. Several hundred nymphs were examined, from many sites and were all female. All 15 nymphs which were sexed as part of the type series were also females. This species seems very likely parthenogenetic or possibly gynogenic (a sexual parasite, using males of another species in mating, but not using the genetic material of the male). Females were taken swarming and the growth and emergence of this species is as well synchronized as other species in similar high mountain streams. Synchronized emergence would seem less advantageous to a purely parthenogenetic species since finding mates is unnecessary. Predator satiation also seems highly unlikely for this species because of its small populations. Eggs obtained from reared females were incubated for over two months at 8° C without hatching. No such delay in hatching occurs in the field. Brittain (1982) found parthenogenesis reported for about 50 mayfly species, but obligatory parthenogenesis to be very rare.

As previously mentioned, the species in this family seldom constitute tight seasonal or longitudinal replacements of one-another. Only a single pair of species seems to represent longitudinal replacements of one-another. In the Gallatin drainage, *Ephemerella inermis* is restricted to the spring creeks in the valley and to the warmer parts of the East Gallatin River. *Ephemerella infrequens* replaces it in the mainstem of the river and all higher tributaries. These two species occur together in the lower parts of the nearby Madison river, where *E. infrequens* inhabits the cleaner riffles and *E. inermis* inhabits the more silted or vegetated areas of the river. Individuals of these two species are difficult to distinguish as nymphs, but the male imagoes are easily separated. Likewise, only a single pair of species in this family is thought to represent seasonal replacements of one-another. *Ephemerella infrequens* and *Serratella tibialis* both occupy the same habitat and have the same longitudinal distribution, but the first has a winter life cycle and the second a summer life cycle. Though belonging to different genera, the nymphs of these two species are morphologically very similar.

The remaining ephemerellid species show obvious niche separation in more dimensions, and may overlap one-another seasonally and longitudinally. For example, *Drunella spinifera* could be considered an upstream replacement for *D. grandis*, except its trophic status is very different. Likewise, *D. coloradensis* could be considered an upstream replacement of *D. flavilinea*, except its life cycle is quite different, it is much larger and it prefers larger substrates.

The three species of *Caudatella*, which occur in the Gallatin drainage, are all highly specialized. Within the Gallatin drainage, *Caudatella edmundsi* is restricted to a short section (20 km) of the mainstem in the Gallatin Canyon, where it is further restricted to large, moss covered rocks in very fast current. Such a narrow distribution on the mainstem of the river occurs for none of the other species studied. Its association with aquatic moss is apparently absolute in agreement with reports by Hawkins (1984), who took the species in abundance in only one of seven sites in western Oregon. *Caudatella edmundsi* does not, however, occur everywhere moss occurs. Adults were reared with great difficulty, compared to the other species of the family as the nymphs are very fragile. The discovery of this species in Montana represents an eastward expansion of its known range. *Caudatella edmundsi* cannot be considered either the downstream replacement of *C. hystrix* or the winter replacement of *C. heterocaudata*.

Members of the family Ephemerellidae have great potential for use as indicator species. The nymphs are specifically identifiable, even when quite young, and the species have diverse and specific environmental requirements. Changes in the zonation of the species, over time, should be especially easy to interpret. The range of *Drunella doddsi*, for example, retreats upstream during low water years, primarily in response to increased rock cluttering. During years with long, warm summers, the range over which *Timpanoga hecuba* completes its growth, extends further upstream than it does during cooler summers.

Family Heptageniidae: The heptageniid fauna of the Gallatin drainage consists of 18 species in six genera (Table 8). In contrast to the ephemerellids, the species are morphologically homogeneous at the generic level, in the nymphal stage. All the species of *Cinygmula* and most of those of *Rhithrogena* cannot be reliably identified as nymphs, even when compared to reared material. Nymphs of many of the other species are recognized only on very close inspection. The family is homogeneous also with regard to feeding. All of the species known from the Gallatin drainage feed primarily on fine, collected detritus. Some of these genera are sometimes referred to as scrapers, but that is reserved here for species more specialized for feeding on tightly attached diatoms. All these heptageniids feed on relatively loosely attached material, and their guts do not contain the very high percentage of diatoms found in species listed here as scrapers. The family is characterized by very tight packing of the species, seasonally and longitudinally. Each species is presumably a temperature specialist, physiologically adapted to a rather narrow temperature regime similar to many of the stonefly species studied. The taxonomy of the Heptageniidae has traditionally been based on the adults, frequently using only color patterns to distinguish the species, yet most of the described species appear to represent ecologically distinct populations.

Table 8. Heptageniidae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Cinygma integrum Eaton	0000223	Uw	M	Cg	CG
Cinygmula gartrelli McDunnough	4433000	Uw	GM	Cg	CG
C. kootenai McDunnough	3444300	Uw	GM	Cg	CG
C. par (Eaton)	0000003	Us	GM	Cg	CG
C. ramaleyi (Dodds)	0000334	Us	GM	Cg	CG
C. reticulata McDunnough	0000440	Uw	GM	Cg	CG
C. tarda (McDunnough)	3443000	Us	GM	Cg	CG
Epeorus albertae (McDunnough)	4400000	Us	GT	Cg	CG
E. deceptivus (McDunnough)	0000233	Us	GT	Cg	CG
E. grandis (McDunnough)	0011343	Uw	GT	Cg	CG
E. longimanus (Eaton)	0443310	Us	GT	Cg	CG
Nixe criddlei (McDunnough)	4420000	Us	M	Cg	CG
N. simplicioides (McDunnough)	3200000	Us	M	Cg	CG
Heptagenia adequata McDunnough	3200000	Uw	GM	Cg?	CG
Rhithrogena futilis McDunnough	3444443	Uw	GT	Cg	CG
R. morrisoni (Banks)	4420000	Uw	G	Cg	CG
R. robusta Dodds	0122343	Uw	GT	Cg	CG
R. undulata Banks	4000000	U?	G	Cg	CG

The heptageniid species from the Gallatin drainage occupy only two major microhabitats. All the species can be classified either as fast-water species or as slow-water species. This classification can be applied at the generic level for the species discussed here. Slow-water species have very limited contacts with fast-water species. They strongly avoid rapid current, and they often have a marked preference for finer substrate, organic substrates or somewhat silty substrates. Slow-water heptageniids must have contact with the rock, and they are displaced by silt which is too deep for them to move through. These species usually concentrate near shore, especially prior to emerging. *Cinygma*, *Cinygmula*, *Nixe* and *Heptagenia* contain only slow-water species.

Fast-water heptageniids occur only on smooth, clean substrate in fast current. *Epeorus* and *Rhithrogena* contain only fast-water species. Of course, a slow-water species in the Gallatin drainage may appear as a fast-water species in a less torrential river system, where true fast-water species are lacking. The heptageniid fauna of any site at a given time usually consists of only two fast-water species and two slow-water species. The two ecologically similar species, in each case, being of rather different sizes. Lamp and Britt (1981) describe in some detail the resource partitioning of two heptageniid species which appear to represent a slow-water species and a fast-water species. Food and the seasonality of growth were very similar for the two species, but the habitat, in terms of depth and especially current velocity was very different. They also correlated several morphological differences with the preferred current velocities.

In the river near Bozeman, seven heptageniid species are sufficiently common to allow following the growth of the nymphs over the course of a year (Figure 9). The pattern here is one of three fast-water species following one-another in time and four slow-water species following one-another in time. In each case, the later species completes its growth in less time than the species before it and tends also to be smaller in final size. This is most apparent for the three *Cinygmula* species. All *Rhithrogena* nymphs at this site, exclusive of the rare individuals of *R. robusta* which are easily recognized, were considered to belong to *R. futilis*. *Rhithrogena undulata* is unknown this far upstream, and while *R. morrisoni* adults can be quite common in this area, mature nymphs of *Rhithrogena* are very rare at this site during the flight period of *R. morrisoni*. Mistakenly mixing the nymphs of *R. futilis* and *R. morrisoni* still seems the most probable explanation for the unusually erratic growth of *R. futilis* seen in Figure 9.

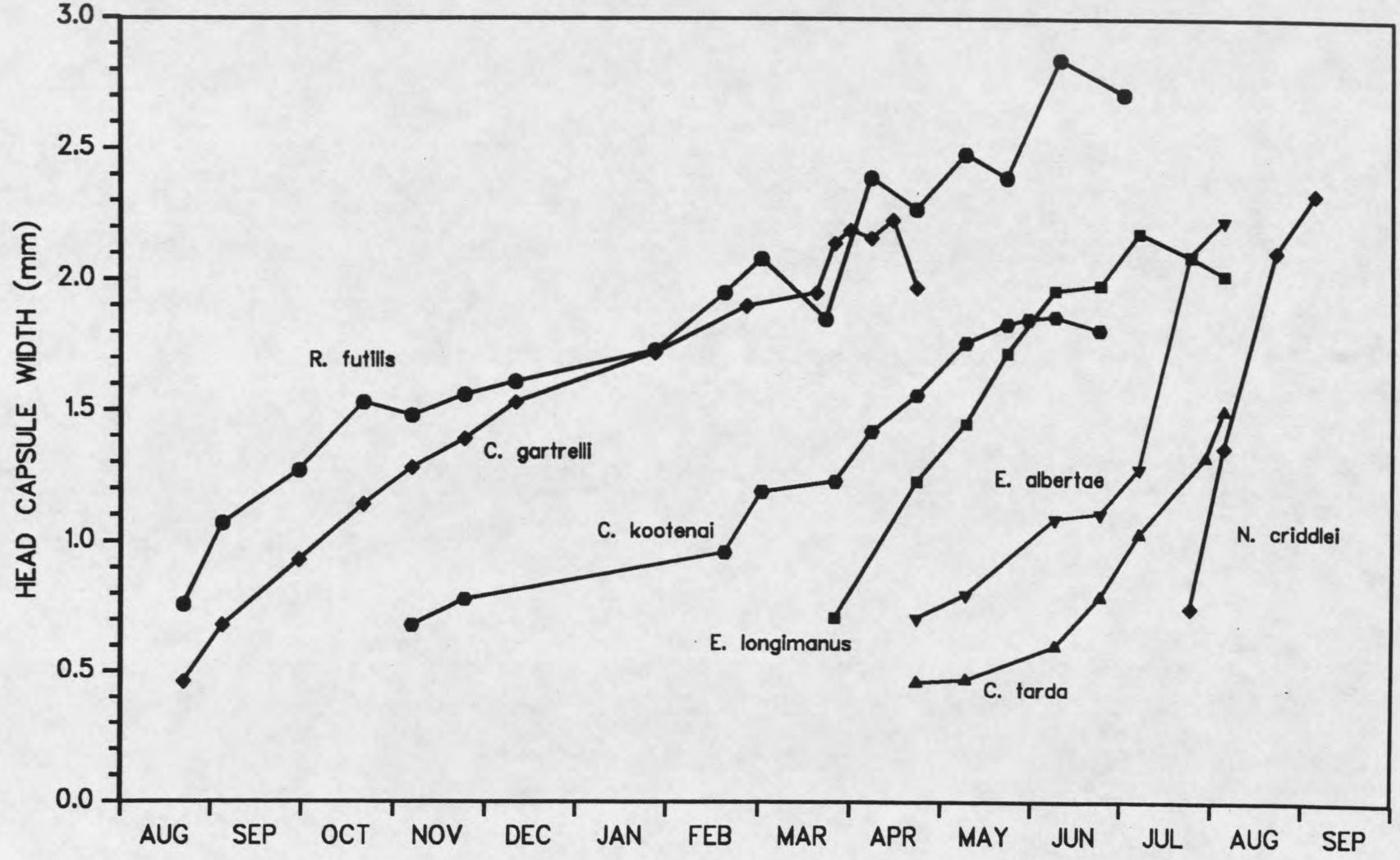

Figure 9. Mean head capsule width of 7 species of Heptageniidae occurring in the Gallatin River near Bozeman. Only nymphs derived from eggs laid in 1984 are shown.

The genus *Cinygma* is represented in the Gallatin drainage by a single species, *C. integrum*. This species occurs in many small mountain streams which have organic debris present. They are seldom very common and they are always found in very reduced current on organic substrates or in areas of accumulating debris. No other heptageniid species is normally collected closely with *C. integrum*.

The genus *Cinygmula* is represented in the drainage by 6 of the 11 described, nearctic species. These species are characterized by very tight spacing, seasonally and longitudinally. They are further characterized by uniformity of the nymphs. All of these species appear to be ecologically identical, but each species is separated from the others seasonally or longitudinally. All species were reared, but positive recognition of the species was not achieved for the nymphs. Nymphs collected from the mainstem of the river directly west of Bozeman can be identified to species based on body size at the collection date. The reliability of these determinations appeared perfect based on numerous reared individuals at that site. Such determinations in other parts of the drainage were less than perfect, but still usually correct. The existence, longitudinal position and seasonality of *C. par* were hypothesized, prior to the discovery of that species, based on the packing of the other species. *Nixe criddlei* probably occupies the position of a fourth species of *Cinygmula* in the mainstem of the river near Bozeman. The *Cinygmula* species of the drainage do not occur in water as warm as do species of *Nixe*. They are otherwise very similar ecologically.

Rhithrogena is represented by one very large and distinctive species, *R. robusta*, and by three smaller species which cannot be reliably distinguished as nymphs. The three small species are seasonal and longitudinal ecological equivalents. *Rhithrogena morrisoni* and *R. undulata* occur in the lower parts of the mainstem, with *R. morrisoni* completing its growth and emerging well before *R. undulata*. *Rhithrogena futilis* occurs in all streams of the drainage except for the lowermost parts of the Gallatin Valley and the most alpine sites. Its longitudinal range overlaps that of *R. morrisoni*, but not that of *R. undulata*. There has been for some time a question as to whether *Rhithrogena futilis* and *R. hageni* Eaton are distinct. In the Gallatin drainage, only one of these species exists, it is very common and widespread, and it morphologically fits the description of *R. futilis* better than *R. hageni*. *Rhithrogena futilis* is junior to *R. hageni* should they be found to be synonymous. *Rhithrogena futilis* completely spans the longitudinal range of *R. robusta*, but it is much smaller and favors less torrential current velocities.

Epeorus, like *Rhithrogena* contains three very similar species, which are ecologically equivalent and separated from one-another seasonally or longitudinally, and a fourth much larger species, which is not ecologically close to the other species. Unlike *Rhithrogena*, all *Epeorus* species are recognizable as nymphs. The large species, *E. grandis* is placed in the subgenus *Ironopsis* and occurs abundantly only in very swift water of cold mountain streams. It does not occur in mountain spring creeks and is very rare in the mainstem of the river. It is frequently aggregated on logs which have lost their bark or on boulders with just a thin sheet of water falling over them. The three smaller species are members of the subgenus *Iron*. *Ironopsis* and *Iron* are sometimes recognized as distinct genera (Allen and Murvosh, 1983). *Epeorus longimanus* and *E. albertae* overlap in the mainstem of the river near Bozeman and exhibit a fairly commonly observed longitudinal shift in habitat. *Epeorus longimanus*, which is near the lower end of its longitudinal range is found in large numbers, highly congregated on rocks in rapid current. *Epeorus albertae*, which is near the upper end of its longitudinal range, is found in smaller numbers, on rocks in more moderate currents. These rocks are, however, very numerous and the swarms of *E. albertae* at this site dwarf those of *E. longimanus*. Each species at the center of its range occupies similar habitat. *Epeorus deceptivus* occurs higher in the drainage sometimes overlapping the range of *E. longimanus*, but not that of *E. albertae*. It completes its growth and emerges later in the year than *E. longimanus*.

All three of the Rocky Mountain species of *Heptagenia* occur in Montana, but only the poorly known *H. adequata* occurs within the Gallatin drainage. This species is commonly encountered in the lower parts of the Gallatin and East Gallatin Rivers as well as the upper Missouri River and the Madison River near its mouth. The nymphs prefer slightly silty rocks in areas of reduced currents. They are never very abundant within the drainage. In the upper, more vegetated parts of the Madison River *H. solitaria* McDunnough occurs abundantly and is frequently associated with organic substrate. These two species were not taken together. *Heptagenia elegantula* (Eaton) is confined to much warmer, more silted streams than occur within the Gallatin drainage.

Two species of *Nixe* occur within the drainage. Both species occur only in the streams of the Gallatin Valley or in foothill streams and are restricted to the summer season. *Nixe criddlei* occurs mostly upstream of *N. simplicioides* and it emerges later in the season. These two species differ as adults primarily in color, but they are distinguishable as nymphs also. They are sometimes taken together, but in those cases one species always greatly predominates numerically. *Nixe simplicioides* is much more common in the warmer rivers adjacent to the Gallatin drainage.

Stenonema terminatum (Walsh) was taken from the mouths of the Jefferson and Madison rivers and from the Missouri River at the mouth of the Gallatin River, but was not taken from even the lowest part of the Gallatin River. Adults undoubtedly range into the Gallatin drainage. It is another slow-water species preferring warmer temperatures than found in the Gallatin drainage. A similar species, ecologically, *Leucrocuta petersi* Allen occurs still further downstream in the prairie streams. Both of these species appeared to be expanding their range upstream during the course of this study.

Family Leptophlebiidae: This family is represented in the Gallatin drainage by a single genus, *Paraleptophlebia*, with four species (Table 9). *Leptophlebia gravastella* (Eaton) and *Traverella albertana* (McDunnough) were taken from neighboring drainages on all sides, but they appear restricted to warmer water than found within the Gallatin drainage. Both of these species, however, expanded their range toward the Gallatin drainage during the course of this study.

Table 9. Leptophlebiidae, Leptohyphidae, and Caenidae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Leptophlebiidae					
Paraleptophlebia bicornuta (McDunnough)	4430000	Us	M	Sp	CG
P. debilis (Walker)	3300000	Us	M	Cb	CG
P. heteronea (McDunnough)	4333000	Uw	M	Cb	CG
P. vaciva (Eaton)	0000024	Uw	M	Cb	CG
Leptohyphidae					
Tricorythodes minutus Traver	4420000	As	M	Sp	CG
Caenidae					
Caenis simulans McDunnough	2000000	As	LM	Sp	CG

All four species of *Paraleptophlebia* in the Gallatin drainage feed as collector-gatherers, and prefer areas of reduced currents. *Paraleptophlebia heteronea* was the most frequently collected species. It takes nearly a full year to complete its growth and it occurs over the widest longitudinal range. It is replaced by *P. vaciva* in very high mountain streams. There is usually a substantial area between the range of these two species, where no species of *Paraleptophlebia* occur. This is probably due to the preferred habitat being rare or unpredictable in high gradient streams. *Paraleptophlebia heteronea* is replaced in the late summer, over the lower half of its range, by a pair of species, *P. bicornuta* and *P. debilis*. These two species are strongly separated spatially. *Paraleptophlebia bicornuta* is found on silty rocks and wood and *P. debilis* is found on submerged vegetation. *Paraleptophlebia bicornuta* exhibits very rapid growth late in the season (Figure 10). *Paraleptophlebia debilis* exhibits unusually large fluctuations in its population density from

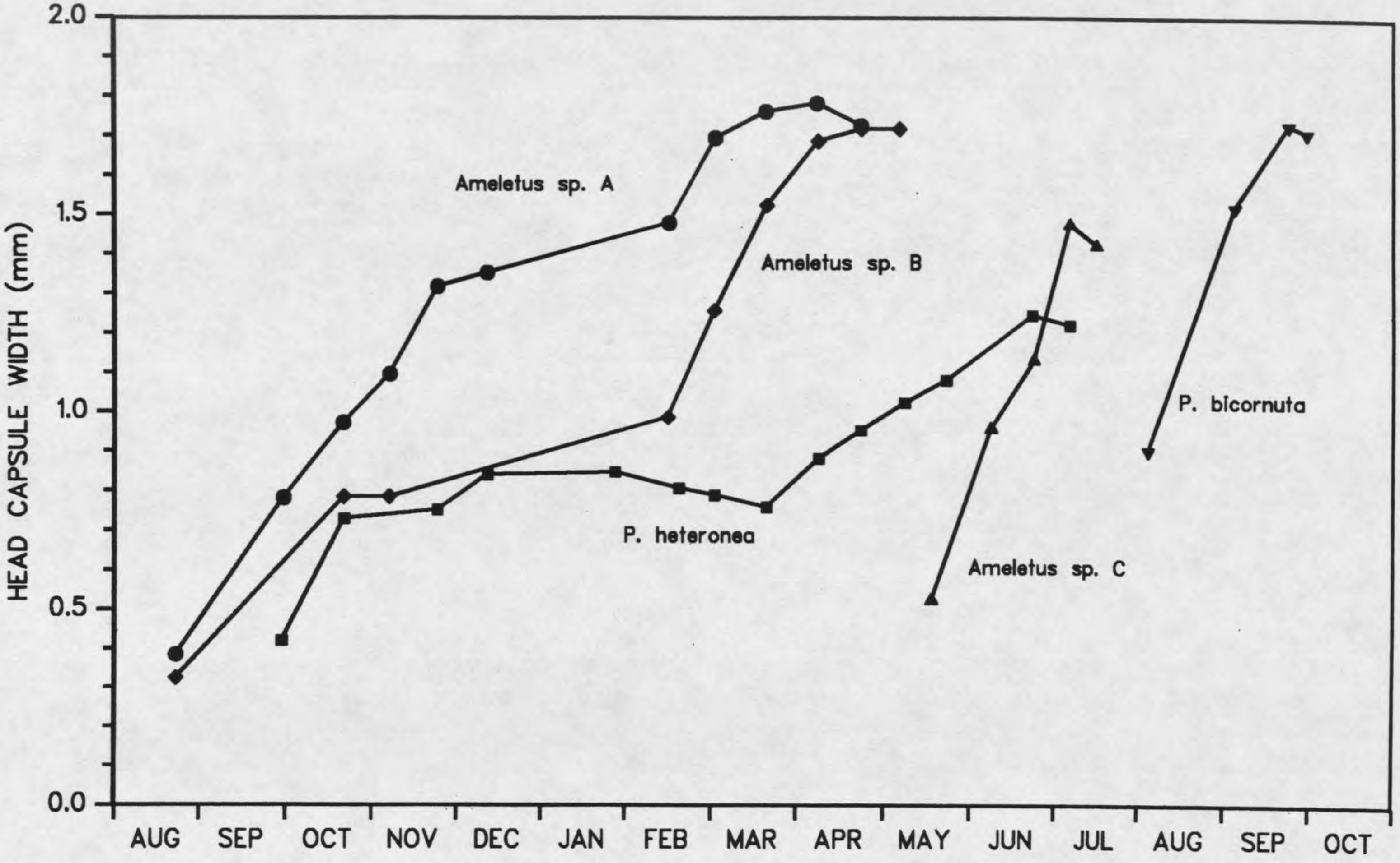

Figure 10. Mean head capsule width of lotic Siphlonuridae and Leptophlebiidae occurring in the Gallatin River near Bozeman. Only nymphs derived from eggs laid in 1984 are shown.

year to year. This is probably in direct response to the availability of submerged vegetation. Submerged vegetation, in turn, depends largely on the magnitude of flooding the previous spring, and also on the water level during the summer. *Paraleptophlebia bicornuta* shows no such population fluctuation, as silty rocks are always to be found during the late summer.

Family Leptohyphidae: This family is not well represented in cold northern waters. A single species, *Tricorythodes minutus*, occurs in the Gallatin drainage. This species is restricted to the lower parts of the mainstem and to warmer streams across the Gallatin Valley (Table 9). It may be extremely abundant. In the uppermost part of its range it occurs only for a very short time during the late summer. In the lower parts of the drainage it occurs throughout the year, but overwintering nymphs are never very abundant. Whether the upper-most populations are derived from eggs deposited on the site the previous year, or derived from individuals migrating upstream each summer is not known.

Family Caenidae: This family is poorly represented in cold waters with rapid current. A single species *Caenis simulans* expanded its range upstream to enter the Gallatin drainage near the conclusion of this study. This species favors warm lentic, or nearly lentic water in the lower Gallatin Valley (Table 9). It is not very common in the drainage. *Caenis youngi* Roemhild occurs in abundance in some of the lakes in the headwaters of the Madison drainage very near the Gallatin-Madison divide and it may eventually be found within the Gallatin drainage. Species of *Brachycercus* and *Cercobrachys* occur downstream of the Gallatin drainage in warmer, more silted rivers.

Family Siphlonuridae: Two genera and at least 10 species of siphlonurids occur in the Gallatin River (Table 10). Most species, of this family, prefer areas with little current. They may be found at the margins of streams or in backwater areas, though none of these species tolerate the very warm, stagnant waters that may be occupied by *Callibaetis*. *Siphlonurus occidentalis* occurs along the shorelines of some lakes and also in cooler ponds of the drainage, but all remaining species of the family are known only from lotic environments.

Table 10. Siphlonuridae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Ameletus sp. A	3333000	Uw	M	Sw	CG
A. sp. B	3333200	Uw	M	Sw	CG
A. sp. C	3300000	Us	M	Sw	CG
A. sp. D	0000034	Uw	MS	Sw	CG
A. sp. E	0000333	?	GM	Sw	CG
A. sp. F	0000320	U?	M	Sw	CG
A. sp. G	0000002	U?	M	Sw	CG
A. sp. H	0000022	U?	M	Sw	CG
Siphlonurus autumnalis McDunnough	3300000	Us	M	Sw	CG
S. occidentalis Eaton	3333332	As	L	Sw	CG

The genus *Ameletus* is represented by at least eight species, none of which were positively identified. Each species either had several names available that could be applied with equal confidence, or none of the available names seemed applicable. All eight species were reared, and they are easily recognized as both adults and nymphs. They were coded in their order of discovery. The naming of these species will remain uncertain until the nearctic species are revised. As a group, species of *Ameletus* are ecologically similar to *Callibaetis* and *Siphlonurus*, but prefer cooler, more lotic waters. All 8 species are active swimmers and feed on fine detritus as collector-gatherers.

The species of *Ameletus* utilize all three of the primary dimensions of ecological separation that are left to species of similar habits and trophic type. They are separated temporally, longitudinally or spatially. Frequently two and rarely three species occur together and even emerge simultaneously. This leaves in doubt several nymphal associations, which were based only upon the simultaneous occurrence of mature nymphs, or exuviae, and freshly emerged subimagoes. In all cases where two species occur, one species favors organic substrates and very reduced current and the other species favors mineral substrates with more pronounced current. If three species occur as mature nymphs at a single site, one is always near the end of its longitudinal range. In the mainstem of the river near Bozeman, three species occur. Species A and B have similar life cycles and body size (Figure 10), but are very well separated spatially. Species A prefers mineral substrates and B prefers organic substrates in very reduced current. Species C, which also occurs at this site, has a summer life cycle. Species E is unusual in favoring stronger currents than the other species. Species E is also the largest of these species and may be semivoltine. Only a single species of *Ameletus* was taken as swarming adults and only upon one occasion. These males were swarming about 20 meters above the water and were netted with a long handled net, while clinging to the face of cliff whenever a gust of wind blew them within range. This may explain why swarming has not been reported in this large genus.

The genus *Siphlonurus* is represented in the Gallatin drainage by two species. *Siphlonurus occidentalis* is widespread in lentic or essentially lentic waters throughout the drainage. It occupies a habitat intermediate to that occupied by *Callibaetis* and *Ameletus*. Like *Callibaetis*, *S. occidentalis* is often represented by spatially separated and asynchronous populations which have a total emergence period second in duration only to *Baetis tricaudatus*. Voltinism for this species cannot be determined in the field. *Siphlonurus autumnalis* was first taken while rearing nymphs presumed to be *S. occidentalis*. The species is very different from *S. occidentalis* as adults, but very similar as nymphs, until the color pattern of the adult becomes visible through the nymphal cuticle. These two species are spatially separated in a manner similar to many *Ameletus* species. *Siphlonurus occidentalis* prefers organic or heavily silted substrates in areas of no or very reduced current while *S. autumnalis* prefers clean mineral substrates with more current. The identity of a newly emerged subimago can be rather reliably predicted at a distance of several meters based on the habitat from which it emerged. The nymphs of *S. autumnalis* may be found quite deep in crevices between rocks, and were found only in small numbers until very near emergence. The emergence of *S. autumnalis* is completed before that of *S. occidentalis* at this site contrary to the situation mentioned in the description of *S. autumnalis* (McDunnough, 1931). Neither of these species is present as active nymphs during the winter months.

Plecoptera

Representatives of all nine nearctic families of Plecoptera or stoneflies occur in the Gallatin River Drainage. Thirty-six genera and 67 species were taken during this study, but a few more species may be present. Stoneflies are by far the best collected order of aquatic insects in Montana. Only for this order are county records currently meaningful in Montana. New county records are, in fact, more difficult to obtain for Plecoptera than are new state records for Ephemeroptera or Trichoptera. Only three species, *Capnia petila*, *Isoperla pinta* and *Paraperla wilsoni* were added to the known fauna of the Gallatin drainage. Twelve species, *Isocapnia vedderensis* (Ricker), *Utacapnia trava* (Nebeker & Gaufin), *Despaxia augusta* (Banks), *Zapada frigida* (Claassen), *Yoraperla mariana* (Ricker), *Kogotus modestus* (Banks), *Megarcys subtruncata* Hanson, *Calineuria californica* (Banks) *Suwallia lineosa* (Banks), *Sweltsa lamba* (Needham & Claassen), *Sweltsa revelstoka* (Jewett) and *Utaperla sopladora* (Ricker) were reported from the drainage by Gaufin *et al.* (1972), but were not collected, or recognized during this study. Two of these, *Yoraperla mariana* and *Calineuria californica* were apparently misidentified and were deleted from the county list by Baumann, Gaufin and Surdick (1977). The occurrence, within the Gallatin drainage of some of the remaining species also seems doubtful. If present, these species must be of limited seasonal or spatial distribution within the drainage.

While stoneflies are relatively well collected, they are not so well known biologically. The majority of specifically identified collections are of adults only. This provides a basis for describing the distribution of the species, the longitudinal zonation of the species, and seasonality of the adults, but provides no information on microhabitat needs, seasonality of growth or even the length of the life cycle.

In the Gallatin drainage 72% of the known Plecoptera life cycles are univoltine-winter, 10% are univoltine-summer, 12% are semivoltine and 5% are largely asynchronous. The asynchronous life cycles all occur in species that are largely restricted to springs. Figure 11 summarizes the seasonality of adults and nymphs of 26 species of Plecoptera that are common in the mainstem of the river near Bozeman. Two main emergence periods are evident. The winter stoneflies emerge mostly during March and April; while the summer stoneflies emerge from mid June through August. The later part of May through the first week of June is remarkably poor collecting for adult stoneflies at that site. Stonefly nymphs are best sampled in late March, while many are well grown, but before the emergence of important early species, *Skwala parallela*, *Taenionema pacifica*, *Zapada cintipes* and *Prostoia besametsa*. Sampling at this time may miss one important species, *Isoperla quinquepunctata*, which is of very small body size at that season. Autumn sampling is plagued by the small size of many specimens and by rapidly changing population sizes.

Even intensive benthic sampling will take only a small fraction of the Plecoptera species that are present at a site. Twelve of the 26 species common in the Gallatin River near Bozeman are significantly represented only by adults. Most of the species which are rare or sporadic at this site are known only from adults or from exuviae. The presence of hyporheic species is one of the reasons for this. Thirty-seven percent of all the stonefly species known from the Gallatin drainage are hyporheic. These species are poorly represented in benthic samples until immediately before they emerge. The emergence of these species is relatively highly synchronized and largely independent of annual variation in flow and temperature regimes. The degree of synchronization and the extent to which emergence is restricted to areas of upwelling water may be an indication of occurrence

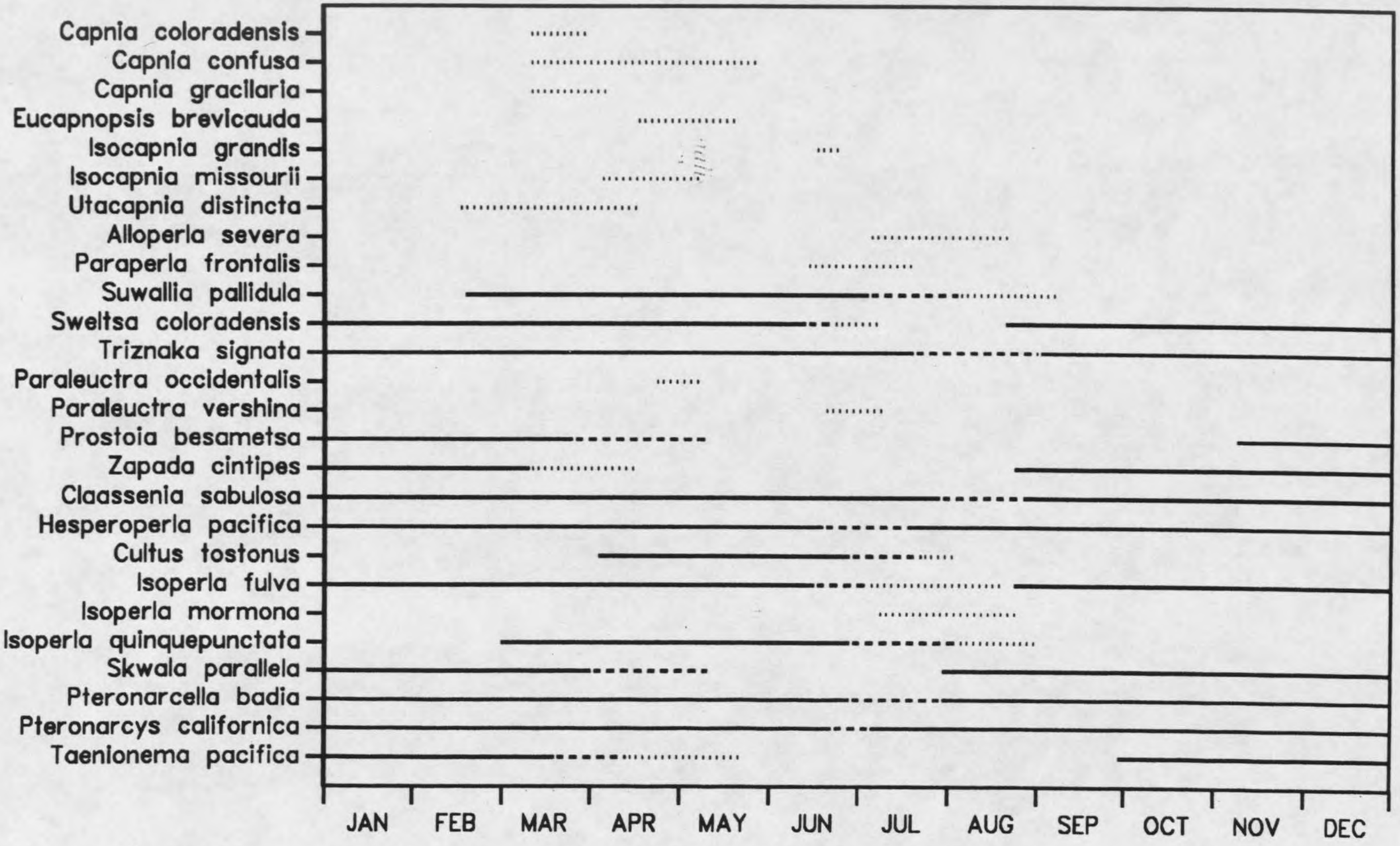

Figure 11. Phenology of 26 Plecoptera species that were common in the Gallatin River near Bozeman during 1984. Solid line represents the occurrence of nymphs only, dotted line of adults only and dashed line the occurrence of both.

deeper in the substrate. The nymphs of hyporheic species are rarely collected, but may be taken at night or in emergence traps. Hyporheic species do not interact substantially with other species and they do not feed while at shallow substrate depths.

Many stonefly species which are not hyporheic occur in the benthos at relatively low densities. This may not be reflected in the abundance designations given to the species, however, because of the general success of early-morning vegetation sweeps in taking Plecoptera adults. Species occurring at low densities may also be concentrated near shore prior to emergence, or leave relatively abundant exuviae along the shorelines. These species are difficult to work with at other times and are poorly represented in the quantitative data sets.

Relatively few species of stoneflies which occur in the benthos have very specialized habitats. Over 80% of the non-hyporheic Plecoptera species are generally distributed in the gravel, cobble or boulder riffles that make up the majority of the lotic substrates within the drainage. Of the remaining species, two are largely restricted to specialized habitats along the stream shorelines and five species are largely confined to springs. All non-hyporheic stoneflies from the drainage are either clingers (62%) or climbers (38%). The unspecialized habitats and habits of most stonefly species may be largely responsible for the relatively low densities of the nymphs compared to the adults.

Plecoptera are well represented in all seven of the longitudinal zones. The greatest number of stonefly species occurs in cold mountain streams (41 species) and the least occur in the highest sites (25 species). Seven species are restricted to a single longitudinal zone and four species occur in all seven of the longitudinal zones.

None of the 67 species of Plecoptera known from the Gallatin drainage have their maximal abundance designation as sporadic and only six species have their maximal abundance designation as rare. Four of these species, *Capnia coloradensis*, *Mesocapnia oenone*, *Isoperla pinta* and *Setvena bradleyi* were all collected many times, but never in very large numbers. This is unlike the situation for mayflies and caddisflies where the most rare species are also very rarely encountered. The remaining two of the six globally rare stonefly species, *Isocapnia hyalita*, and *Paraperla wilsoni* are hyporheic and probably not really rare. These species have a short emergence period.

Analysis of gut contents supports the usual separation of stoneflies into two trophic groups. The families Perlidae, Perlodidae and Chloroperlidae are primarily carnivores, while the remaining five families are shredders, primarily detritivorous, or less frequently, herbivorous. For the 67 species known from the drainage, 48% are predators and 52% are shredders. Chironomids and simulids are by far the most frequently taken prey, but essentially all taxa of suitable size may be taken. Carnivorous stoneflies generally swallow their food whole, making identification of the prey very simple. Many specimens were fixed with a half swallowed chironomid larva in their mouths. The nymphs of hyporheic species were always found to contain no food. The trophic status of these cannot be confirmed, but likely follows taxonomic lines. Sometimes an individual perlid or perlodid was found to take up herbivorous feeding, packing the gut with filamentous algae or detritus with minimal intake of animal material. Richardson and Gaufin (1971) reported this for 6 of 133 specimens of *Hesperoperla pacifica* and *Claassenia sabulosa*. The significance of this is unknown. Individual feeding specialization appears to be common, even in insects, based on gut contents observed.

As carnivorous stonefly species are rather unspecialized in terms of food taken, it is their microhabitat, seasonality and longitudinal zonation which must account for the resource partitioning among the species. Close encounters of similarly sized carnivorous stoneflies of any species usually results in evasive or aggressive behavior resulting in wasted energy and lost feeding time. Peckarsky and Penton (1985) concluded from experimental studies that interference is the major mechanism of competition among carnivorous stoneflies. Competition is probably responsible for the limited number of similar sized species of carnivorous stoneflies at any site. The families of carnivorous stoneflies as represented in the Gallatin drainage are ecologically isolated in terms of microhabitat. Perlids occupy large boulders in fast water, chloroperlids are either hyporheic or occupy gravel and cobble substrates in moderate current and perlodids occupy intermediate habitats.

The detritivorous Plecoptera are also unspecialized in terms of food taken. Individuals living on rotten wood eat mostly wood, those living in leaf packs eat leaf material, while those living in mats of algae or moss, eat algae or moss. All of the detritivores occasionally take animal food and may become fiercely carnivorous when held in captivity. Detritivorous stoneflies are frequently highly aggregated in areas of organic debris accumulation. They are poorly represented in the quantitative data sets.

Most species of detritivorous stoneflies in the drainage appear in the benthos as small nymphs in late summer or fall, grow throughout the winter and emerge before spring run-off. This closely parallels the accumulation and flushing of organic debris in the stream. In the mainstem of the river near Bozeman only four species of detritivorous stoneflies are common in benthic samples. These species are taxonomically unrelated, with each in its own genus and three families represented. The seasonality of growth of these species (Figure 12) suggests that body size is of great importance in resource partitioning.

Family Capniidae: This family is represented in the Gallatin drainage by 13 species (Table 11). All are mostly hyporheic and are taken in the benthos in significant numbers only near or during the emergence of the adults. The genus *Capnia* is represented by six species. These small, winter stoneflies emerge from mid February to early June and are frequently very abundant. All species overlap longitudinally and seasonally to some extent except for the two longitudinal extremes. *Capnia petila*, known from small mountain streams, was not taken with *C. vernalis*, which is very rare as far upstream as Bozeman. *Capnia confusa* is largely confined to the mainstem and to the larger tributaries and is

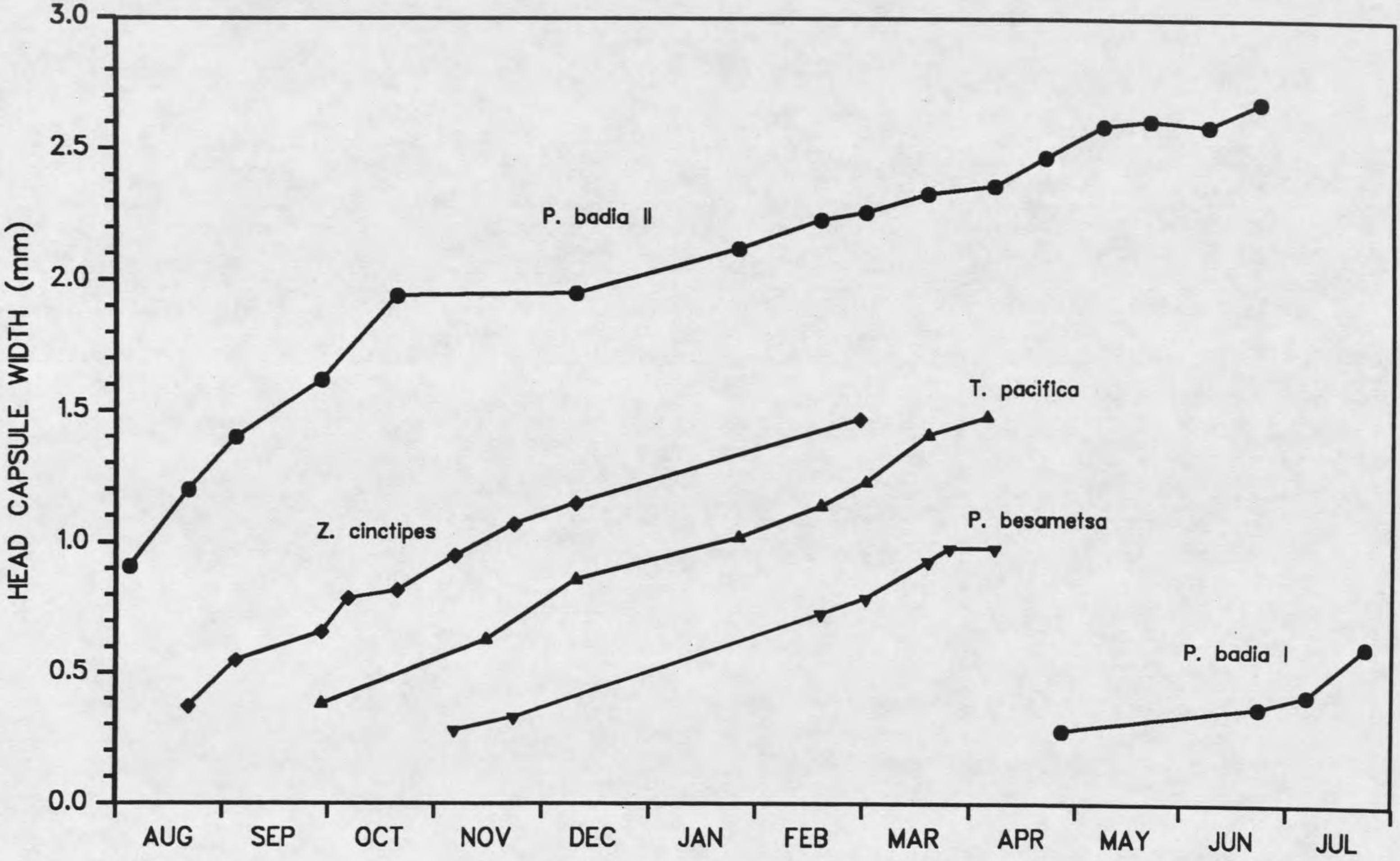

Figure 12. Mean head capsule width of detritivorous stoneflies occurring in the Gallatin River near Bozeman during 1984 and 1985.

replaced by *C. gracilaria* in smaller streams. *Capnia nana* occurs abundantly in the same streams as *C. gracilaria*, and also occurs in much smaller headwater streams, and is sometimes associated with mountain lakes and seeps. *Capnia coloradensis*, while widespread in occurrence is never dominant numerically. This species has a relatively short emergence period. This may indicate that the nymphs occur relatively deep in the substrate. None of the nymphs of *Capnia* were identified to species unless taken just prior to emergence when the adult characters are fully formed under the nymphal skin. The nymphs are, however, only rarely taken in significant numbers at other times.

Table 11. Capniidae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Capnia vernalis Newport	3300000	Uw?	H	?	SD?
C. confusa Claassen	4444320	Uw?	H	?	SD?
C. gracilaria Claassen	2234432	Uw?	H	?	SD?
C. coloradensis Claassen	1222200	Uw?	H	?	SD?
C. nana Claassen	1222344	Uw?	H	?	SD?
C. petila Jewett	0000223	Uw?	H	?	SD?
Eucapnopsis brevicauda (Claassen)	4444433	Uw?	H	?	SD?
Isocapnia crinita (Needham & Claassen)	3200000	?	H	?	SD?
I. missourii Ricker	3200000	?	H	?	SD?
I. grandis (Banks)	0300000	?	H	?	SD?
I. hyalita Ricker	0000020	?	H	?	SD?
Mesocapnia oenone (Neave)	0000022	Us?	H	?	SD?
Utacapnia distincta (Frison)	4444310	Uw?	H	?	SD?

The genus *Isocapnia* is frequently used as an example of hyporheic stoneflies and is represented in the Gallatin drainage by four species. Two of these, *I. crinita* and *I. hyalita*, have their type locality within the Gallatin drainage. The type locality of *I. missourii* is just downstream of the Gallatin drainage. The large, elongate nymphs can be collected at night while headlamping around springs, but are more easily taken in emergence traps as they emerge from the hyporheos and from the river in a single night. They emerge most heavily in areas of upwelling water, but may also emerge some distance from the stream even in areas of standing water. The emergence period appears completely independent of annual variation in temperature and flow and it is very predictable and also of very short duration. *Isocapnia missourii* and *I. crinita*, can be common in the lower reaches of the river during their short emergence periods. The large adults are conspicuous on snow or bridges. Both species are rare as far upstream as Bozeman. *Isocapnia grandis* has been taken only from the mainstem of the river immediately west of Bozeman. There it was consistently taken in large numbers each year, from the 15th to 23rd of June regardless of flow and temperature conditions. This species appears to have only normal males, while the remaining three species have both normal and dwarf males. *Isocapnia grandis* emerges simultaneously with the large hyporheic chloroperlid, *Paraperla frontalis*. The remaining species *I. hyalita*, occurs in smaller streams and was never collected in large numbers.

The remaining three genera of the Capniidae are each represented by a single species. *Utacapnia distincta* emerges abundantly from the mainstem upstream well into Yellowstone National Park. It also occurs in the larger tributaries but not in small mountain streams. It is the first stonefly to emerge from the lower sites, appearing by mid February. *Capnia nana* emerges just as early from much higher sites. The majority of capniid nymphs taken in routine fall and winter samples belong to this species. Its relatively long emergence period probably also reflects its shallow occurrence in the substrate. The emergence of *U. distincta* precedes upstream and is completed by the middle of May. *Utacapnia trava* occurs abundantly in the neighboring Yellowstone River drainage, but was not taken in the Gallatin drainage. *Eucapnopsis brevicauda* is abundant throughout much the drainage. This species emerges later in the season than most of the previous species. The emergence of *Eucapnopsis* starts around the middle of April and is unusually simultaneous throughout its broad longitudinal range in the drainage. *Mesocapnia oenone* occurs only in small mountain streams and emerges from late August into November. It is seldom common.

Family Leuctridae: The family Leuctridae is represented by six species in two genera (Table 12). Like the Capniidae, all species are hyporheic and are only rarely taken in benthic samples except during the emergence of the adults. The species of this family are most abundant near spring seeps. Emergence of the species in this family occurs later in the season and more synchronously than in the family Capniidae. This may indicate that they occur deeper in the substrate than the family Capniidae. *Paraleuctra occidentalis* extends the furthest downstream, and is by far the most frequently collected species of the family.

Table 12. Leuctridae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Paraleuctra occidentalis (Banks)	2333333	Uw?	H	?	SD?
P. vershina Gaufin & Ricker	0232200	Uw?	H	?	SD?
P. forcipata (Frison)	0000033	Uw?	H	?	SD?
P. purcellana (Neave)	0000033	Uw?	H	?	SD?
P. rickeri Nebeker & Gaufin	0000033	Uw?	H	?	SD?
Perlomyia utahensis Needham & Claassen	0000030	Uw?	H	?	SD?

Family Nemouridae: The family Nemouridae consists of stout bodied species, poorly adapted to deep penetration of the substrate. They are frequently abundant in benthic samples. Ten species in six genera are known from the Gallatin drainage (Table 13). Several species are relatively specialized. Both *Podmosta decepta* (Frison) and *P. delicatula* (Claassen) have been reported from the drainage, but only nymphs of this genus were taken during this study. They are abundant only in certain mountain springs choked with *Fontinalis* sp. They do not occur in direct association with other species of stoneflies. The same is true of the two species of *Malenka*. Both species have been taken only from watercress or moss choked springs at a wide variety of elevations. *Amphinemura banksi*, though never abundant, is widely distributed in small mountain streams again mostly in association with springs and dense bryophyte growth. All of the nemourids associated with springs are prone to herbivorous feeding. *Visoka cataractae* is commonly present in small, high gradient streams, but is seldom very abundant.

Table 13. Nemouridae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Amphinemura banksi Baumann & Gaufin	3330000	A	S	Cb	SH
Malenka californica (Claassen)	3330000	A	S	Cb	SH
M. flexura (Claassen)	0000033	A	S	Cb	SH
Podmosta sp.	0000030	Uw?	S	Cb	SH
Prostoia besametsa (Ricker)	4444320	Uw	G	Cb	SD
Zapada cintipes (Banks)	4444430	Uw	G	Cb	SD
Z. haysi (Ricker)	0000333	Uw	G	Cb	SD
Z. columbiana (Claassen)	0000033	Uw	G	Cb	SD
Z. oregonensis (Claassen)	0000033	Uw	G	Cb	SD
Visoka cataractae (Neave)	0000033	Uw	G	Cb	SD

Prostoia besametsa is found abundantly throughout the mainstem of the Gallatin River and in its larger tributaries. This species occurs in smaller streams across the Gallatin Valley. The nymphs are active and very abundant in benthic samples during the fall and winter until the spring emergence. It is absent from smaller mountain streams and is an important component of the winter detritivore community where it occurs. Gut contents consist of fine detritus of both shredded and collected origins.

Four species of *Zapada* are known from the drainage (Table 13). These are the dominant winter benthic detritivore in smaller mountain streams where *Prostoia* does not occur. One species, *Z. cintipes* also occurs in downstream areas coexisting with *Prostoia*, but is much larger. The remaining three species are morphologically and ecologically very similar. All are frequently collected simultaneously, though usually a single species greatly predominates numerically.

Family Pteronarcyidae: The giant stoneflies are represented in the Gallatin River system by two species (Table 14). Both species are confined to the mainstem and to the lower reaches of the larger tributaries. *Pteronarcys californica*, the salmonfly is abundant only in the mainstem of the river throughout the Gallatin Canyon. *Pteronarcys* is rare downstream of the canyon in the Gallatin Valley, probably because of the frequency and magnitude of substrate movements in this area. *Pteronarcys* occurs in nearby rivers much larger and warmer than the lower Gallatin if such drastic substrate movement does not occur. The distribution of this species in still lower parts of the river is also affected by periodic low summer flows which may result from irrigation diversions. Salmonflies were observed to die well before trout during periods of reduced flow and increased temperature. Visual inspection of large samples of nymphs suggests that 4 years are needed to complete growth in the Gallatin Canyon. Quantitative analysis of these data is unconvincing, probably because of the large number of instars and differences between sexes. Even the final instar nymphs show a large variation in size, with some overlap between sexes.

Table 14. Smaller families of Plecoptera known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Pteronarcyidae					
Pteronarcella badia (Hagen)	4434200	S	G	Cb	SD
Pteronarcys californica Newport	3343000	S	G	Cb	SD
Taeniopterygidae					
Taenionema pacificum (Banks)	4430000	Uw	G	Cg	SD
T. nigripenne (Banks)	0000342	Uw	G	Cg	SD
Doddsia occidentalis (Banks)	0002442	Uw	G	Cg	SD
Peltoperlidae					
Yoraperla brevis (Banks)	0000134	S	G	Cg	SD

Pteronarcella has a rare bimodal distributional pattern being abundant in the lower river and in the upper river including the lower parts of the larger tributaries. It exhibits depressed population levels in the Gallatin Canyon. This is probably due to direct replacement by *Pteronarcys*. The young nymphs of *Pteronarcys* completely span the size of *Pteronarcella*. *Pteronarcella* has a two-year life cycle in all parts of the river, though this is not immediately apparent because of the delayed appearance of the young nymphs in the benthos (Figure 12). *Pteronarcella* and *Pteronarcys* grow and emerge during warmer seasons than most other detritivorous stoneflies. They also take algae as food more frequently than the other detritivorous stoneflies.

Family Taeniopterygidae: This family is represented in the drainage by three species of important benthic detritivores (Table 14). *Taenionema pacificum* is enormously abundant in the lower river extending upstream into the canyon. It grows throughout the winter and is not adversely affected by complete summer dewatering. It may well respond positively to summer dewatering in terms of density the next winter. In many smaller streams both *Doddsia occidentalis* and *Taenionema nigripenne* are abundant. *Doddsia occidentalis* grows slowly during the fall and winter, emerging mostly in April, while *T. nigripenne* grows more rapidly later in the season and emerges primarily in July.

Family Peltoperlidae: A single species of the family Peltoperlidae is known from Montana and it is common in the Gallatin drainage (Table 14). *Yoraperla brevis* is predictably present in the highest, small mountain streams, which flow throughout the year and is often quite abundant. Unlike most stoneflies, which can be found in small numbers far downstream of their usual habitat, this species seems entirely restricted to alpine sites. It likely has low tolerance to even moderately warm temperature. Despite its small size, numerous collections spanning the emergence period indicate that most individuals require 2 years to complete growth. The species shows considerable variation in adult body size, which probably accounts for the reports of *Yoraperla mariana* in the Gallatin drainage (Gaufin *et al.*, 1972). Possibly some individuals emerge after only 1 year of growth.

Family Perlidae: This family is represented in the Gallatin drainage by three species of large predators (Table 15). All three species require 3 or 4 years to complete growth. Exact determination of the length of the life cycle is impossible based on field data alone because of the uncertain timing of egg hatching and because of the large size range within a single instar and between the two sexes. The three perlid species in the Gallatin drainage as well as a fourth species in the upper parts of the Missouri River are for the most part altitudinally disjunct, but frequently have considerable overlap between adjacent species. This overlap is noticeably greater than occurs in large perlodid stoneflies.

Claassenia sabulosa is dominant in the lower reaches of the mainstem and can be taken only with great effort as far upstream as Bozeman. It occurs in small numbers, as far upstream as the mouth of the canyon, based on collected exuviae. Collection and enumeration of all exuviae from a stretch of the river near Bozeman during 1985 suggest that the species emerges from the river at a density of less than one fully grown individual per 150 m^2. A partial replication of this census in 1989 indicated that this species had become much more common in this section of the river. As growth requires 3 or 4 years and they occur only in fast riffles on large boulders, they may be taken, in benthic samples, more easily than calculated above.

Hesperoperla pacifica is the dominant species of the family in the mainstem of the river upstream of Bozeman and in the warmer tributaries. It occurs with *Claassenia sabulosa* for some distance in the lower river. The distribution of these two species in the lower river is disturbed by periodic dewatering for irrigation diversions. *Hesperoperla pacifica* is dominant above the dewatered area and *C. sabulosa* below. Individuals of both species were found dead in large numbers following hot days with no flow. A new year class appears in the fall when flow resumes. At first, *H. pacifica* predominates, arriving from upstream sources. If flow is maintained throughout the next summer, *C. sabulosa* becomes increasingly abundant, achieving eventual dominance. Emergence of adults is very limited from this area for two summers following dewatering. *Hesperophylax pacifica* occurs also in large, nearly isothermal springs within the drainage. Here the size of the adults, form of the wings and season of emergence are all extremely variable compared to the rest of the drainage.

Table 15. Perlidae and Perlodidae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Perlidae					
Claassenia sabulosa (Banks)	3200000	S	G	Cg	Pr
Hesperoperla pacifica (Banks)	2344310	S	G	Cg	Pr
Doroneuria theodora (Needham & Claassen)	0111232	S	G	Cg	Pr
Perlodidae					
Isoperla mormona Banks	4300000	Us	G	Cg	Pr
I. quinquepunctata (Banks)	4432000	Us	G	Cg	Pr
I. fulva Claassen	4444300	Uw	G	Cg	Pr
I. fusca Needham & Claassen	0000024	Uw	G	Cg	Pr
I. pinta Frison	2200000	Uw	S	Cb	Pr
I. petersoni Needham & Christenson	0002230	Uw	GM	Cg-Cb	Pr
I. sobria (Hagen)	0000333	Uw	M	Cb	Pr
Isogenoides elongatus (Hagen)	3000000	Uw	G	Cg	Pr
Skwala parallela (Frison)	3443100	Uw	G	Cg	Pr
S. curvata (Hanson)	0002330	Uw	G	Cg	Pr
Megarcys signata (Hagen)	0003200	Uw	G	Cg	Pr
M. watertoni (Ricker)	0000034	Uw	G	Cg	Pr
Setvena bradleyi (Smith)	0000002	S	GS	Cg	Pr
Cultus tostonus Ricker	4320000	Us	G	Cg	Pr
Diura knowltoni (Frison)	0112320	Uw	G	Cg	Pr
Pictetiella expansa (Banks)	0112230	Uw	G	Cg	Pr
Kogotus nonus (Needham & Claassen)	0003331	Us	G	Cg	Pr

Doroneuria theodora is the most alpine species of perlid in the Gallatin drainage. It occurs commonly in smaller and colder streams than does *Hesperoperla pacifica*, but it does not extend into the most upstream tributaries. *Hesperoperla pacifica* and *D. theodora* overlap for some distance in larger mountain streams. *Doroneuria theodora* is only very rarely taken from the longitudinal zone where *Claassenia sabulosa* occurs. These probably represent individuals washed into the river from smaller tributaries. *Doroneuria theodora* is rather frequently represented by a sporadic individual downstream of larger populations. This may indicate that its distribution is limited by biological interactions rather than directly by physical conditions.

Another perlid species, *Acroneuria abnormis* (Newman) has been greatly expanding its range across Montana. It now occurs abundantly in the Missouri River just 40 km downstream of the Gallatin River. It occurs with *Claassenia sabulosa* and may be replacing that species in the lower part of its range. As mentioned earlier, *Claassenia sabulosa* is itself extending its range upstream in the Gallatin drainage.

Family Perlodidae: The family Perlodidae is well represented in the drainage with nine genera and 18 species (Table 15). Ecologically they are best discussed in three size groups, small, medium and large. The large perlodids in the river are all rather similar in size with head capsule widths near 4.0 mm when fully grown. The medium sized perlodids have ultimate head widths between 2.5 and 3.3 mm. The small perlodids have maximal head capsule widths between 1.3 and 2.2 mm. Most sites, at a given time, have only one common species of perlodid in each size category. This count excludes the few species which have specialized habitats and those at grossly different stages of body growth.

The large perlodids frequent smaller substrate sizes than their perlid counterparts. The large perlodids form a longitudinal progression similar to the perlids. Six species are involved with *Isogenoides elongatus* occurring lowest within the drainage. This species was recorded in the river near Bozeman in 1951, but does not seem to approach that far upstream currently. It occurs with *Skwala parallela* for some distance in the lower river and is clearly the more dominant below the confluence with the East Gallatin. The distribution of these two species may be affected in a way similar to the perlids *Hesperoperla pacifica* and *Claassenia sabulosa* by periodic dewatering of part of the river. *Skwala. parallela* is the only large perlodid to occur in the mainstem of the river from Bozeman upstream to Yellowstone National Park. It does not occur in any of the tributaries upstream of Bozeman except the lower reaches of Taylor Creek and West Creek. *Skwala parallela* is however, abundant in small, but warmer tributaries of the East Gallatin drainage. Both *S. parallela* and *Isogenoides* complete their growth in a single year. Near Bozeman, *S. parallela* grows very rapidly in the late summer and fall, reaching the final instar by mid-winter (Figure 13). The final instar takes about 3 months to complete body growth. Females are substantially larger than males.

Skwala parallela is replaced upstream by *S. curvata*. These two species occur very near one-another throughout the canyon area, where *S. parallela* occupies the mainstem and *S. curvata* the larger mountain streams. The nymphs of both were reared many times and can be reliably distinguished by color pattern. The nymphs have not been taken together at any site. The adults were taken together, though only near the mouths of tributary streams.

In the mainstem of the Gallatin River, West Fork Creek and Taylor Creek, *Skwala curvata* is replaced upstream by *Megarcys signata*. Unlike the two species of *Skwala*, which appear to have no overlap, *S. curvata* and *M. signata* do overlap for a short distance on many streams. *Megarcys signata* is replace in turn upstream by *M. watertoni*, which is ubiquitous in the headwater streams of the drainage. Again, like the two species of *Skwala*, the two species of *Megarcys* do not occur together. However, unlike the *Skwala* species, the two species of *Megarcys* could not be reliably distinguished as nymphs, so records of each species are based only on reared nymphs and adults. A third species of *Megarcys*, *M. subtruncata* was reported from Cascade creek by Gaufin *et al.* (1972), but only *M. watertoni* was taken at that site during this study. The status of *M. subtruncata* in the drainage is unclear. Based on the very large number of *Megarcys* adults collected and reared from many sites, *M. subtruncata* must be highly restricted within the drainage if it occurs there at all. It could be associated with lakes.

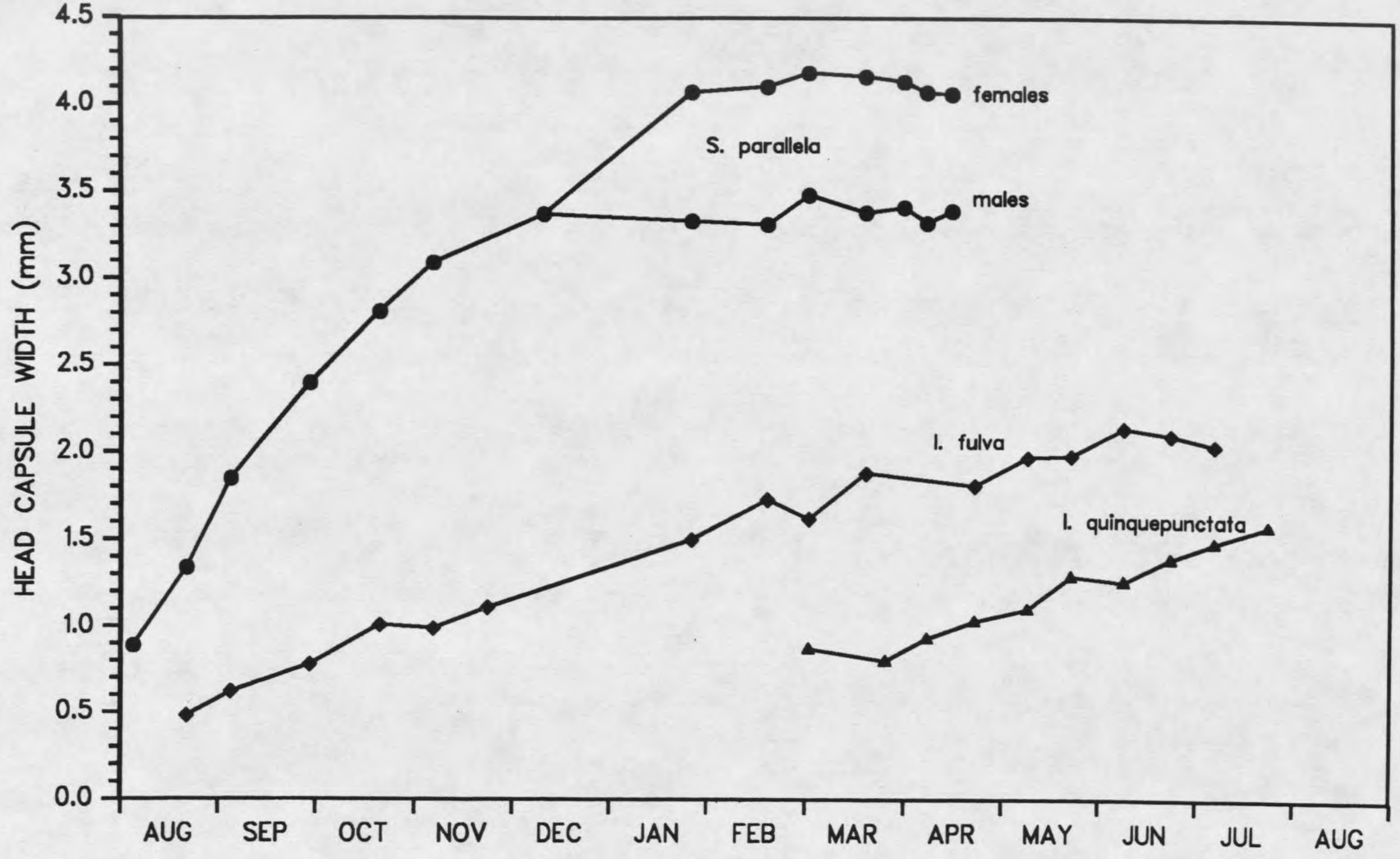

Figure 13. Mean head capsule width of perlodid stoneflies occurring in the Gallatin River near Bozeman during 1984 and 1985.

Setvena bradleyi is the most alpine of the large perlodids. It was collected many times, but always in small numbers. It is morphologically quite distinct, but easily lost among the vast numbers of *M. watertoni*. This may be a common mistake, as this species was not reported in the well-collected drainage until very recently (Stewart and Stanger, 1985). It occurs only in the highest streams with minimal discharge fluctuation. These sites are always isothermal, cold and choked with bryophytes. It occurs with *M. watertoni* and dominates that species numerically only very near the stream source. *Setvena bradleyi* is the only species of large perlodid known from the drainage that requires 2 years to complete its growth. Both species of *Megarcys* as well as *Skwala curvata* appear to complete growth in a single year, but it is possible that a small fraction of a second year is used, similar to *Pteronarcella badia*. With the late discovery of *S. bradleyi*, it now seems possible that *Arcynopteryx compacta* (MacLachlan) may be taken in the drainage. This species is known from southeast and northwest of the Gallatin drainage. It is expected only at still higher elevations associated with alpine lakes. It also requires 2 years to complete its growth in lake outlets on the Beartooth plateau. The highest lake systems of the Gallatin drainage were not well explored during this study.

Skwala curvata and *Megarcys signata* both occupy a longitudinal zone which is frequently missing in the transition from the mainstem to a tributary stream. *Megarcys signata* is limited to the mainstem, West Fork Creek and Taylor Creek. Thus the transition from *Skwala* to *Megarcys* in the Gallatin drainage usually skips *M. signata*. Less frequently is *S. curvata* skipped. In the latter case, *M. watertoni* occurs in tributaries immediately adjacent to the mainstem occupied by *S. parallela*. These two species have not been taken together, probably due to physical factors. The ideal succession of all six large perlodids thus has some overlap between adjacent species of different genera, but very little, if any, overlap between adjacent species of the same genus. Members of the same genus are always adjacent longitudinally.

The four medium sized perlodids in the drainage, *Diura knowltoni*, *Isoperla sobria*, *Kogotus nonus*, and *Pictetiella expansa*, are widely distributed throughout the tributaries and the upper mainstem, but are seldom very common. Each species, however, can be common or even abundant in some circumstances. They are all probably more specialized in one way or another than are most stonefly species. *Isoperla sobria* is obviously specialized. It is exclusively found in association with organic debris; especially soft rotting wood. The nymphs sometimes exit in large numbers from crevices in wood when it is removed from the water. They are rarely taken in association with the usual rocky riffle areas favored by most stoneflies, and are very poorly represented in normal benthic samples. They may also occur in dense growths of bryophytes. *Isoperla sobria* occurs in cold streams wherever the proper habitat is found, and is usually common or even abundant wherever the habitat is similarly common or abundant. The remaining three species are more typical in terms of preferred habitat, but are still relatively rarely collected. Two species are common only in a single stream. *Pictetiella expansa* is common in the lower parts of the Squaw Creek drainage, but rare elsewhere while *Diura knowltoni* is common in the lower reaches of West Creek, but again is rare everywhere else. The remaining species, *Kogotus nonus* is much more widely distributed and more frequently common. This species appears in the benthos in early fall as small, rather peculiar looking nymphs which were not recognized initially. They grow very little until mid-summer of the next year, after most other stoneflies have completed their growth. A second species, *K. modestus*, has been reported in the drainage (Gaufin *et al.*, 1972), but all of the many specimens examined during this study are better referred to as *K. nonus*. Within the Gallatin drainage, the genus *Kogotus* has a longitudinal distribution and seasonal emergence consistent with a single species.

The small perlodids include the remaining species of *Isoperla* and *Cultus tostonus*. *Cultus tostonus* is abundant only in the lower reaches of the river and is rare as far upstream as Bozeman. *Isoperla mormona* is the smallest species of the genus in the drainage and is also common only in the lowest reaches of the river. Both *C. tostonus* and *I. mormona* were relatively poorly studied because of their limited distribution within the drainage. *Isoperla fulva* is abundant throughout the mainstem of the river and in the larger tributaries. It shares the lower half of its range with *I. quinquepunctata* which completes its growth quickly with warmer temperatures after *I. fulva* has completed its growth (Figure 13). Dosdall and Lehmkuhl (1979) concluded that this species, as *I. patricia* Frison, requires 2 years to complete its growth in Saskatchewan. This was based on the occurrence of relatively small nymphs and mature nymphs at the same time. That observation is, however, also consistent with the one-year life cycle with very rapid and poorly synchronized growth, which occurs in the Gallatin River. The emergence period of *I. quinquepunctata*, while qualitatively similar to that of *I. fulva* (Figure 11) is both longer and later in the season when examined quantitatively (Figure 14).

Isoperla petersoni has an unusual dual nature in the drainage. In the mainstem of the river it is generally distributed in rocky riffles from near the border of Yellowstone Park upstream for about 15 km. This is mostly upstream of the zone occupied by *I. fulva* and is an area of the river not well populated with other carnivorous stoneflies. In many smaller streams, *I. petersoni* is restricted to organic debris occurring with the much larger *I. sobria*. Biological interactions are the most likely explanation for this habitat shift. *Isoperla fusca* is abundant only in very small alpine streams, associated with *Yoraperla*. The last species, *I. pinta* is recorded as new from the drainage and the county. It has a sporadic occurrence in the lower parts of the drainage existing only as local, small populations entirely restricted to springs.

Family Chloroperlidae: The green stoneflies are represented in the Gallatin drainage by seven genera with 15 species (Table 16). These are the smallest of the predatory stoneflies. The species prefer finer substrates than the perlodids. Many occur in gravel while others are hyporheic.

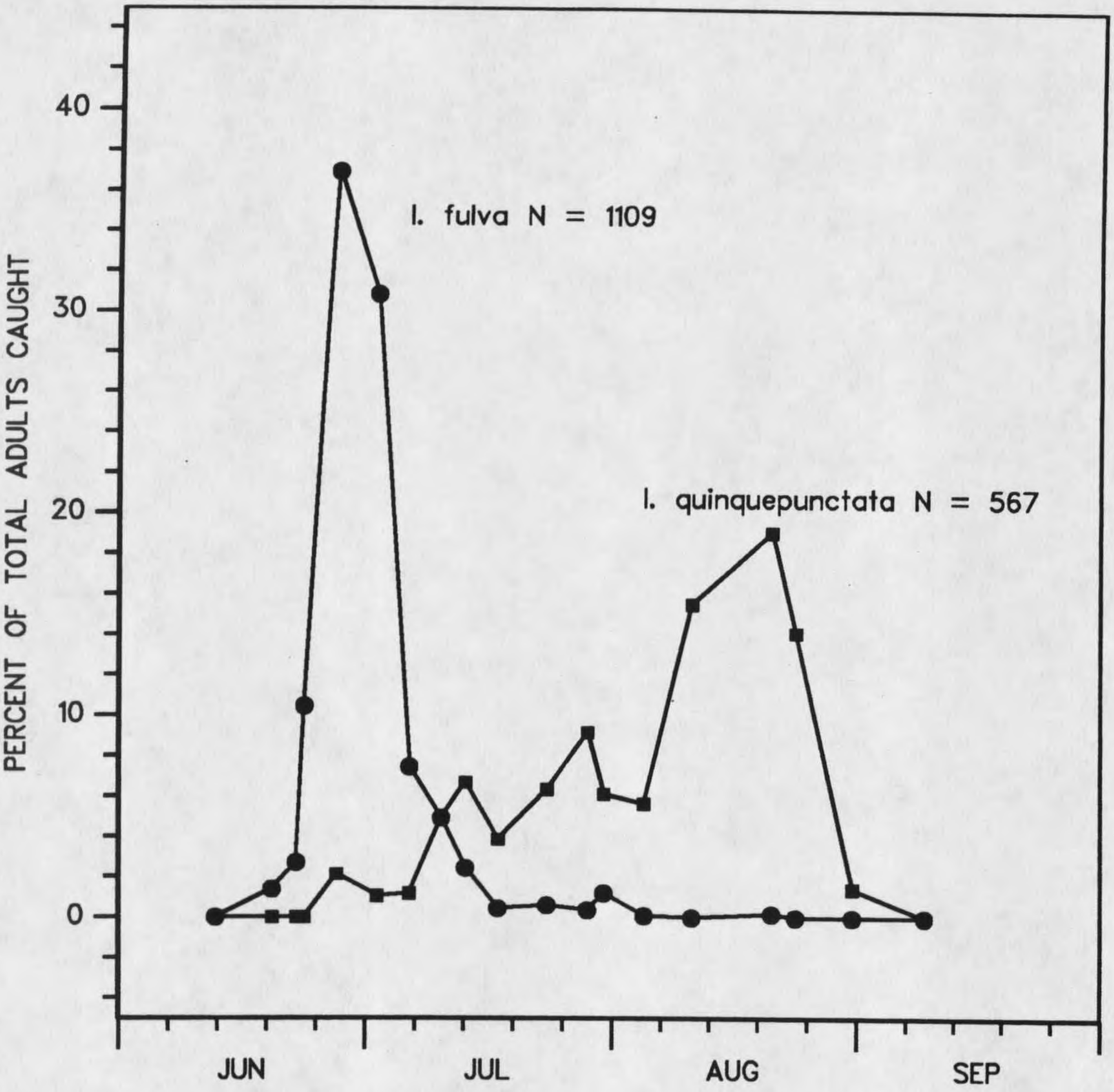

Figure 14. Seasonal abundance of adults of two species of *Isoperla* caught in morning vegetation sweeps along the Gallatin River west of Bozeman during 1984 and expressed as a percent of the annual total.

Table 16. Chloroperlidae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Alloperla severa (Hagen)	4433000	U?	H	?	Pr?
A. medveda Ricker	0000032	U?	H	?	Pr?
A. serrata Needham & Claassen	0000320	U?	H	?	Pr?
Suwallia pallidula (Banks)	4433000	Us	G	Cg	Pr
Sweltsa coloradensis (Banks)	4444320	Uw	G	Cg	Pr
S. fidelis (Banks)	0122334	Uw	G	Cg	Pr
S. albertensis (Needham & Claassen)	0003440	Uw	G	Cg	Pr
S. borealis (Banks)	0000033	Uw	G	Cb	Pr
Triznaka signata (Banks)	4433000	Uw	G	Cg-Cb	Pr
Kathroperla perdita Banks	0000332	?	H	?	Pr?
Paraperla frontalis (Banks)	4422000	?	H	?	Pr
Paraperla wilsoni Ricker	0000002	?	H	?	Pr?

The subfamily Paraperlinae is represented by two hyporheic species. *Paraperla frontalis* occurs abundantly on the mainstem from the canyon downstream. The large nymphs emerge most abundantly in areas of upwelling water during the night. They can be easily collected from such areas during the night using a light. They may accumulate in large numbers before midnight. By morning, only cast skins and adults are normally found. The emergence at a single spring is highly synchronous, and emergence from different springs within an area is only slightly less so. The nymphs can be taken in numbers by trapping. A single emergence trap 30 cm in diameter fitted over a small spring took no specimens prior to June 19, 484 individuals by the morning of June 21, 36 individuals over the next two nights and none after that. The emergence period is remarkably consistent from year to year. The nymphs of *Paraperla frontalis* are occasionally found in areas of upwelling water far before emergence. Gut contents of these nymphs consist primarily of copepods. *Paraperla wilsoni* is known in the drainage only from adults taken in traps on high mountain spring seeps. *Kathroperla perdita* is known mostly from exuviae, which indicate that this species is common and widespread in mountain streams above the zone occupied by *Paraperla frontalis*. Nymphs are not taken in routine benthic samples.

Three species of *Alloperla* are present in the drainage. All are species are hyporheic and do not normally turn up in benthic samples. The mature nymphs were taken in sites typical of hyporheic species. The three species form a simple longitudinal progression with *A. severa* the lowest and most widely collected. *Alloperla serrata* occurs in larger tributaries and from some smaller tributaries at low elevations. *Alloperla medveda* occurs only in more alpine situations.

The species of *Sweltsa* are the most frequently collected nymphs of the family. Four species are abundant in the drainage (Table 16). The species show rather clear longitudinal differences in occurrence. *Sweltsa borealis* is considerably larger than the remaining species and is frequently associated with wood. The nymphs of the four known species can be separated only in direct comparisons with exuviae of reared individuals.

Triznaka signata is enormously abundant in the mainstem and in the lower parts of the larger tributaries. This species occurs with *Sweltsa coloradensis*, but is smaller and occupies finer substrates and shows a preference for organic substrates. It is frequently found in large numbers in overhanging grasses at the stream margins.

The last species of the family, *Suwallia pallidula* occurs with both *Triznaka signata* and *Sweltsa coloradensis*. It shares the habitat of *S. coloradensis*, but occurs and grows later in the season than the previous two species (Figure 15).

Trichoptera

The known caddisfly fauna of the Gallatin River drainage consists of 97 identified species placed in 14 families and 45 genera. Unlike mayflies and stoneflies, caddisfly species new to the drainage continue to be found regularly each year. The ultimate number of Trichoptera species in the drainage may be significantly higher. Eleven of the identified species, *Rhyacophila belona*, *R. oreia*, *R. rotunda*, *R. vofixa*, *Neotrichia osmena*,

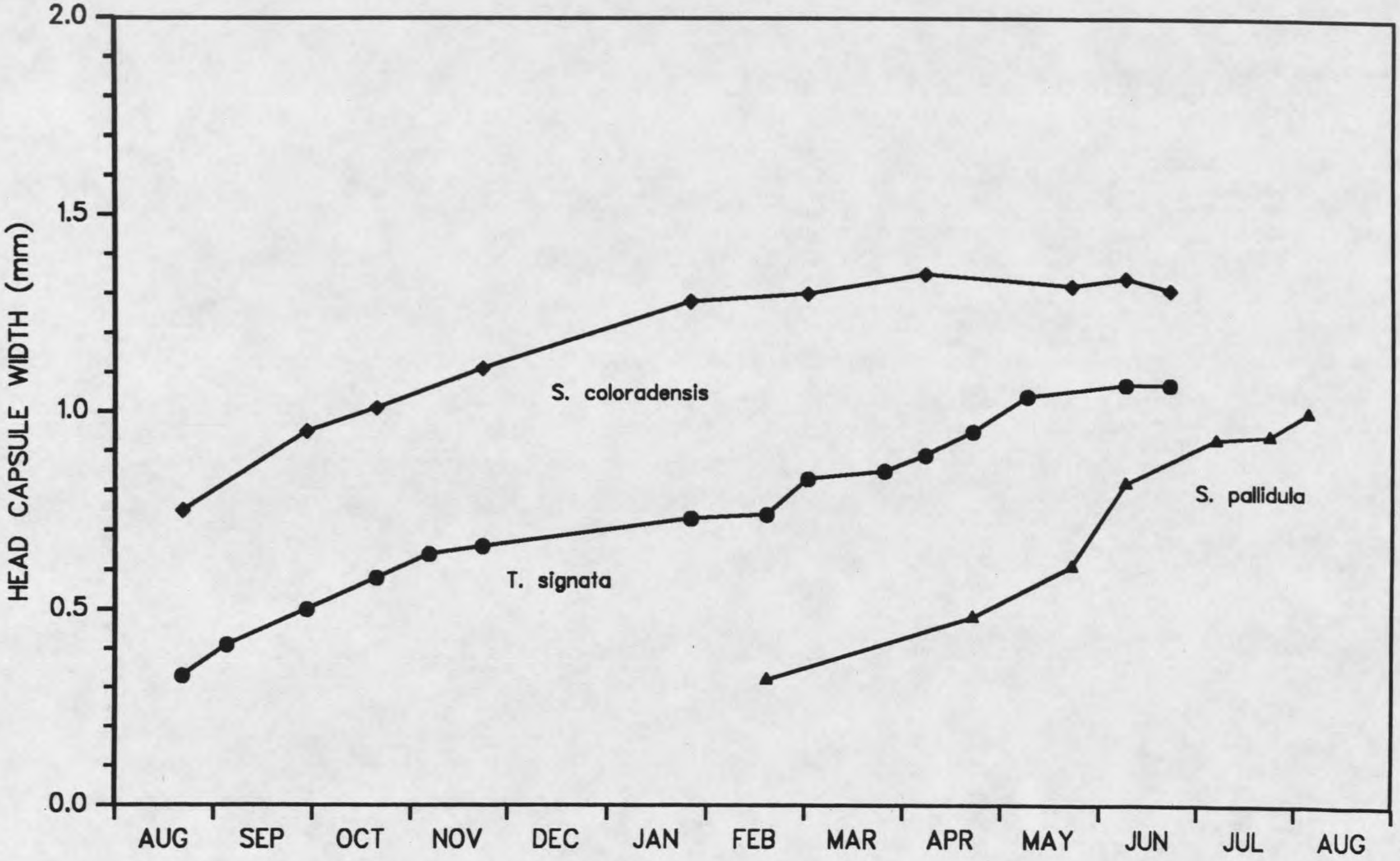

Figure 15. Mean head capsule width of chloroperlid stoneflies occurring in the Gallatin River near Bozeman during 1984 and 1985.

Ochrotrichia logana, *Limnephilus morrisoni*, *L. sitchensis*, *L. perpusillus*, *Philocasca antennata*, and *Allomyia picoides* represent new Montana records. Two genera, *Homophylax* and *Cryptochia* are known only from larvae and are not yet identified to species, though each is thought to be represented by a single species. One species of *Rhyacophila* is undescribed and two forms of *Rhyacophila* larvae are without positive identification. Several additional species of limnephilids are known from the drainage, but have not yet been identified. Most of these are probably restricted to lentic habitats or mountain spring seeps. A fair number of limnephilid larvae from standing water also remain unidentified. All of the unidentified limnephilids have minimal ecological data available and they are excluded from the present discussion.

The number of Trichoptera adults collected during this study far exceeds the number of Ephemeroptera and Plecoptera adults that were collected. This is primarily due to the affinity of caddisfly adults for light traps. Many millions of caddisflies were obtained in these traps. Only 13 of the 97 species known from the drainage were not taken in light traps. Most of these occur in areas or during seasons that are very cold at night. Sixteen species were taken, as adults, only in light traps. Many caddisfly species in the drainage are known only from adult specimens and are thus very poorly known biologically.

Despite the large number of large light trap collections, many Trichoptera species appear to be rare or locally distributed within the Gallatin drainage. The mean abundance designation for all 97 Trichoptera species is a half unit lower than that for Ephemeroptera and Plecoptera. The mean number of longitudinal zones occupied by Trichoptera species is also smaller than that for Ephemeroptera and Plecoptera. Some caddisfly species are known from a single locality, some from a single collection or even from a single individual. Eleven caddisfly species have their maximal abundance designation as sporadic; that is, they cannot yet be predictably found at any time, at any site. This situation did not occur for any species of Ephemeroptera or Plecoptera. Twenty caddisfly species have their maximal abundance designation as rare. This occurred for only three species of mayflies and six species of stoneflies.

Sixteen of the 97 Trichoptera species known from the Gallatin drainage are known from only one of the seven longitudinal zones. Only three species, *Rhyacophila angelita*, *Dicosmoecus atripes* and *Hesperophylax occidentalis*, are known from all seven zones. The upper parts of the mainstem and the larger, warmer tributaries (longitudinal zones c, d and e) have fewer Trichoptera species (about 35) than either the lower parts of the drainage or than the cold mountain streams (about 45 species each).

The taxonomic diversity of the Trichoptera within the Gallatin drainage is reflected also in its ecological diversity. All trophic groups are well represented within this order. For the Gallatin drainage species, approximately 28% are collectors, 24% are predators, 20% are scrapers and 28% are shredders. Trichoptera species also occupy all types of aquatic habitats. In the Gallatin drainage, 68% of the Trichoptera species are generally distributed on rocks in moderate current, 13% are restricted to springs, 11% are restricted to the margins of streams and 8% are known only from lentic water. None of the Trichoptera species in the Gallatin drainage are restricted to torrential current velocity, though some species occur there. The number of lentic species in the drainage will undoubtedly increase when the lakes and ponds of the drainage are better studied.

Approximately 83% of the Trichoptera species known from the Gallatin drainage are univoltine and rather well synchronized in larval growth and adult emergence. Only ten species are known to have summer life cycles. Five species from the drainage are semivoltine and seven species, which occur only in springs, are so asynchronous in growth and emergence that their life cycle cannot be determined from field collections. One additional species has a variable life cycle being univoltine in parts of the drainage and semivoltine in other parts. In the mainstem of the Gallatin River west of Bozeman, 16 Trichoptera species are sufficiently abundant to allow description of their seasonality

(Figure 16). Both short summer cycles and long winter cycles are represented, but most species exhibit the first type.

In contrast to mayflies and stoneflies, caddisfly body growth is very poorly described by measuring head capsule width over time. Trichoptera species typically have only five larval instars, body size varies greatly within an instar, and most or the growth is achieved by the final instar alone. Young members of an instar are usually recognized by the over-sized appearance of their head. Each caddisfly instar, unlike mayflies or stoneflies, is usually, sufficiently different in head capsule size to be easily sorted and recognized when all are available for direct comparison. Indeed, larval appearance and case construction frequently differ so greatly between instars that they are not easily recognized as belonging to a single species. The different instars of a caddisfly species may not even key to the same genus. There is probably very little competition between the different instars of the same species because of these differences. The head capsule widths of the sub-ultimate instars of Trichoptera species appear rather uniform when expressed as a percentage of the final instar's head capsule width (Table 17). The seasonality and duration of the five instars vary considerably among the species (Figure 17). Many species pass through the first 3 instars very rapidly. The fifth instar is generally the most frequently encountered caddisfly instar because it has the longest duration for most of the species.

Family Hydropsychidae: This important family of net-spinning caddisflies is represented in the drainage by four genera and nine species (Table 18). All species function as filter-feeding collectors, but may readily include animals in their diet. The two species of *Chematopsyche* are common only in the warmer waters of the East Gallatin drainage and in the spring creeks of the Gallatin Valley. They have been taken only as sporadic adults upstream of Bozeman. Five species of *Hydropsyche* occur in the drainage. These are all identifiable as larvae. All but *H. occidentalis* are members of the *morosa* species group which has been placed in *Symphitopsyche* and *Ceratopsyche* recently

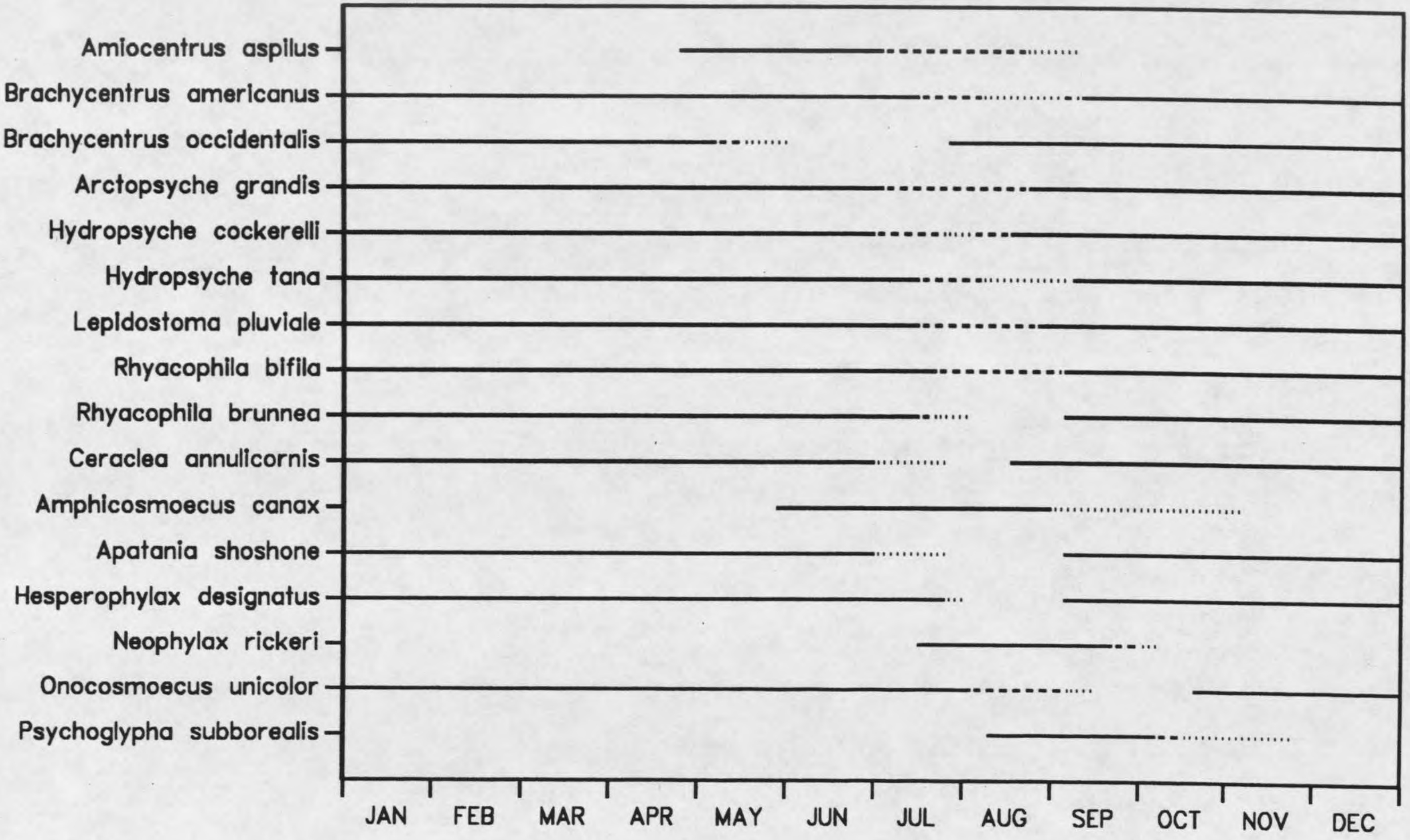

Figure 16. Phenology of 16 Trichoptera species that were common in the Gallatin River near Bozeman during 1984. Solid line represents the occurrence of larvae only, dotted line of adults only and dashed line the occurrence of both.

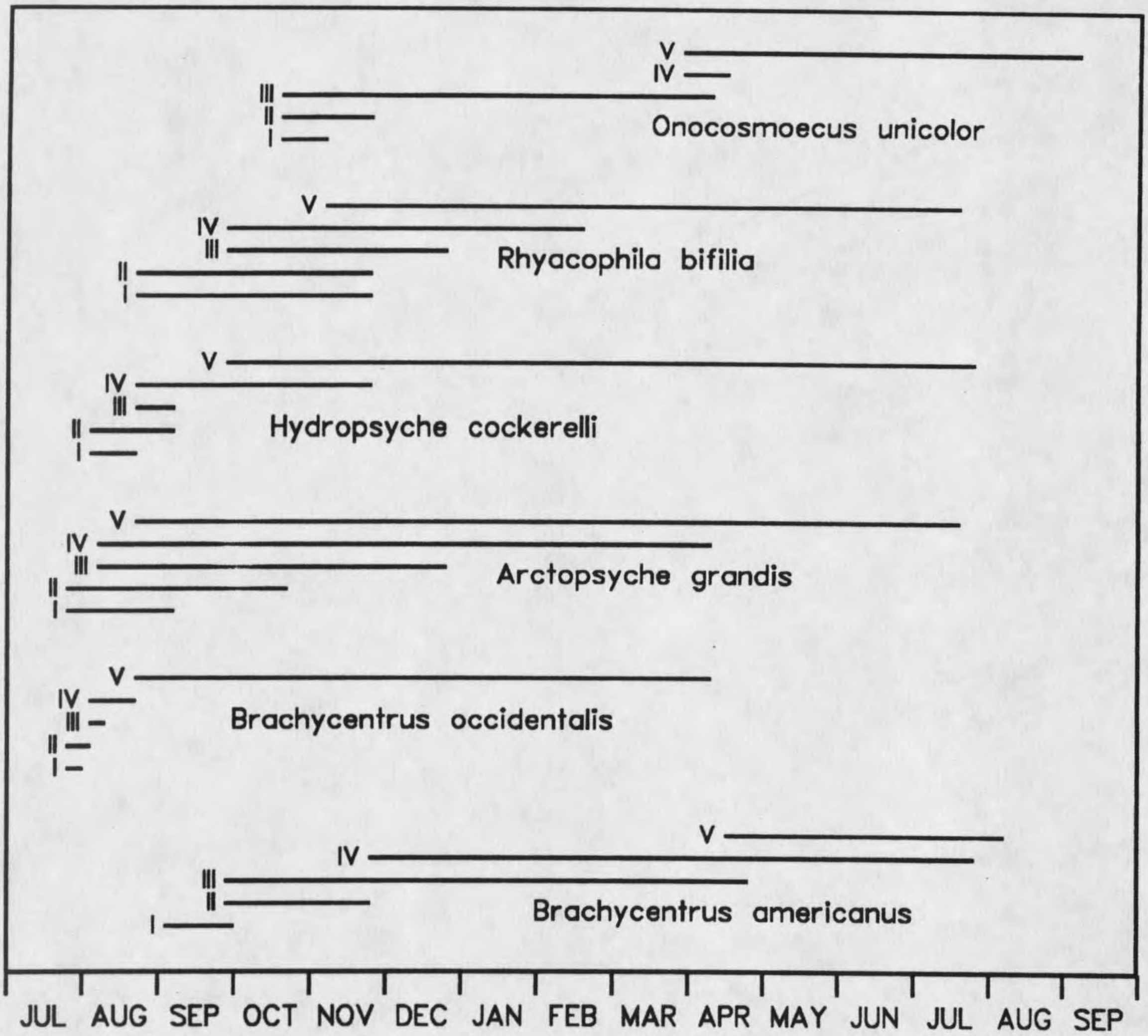

Figure 17. Seasonality of larval occurrence, by instar, of six Trichoptera species occurring in the Gallatin River west of Bozeman during 1984.

(Schuster, 1984). Schefter and Wiggins (1986) review the arguments for retaining these species as a group within *Hydropsyche*. *Hydropsyche oslari* and *H. slossonae*, while taken many times, are normally taken only in small numbers as adults and larvae. Both species are most common in warmer streams or those with considerable spring influence.

Table 17. Mean head capsule widths of some Trichoptera larvae from the Gallatin River drainage. The value for the final instar (V) is the mean width in millimeters measured at the widest point in dorsal view. Those for remaining instars are similarly measured, but expressed as a percent of the value for the final instar. All values are based on 10 to 50 measurements. Dashes indicate that insufficient material was available or that identification was uncertain.

Species	V	VI	III	II	I
Amiocentrus aspilus	0.76	64	43	29	--
Brachycentrus americanus	1.06	67	44	29	18
Brachycentrus occidentalis	1.02	70	45	31	--
Arctopsyche grandis	2.31	63	39	23	15
Hydropsyche cockerelli	1.31	63	47	29	17
Hydropsyche tana	0.92	71	48	--	--
Lepidostoma pluviale	0.69	62	40	26	16
Apatania shoshone	0.70	73	49	--	--
Hesperophylax designatus	1.65	71	42	--	--
Onocosmoecus unicolor	1.67	65	41	26	17
Rhyacophila bifila	1.20	75	53	40	22
Rhyacophila brunnea	1.04	71	52	34	--
Rhyacophila hyalinata	1.91	73	49	--	--
Rhyacophila verrula	1.47	78	50	32	22
Means for the above	----	69	46	30	18

The remaining species of the family are abundant and dominant elements of the lotic community. The two species of the subfamily Arctopsychinae are largely allopatric with *Parapsyche elsis* restricted to small cold streams mostly above the zone occupied by *Arctopsyche grandis*. *Arctopsyche grandis* completes its growth in 1 year in all parts of the Gallatin drainage, but requires 2 years in some small streams in isolated mountain ranges of the neighboring Yellowstone drainage. *Parapsyche elsis* appears to be absent from these streams, which may allow *A. grandis* to exist higher than it does in the Gallatin drainage. Alstad (1980) similarly reports *Arctopsyche grandis* occurring higher in Utah streams, where

Table 18. Hydropsychoidea known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Hydropsychidae					
Arctopsyche grandis (Banks)	3443320	Uw	G	Cg	CF
Parapsyche elsis Milne	0000343	S	G	Cg	CF
Chematopsyche enonis Ross	3100000	?	?	Cg	CF?
C. pettiti (Banks)	3111000	?	?	Cg	CF?
Hydropsyche cockerelli Banks	4433100	Uw	G	Cg	CF
H. occidentalis Banks	4143000	Uw	G	Cg	CF
H. oslari Banks	2121200	Uw	G	Cg	CF
H. slossonae Banks	2110100	Uw	G	Cg	CF
H. tana Ross	3443100	Uw	G	Cg	CF
Philopotamidae					
Dolophilodes aequalis (Banks)	0003320	Uw	G	Cg	CF
D. novusamericanus (Ling)	0003000	Aws	S	Cg	CF
Wormaldia gabriella (Banks)	3100000	Us	G	Cg	CF
Polycentropodidae					
Polycentropus halidus Milne	0000100	?	?	?	Pr?
Psychomyiidae					
Psychomyia flavida Hagen	1000000	?	?	?	CF?

Parapsyche elsis does not occur than in drainages where *P. elsis* does occur. The young larvae of *Arctopsyche* appear quickly, after the first adults and grow rapidly. Some of the young larvae reach the final instar within a month while others take much longer (Figure 17). Sometimes the new first instar larvae are taken simultaneously with the fifth instar larvae of the previous year. Overlapping generations, in this case, do not imply a two-year life cycle, as all of the fifth instar larvae emerge or perish before fall. Cuffney and Minshall (1981) report essentially the same life history for *A. grandis* from an Idaho stream. Some of the reports of two-year life cycles in this species may be misinterpretations. Collections must completely span the emergence period and make some quantitative accounting of instars to reach sound conclusions on the length of the life cycle. Many species of Trichoptera were observed to have a few individual larvae live through the emergence period without emerging. *Parapsyche elsis*, on the other hand, clearly takes 2 years to complete its growth. Both species feed on rather coarse material compared to the other members of this family.

The remaining three species of Hydropsychinae are frequently very abundant. All are confined to the mainstem and the lower parts of the larger tributaries. *Hydropsyche cockerelli* and *H. tana* occur abundantly together with the same seasonality of growth and emergence. They are, however, quite different in size (Table 17), construct capture nets of different mesh size, and tend to be differentially aggregated on rock surfaces. The stimulus used in aggregating is not clear. The last species, *Hydropsyche occidentalis*, has a very unusual longitudinal distributional. It is very abundant in the warmer streams of the Gallatin Valley, including the mainstem below its confluence with the East Gallatin River, but becomes rare in the mainstem above this point, and very rare west of Bozeman upstream to the Gallatin Canyon. In much of the Gallatin Canyon, *H. occidentalis* is abundant. This distribution suggests that two species are involved, but morphology supports a single species.

Family Philopotamidae: The family Philopotamidae constructs the finest mesh capture nets of the order (Wiggins, 1977). Three allopatric species are known from the Gallatin drainage (Table 18). *Dolophilodes aequalis* is widespread and common in small and medium mountain streams, but is absent from both the mainstem and from very alpine streams. Larvae are fully grown by late summer, but emergence is delayed until the next spring. *Dolophilodes novusamericanus* is known only from large springs where it may be taken as adults throughout the year. *Wormaldia gabriella* is restricted to the lower sections of the mainstem and to the warmer East Gallatin drainage. Larvae are present only in summer, and the adults emerge late in the season. *Chimarra utahensis* Ross occurs in southwest Montana, but is restricted to warm thermal springs, where it emerges throughout the year. It has not been taken within the Gallatin drainage. All these species, while actively feeding, occur only in streams of very low turbidity. Their fine capture nets may restrict them to this situation.

Family Polycentropodidae: This family favors warmer, less torrential waters than are found within the Gallatin drainage. A single species, *Polycentropus halidus* is known from the drainage (Table 18). It is known only from sporadic larvae and adults and is very poorly known within the drainage. It was always taken in productive mountain streams near the edge of the forest. Another species *P. variegatus* Banks occurs in similar streams just downstream of the Gallatin drainage.

Family Psychomyiidae: This family like the last one is known from a single species, *Psychomyia flavida* (Table 18). It is known in the drainage only from adults taken at black light. It is not predictably taken at any time or in any place within the drainage. This species is very common in the neighboring Madison River drainage, which may well have been the source of the individuals captured.

Family Rhyacophilidae: This large family is represented in the Gallatin drainage by a single genus with at least 21 species (Table 19) including one which is undescribed. All are known from adults and 17 are known as larvae. The larval associations of *R. alexanderi*, *R. belona*, *R. robusta*, *R. vofixa* and *R.* n. sp. are new. Two additional forms of larvae are known but are not associated with adults. One is probably the undescribed larvae of *R. pellisa* the remaining two probably represent additional species. All of the known larvae can be specifically recognized except for those of the *brunnea* branch, *R. brunnea*, *R. vao*, *R.* n. sp. and *R. robusta*.

As many as eight species of *Rhyacophila* can be taken simultaneously as active larvae at a single site, and it is uncommon to take less than five species in small mountain streams. This situation is true of no other genus in the Gallatin drainage since the subgenera of *Ephemerella* were elevated to generic status. The genus *Rhyacophila* has an informal

Table 19. Rhyacophilidae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Rhyacophila verrula Milne	0000333	Uw	G	Cb	SH
R. oreta Ross	0030000	Aws	S	Cb	Pr
R. bifila Banks	3443200	Uw	G	Cg	Pr
R. coloradensis Banks	0223300	Us	G	Cg	Pr
R. hyalinata Banks	0000332	S	G	Cg	Pr
R. brunnea Banks	2344430	Uw	G	Cg-Cb	Pr
R. vao Milne	0002332	Uw	G	Cg-Cb	Pr
R. n. sp.	0000013	S	G	Cg-Cb	Pr
R. robusta Schmid	0000023	S	G	Cg-Cb	Pr
R. alberta Banks	0000001	Uw?	?	?	Pr?
R. tucula Ross	0003231	Uw	G	Cg	Pr
R. narvae Navas	0000233	Uw	G	Cg	Pr
R. pellisa Ross	0000032	Us?	?	?	Pr?
R. belona Ross	0000003	Uw	G	Cg	Pr
R. alexanderi Denning	0000012	Uw	G	Cg	Pr?
R. angelita Banks	1123332	Us	G	Cg	Pr
R. oreia Ross	0000003	Uw	G	Cg	Pr?
R. rotunda Banks	0000002	Uw?	?	?	Pr?
R. vaccua Milne	0112233	Uw	G	Cg	Pr
R. vagrita Milne	0000220	Us?	?	?	Pr?
R. vofixa Milne	0000332	Uw	G	Cg	Pr

subgeneric classification with divisions, branches, groups and subgroups (Schmid, 1970), which may someday be formalized or elevated in rank. The larvae, while structurally diverse, are relatively uniform in terms of feeding and habitat preferences. Larvae for all observed species, except *R. verrula*, appear to be primarily predatory. In captivity, the larvae usually consume only the soft parts of their prey, making gut contents impossible to interpret. Martin and Mackay (1981) report similar observations, and speculate that the small head and mouth gape may predispose *Rhyacophila* species to feed by only partially consuming their prey. In captivity, and like most other aquatic predators observed, they usually take chironomid and simulid larvae which are easily handled and normally numerous. Most of the species are generally distributed in clean riffles on inorganic substrates. Exceptions to this are discussed below. Many species are seasonally isolated in larval occurrence, growth and adult emergence. Body size varies greatly among the species and is probably responsible for much resource partitioning among sympatric species. Head capsule widths for final instar larvae range from 0.58 in *R. oreia* to 1.91 in *R. hyalinata*.

Two species of *Rhyacophila* are ecologically isolated from the rest. *Rhyacophila verrula* is isolated with regards to trophic feeding group. The larvae are herbivorous, feeding primarily on bryophytes. This species is very abundant in the drainage wherever bryophytes are abundant, except in the mainstem canyon area. Its absence here is probably due to temperature or flow fluctuations. *Rhyacophila verrula* is most abundant in mountain spring creeks. Larval growth is relatively asynchronous with most instars present during much of the year. The adults emerge mostly in the fall. *Rhyacophila oreta* is isolated by habitat, occurring only in large springs choked with watercress. It can be very common at these sites, emerging throughout the year, as do many spring-inhabiting Trichoptera. Adults are commonly collected in mid-winter at high elevations.

Rhyacophila bifila, *R. coloradensis* and *R. hyalinata* form a group of ecologically, and taxonomically related species. All prefer large boulders in very fast current. They may be heavily aggregated on such rocks, especially those with rough surfaces. All three species have a similar, distinctive body shape, and are recognizable to species in the field. All three species form the same type of pupation chamber which consists of an elongate dome constructed of coarse sand which completely covers the pupa. *Rhyacophila bifila* is limited to the mainstem of the river and the lower parts of the three largest tributaries. The larvae accomplish much of their growth during the fall and overwinter as fourth or fifth instars (Figure 17). Pupation and emergence take place during the midsummer. *Rhyacophila coloradensis* does not extend as far downstream as *R. bifila* and is not very abundant as far downstream as Bozeman. It also extends further upstream, but does not occur in small mountain streams. The two species are clearly separated seasonally. Larvae of *R.*

coloradensis appear during the early summer, grow rapidly and begin pupating in late summer or fall. In the lower sections of the river the adults emerge in late summer or fall. In the lower parts of the Gallatin Canyon a few adults may be found in the fall, but most emerge in April or May. In the upper parts of the river and in the tributaries, all individuals of this species emerge in the spring. These zones of autumn, mixed autumn and spring, and spring emergence may be substantially shifted upstream or downstream by annual variation in temperature. In smaller and colder tributaries, *R. hyalinata* is found. Its distribution overlaps with *R. coloradensis* only in small streams near the mainstem. This species takes 2 years to complete its growth and is the largest species in the drainage based on head capsule width. The two-year life cycle has the effect of effectively replacing both *R. bifila* and *R. coloradensis*. Adults emerge in midsummer.

The most frequently collected *Rhyacophila* larvae in the drainage are those with branched gills on the abdomen. They occur in nearly every stream and are frequently abundant. These were identified as members of the *brunnea* subgroup of the *brunnea* group. Larvae of this subgroup are easily recognized collectively by the presence of three pairs of branched gills on abdominal segments II through VII, and two pairs on the segment VIII, but they cannot yet be identified to species (Smith, 1984). Smith and Manuel (1984) reviewed the nearctic species of this subgroup and reduced the number of species from seven to three. The description of *R. starki* by Smith and Weaver (1984) brought the total to four, but with only two species, *R. brunnea* and *R. vao*, known from Montana.

Many populations of these larvae were followed through time and identified to species when the adult matured within the pupal cocoon. Two species were obtained in addition to *R. brunnea* and *R. vao*. The first of these was *R. robusta*, a member of the related *vemna* group, for which larvae were previously unknown, though thought likely to be similar to those of *R. brunnea* by Wold (1974). The second species is a new species of the *brunnea* subgroup (*R.* n. sp.). These four species, unlike all other *Rhyacophila* in the Gallatin drainage are currently indistinguishable as larvae. These larvae are also unusual in preferring organic substrates, especially rotting logs, or rocks heavily cluttered with organic material.

Rhyacophila n. sp. is known only from high mountain, moss choked streams with pronounced ground water influence. It is most abundant in the coldest streams. *Rhyacophila* n. sp. appears to share more morphological features with the Asian *R. vaoides* Ross and *R. sakhalinica* Schmid than do the other Nearctic species. It may represent a relic species. This hypothesis is supported by its restricted habitat. Its life cycle has not been determined with certainty, because at all sites where it has been taken *R. robusta* also occurs and always in greater numbers. Both *R.* n. sp. and *R. robusta* pupate over the winter and emerge simultaneously and relatively synchronously during the last third of May and the first third of June. The presence of numerous active larvae during the long pupation period indicates that either *R. robusta* or *R.* n. sp. or both require 2 years to complete larval growth. Because none of the young larvae which appear in early summer approach full size by winter, probably both species have a two-year life cycle. This explains the larger size of both of these species when compared to *R. brunnea* or *R. vao*, both of which occur in warmer, more productive streams, but are univoltine. No ecological separation for *R.* n. sp. and *R. robusta* has been noted.

Neither *R. brunnea* nor *R. vao* have been taken with *R.* n. sp., though both may be present in nearby streams of the same drainage. *Rhyacophila robusta* may occur with both *R. brunnea* and *R. vao* but is never common in these situations. *Rhyacophila brunnea* and *R. vao* overlap extensively in the upper reaches of the mainstem of the Gallatin and in many larger tributaries where both species may be abundant. In this situation two clear cohorts of larvae are present: those of *R. brunnea* mostly reach the fourth instar by winter, finish growth in the spring and emerge mostly during July; and those of *R. vao* appear as early instars by midwinter, grow rapidly during the spring and summer and emerge during August and September. *Rhyacophila vao* occurs also in many smaller streams where *R. brunnea* is not found. In these situations, the larvae sometimes do not emerge during the fall, emerging instead during the next spring or early summer. As a result, adults of *R. vao* may be taken at almost any time from early spring through late fall within the drainage. The other three species have much more restricted adult emergence. *Rhyacophila brunnea* extends much further downstream than the other species. It is the only species to occur outside the forested part of the drainage. Adults of this species range far from the river across the valley, making it not unexpected that it is the only species of the branch to occur in both eastern and western states.

Contrary to Smith's (1968) and to Nimmo's (1971) findings, *R. brunnea* can be taken at light. It and *R. vao* sometimes occur in light traps in great numbers. *Rhyacophila robusta* and *R. n. sp.* may also be taken at light, but only on warmer nights, that are uncommon during the early season at high elevation. *Rhyacophila robusta* and *R.* n. sp. are taken mostly toward dawn, while *R. brunnea* and *R. vao* are taken mostly at dusk. Males of all four species were at least as well represented as females in light trap collections. In hand collecting, males were always much better represented than females.

Two of the four species of the *alberta* group occur in the drainage. *Rhyacophila tucula* is abundant in small streams and emerges late in the season. *Rhyacophila alberta* is known only from rare adults. It may be more alpine that *R. tucula*. Three species of the large *sibirica* group occur in the drainage. *Rhyacophila belona* is restricted to cold mountain spring creeks and emerges in early spring while *R. narvae* and *R. pellisa* are widespread in mountain streams and emerge in mid summer. The remaining species are unrelated by group. *Rhyacophila angelita*, *R. vaccua* and *R. vagrita* emerge late in the season.

Family Glossosomatidae: This family is represented in the drainage by eight species placed in three genera (Table 20). The family is morphologically and ecologically uniform. All species construct the characteristic saddle-case, cling tightly to rock surfaces and feed on closed attached organic material. Abandoned cases sometimes accumulate on rock surfaces to such an extend that many clinger species are largely excluded from the rock.

Table 20. Glossosomatidae and Hydroptilidae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Glossosomatidae					
Agapetus montanus Denning	1100000	Us	S	Cg	Sc
Anagapetus debilis Ross	0000023	Uw	G	Cg	Sc
Glossosoma alascense Banks	0033332	Uw	G	Cg	Sc
G. excitum Ross	0012000	U?	?	Cg	Sc?
G. montana Ross	3100000	Uw	G	Cg	Sc
G. traviatum Banks	3100000	U?	G	Cg	Sc
G. velona Ross	3110000	Uw	G	Cg	Sc
G. verdona Ross	0033332	U?	G	Cg	Sc
Hydroptilidae					
Hydroptila rono Ross	0030000	Aws	S	Cb	?
Neotrichia osmena Ross	2000000	Us?	?	?	?
Ochrotrichia logana (Ross)	3333000	Uw?	G	Cg	?
Oxyethira dualis Morton	0030000	Aws	S	Cb	?

Two of the three genera are represented by a single species each. *Agapetus montanus* is of sporadic occurrence in areas of spring influence across the Gallatin Valley. It is sometimes common, but not predicable from year to year. Larvae are present only in summer and the adults emerge late in the season. *Anagapetus debilis* is common in very small high mountain streams throughout the drainage.

Glossosoma is the dominant genus of the family in the drainage with six species, one or more of which can be found at almost every site. Species recognition of the larvae is not yet possible so the following comments are based on collections containing adults or pharate adults. *Glossosoma alascense* and *G. verdona* were the most frequently identified species. Both are generally distributed in the upper parts of the mainstem and in medium sized mountain streams. They may be found mixed together in aggregated clusters during the pupation period, which lasts through much of the winter and into the spring, prior to emergence. As the larvae cannot be distinguished it is unknown how such similar species coexist in both time and space. The remaining species of *Glossosoma* are more limited in distribution within the study area. *Glossosoma montana* exhibited rarely observed shifts in zonation during the course of this study. It was very abundant in the mainstem of the River directly west of Bozeman during 1982 and 1983 and disappeared in 1984. It remained very sporadic in this area until 1989 when it suddenly became quite common again. This species remained common in the warmer parts of the East Gallatin drainage, in spring creeks of the Gallatin Valley and in the nearby Madison River throughout this period. *Glossosoma traviatum* is restricted to the lower parts of the river, but was seldom very common. *Glossosoma velona* appears restricted to the spring creeks in the Gallatin Valley, but may also be found in large springs at higher elevations. The last species, *G. excitum* has been collected from the Gallatin Canyon area, but was not taken as part of this study. It is the only Trichoptera species recorded from the drainage not collected during this study, and is probably restricted to springs.

Family Hydroptilidae: The microcaddisflies are very poorly represented in unvegetated, cold mountain rivers such as the Gallatin. Only four species were identified from the drainage (Table 20). Two of these, *Oxyethira dualis* and *Hydroptila rono* are restricted to large springs where they emerge in large numbers throughout the winter months. *Ochrotrichia logana* occurs throughout the mainstem and larger tributaries, but is seldom very abundant. *Neotrichia osmena* occurs in the East Gallatin drainage. Several more species are probable in the East Gallatin drainage and the spring creeks of the Gallatin Valley, based on collections from outside the drainage.

Family Limnephilidae: This large family is represented in the Gallatin drainage by 19 genera with 34 identified species (Table 21). Some species are important elements of the benthic community, but many are restricted to the margins of streams or to entirely lentic waters and not associated with lotic species.

Table 21. Limnephilidae known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Amphicosmoecus canax (Ross)	3322000	Uw	M	Cb	SD
Anabolia bimaculata (Walker)	3330000	U?	LS	Cb	SD-SH
Asynarchus aldinus (Ross)	0000023	?	L	Cb	SD
Chyranda centralis (Banks)	0000033	Uw	M	Cb	SD
Cryptochia sp.	0000022	Uw	M	Cb	SD
Goereilla baumanni Denning	0000003	?w	S	?	SD?
Homophylax sp.	0000003	Uw	M	Cb	SD-CG
Glyphopsyche irrorata (Fabricius)	1100000	?	?	?	SD?
Limnephilus alberta Denning	0000022	U?	LM	Cb	SD
L. cockerelli Banks	0000022	?	?	?	SD?
L. externus Hagen	2220000	U?	L	Cb	SD
L. fagus Ross	0022220	?	L	Cb	SD
L. indivisus Walker	1100000	?	?	?	SD?
L. morrisoni Banks	1100000	?	?	?	SD?
L. sitchensis (Kolenati)	1100000	?	?	?	SD?
L. perpusillus Walker	1100000	?	?	?	SD?
L. spinatus Banks	1100000	?	?	?	SD?
Onocosmoecus unicolor (Banks)	3333320	Uw	M	Cb	SD
Philocasca antennata (Banks)	0000002	Uw?	S	?	SD?
Psychoglypha subborealis (Banks)	3332200	Uw	M	Cb	SD
P. prita (Milne)	0000022	Uw	M	Cb	SD
Allomyia tripunctata (Banks)	0000022	U?	G	Cg	Sc
A. picoides (Ross)	0000022	U?	G	Cg	Sc
Apatania chasica (Denning)	0001332	Uw	G	Cg	Sc
A. shoshone Banks	2440000	Uw	G	Cg	Sc
Dicosmoecus atripes (Hagen)	3122332	S	G	Cg	Sc-CG
Ecclisiomyia conspersa Banks	0000233	Uw	G	Cg	CG
E. maculosa Banks	0000234	Uw	G	Cg	CG
Hesperophylax designatus (Walker)	3200000	Uw	G	Cg	Sc-CG
H. occidentalis (Banks)	3232223	Aws	S	Cg	Sc-CG
Neophylax occidentis Banks	0000232	Uw	G	Cg	Sc
N. rickeri Milne	3332000	Us	G	Cg	Sc
Oligophlebodes minutus(Banks)	0044330	Uw	G	Cg	Sc
O. ruthae Ross	0000333	Us	G	Cg	Sc

The marginal and lentic species are mostly large bodied and occur on organic substrates upon which they feed as shredders. These species are seldom very common. Many are poorly known or known only as adults or only as larvae. *Onocosmoecus unicolor* is the most common and widely distributed of these species. It occurs throughout the lower parts of the drainage and extends upstream well into the canyon and the larger tributaries. Larvae are usually found in organic debris at the margins of streams. The adults are more easily collected in numbers, being strongly attracted to light. In the lower half of its range *O. unicolor* occurs with *Amphicosmoecus canax*. These two species are distinguished only on close inspection. *Amphicosmoecus canax* sometimes uses a hollow twig up to four times its length as a case. *Amphicosmoecus canax* completes its growth after *Onocosmoecus unicolor*, is present as larvae only during the summer, and is one of the last species to emerge. Adults were taken well into November. Unlike many of the other late season species, adults of *A. canax* were never taken early in the spring.

Asynarchus aldinus occurs only in alpine situations, and may be very common in high mountain meadows with spring seeps and ponds. It is rare in mountainous areas without these wet meadows. *Chyranda centralis* occurs in many mountain streams, and can be quite common in streams with an abundance of organic debris at the margins. An undetermined species of *Homophylax*, known only from larvae, occurs commonly in small spring creeks very high in the mountains, and is most common on wood. At least 10 species of *Limnephilus* occur in the drainage. These are mostly known only from adults. Several additional species are not yet identified. Larvae of the genus are seldom taken in number, but are most common in ponds and seeps. *Anabolia bimaculata* also occurs sporadically in ponds and in quiet waters of springs. *Psychoglypha* is represented in the drainage by two species, which occupy the marginal areas of streams, and are most abundant near springs. Adults of these species emerge late in the year or early the following spring or split between fall and spring, depending on the autumn conditions.

Philocasca antennata occurs only near high mountain springs and is known only from adults. *Cryptochia* is known in the drainage only from larvae. The distribution and seasonality of the larvae are consistent with the presence of a single species, but more could be present. *Cryptochia* is widely distributed in mountain streams, but never common. They are most frequently found at the water line on partially submerged logs and are most abundant in very small mountain streams with few other species present. The early instars occur on rocks in areas of greater current than the final instar prefers. *Cryptochia* is the smallest of the species treated here as shredders.

Goereilla baumanni is known only from high mountain seeps and can be quite common during the last half of May and early June. Wiggins (1976) described the larval habitat as moss covered, water saturated organic muck at the edges of springs. This is exactly applicable to the situation in the Gallatin drainage. Wiggins (1976) also describes the life cycle as annual with a few of the larvae sealing their cases in preparation for pupation as early as August, and he reports that few if any caddisflies are known to have periods of inactivity of this length. This phenology is however common and perhaps typical of early emerging caddisflies from high mountain sites throughout the Gallatin drainage. *Apatania chasica*, *Ecclisiomyia conspersa*, *Psychoglypha subborealis* and *Neophylax occidentis* are other limnephilid species which can spend very long periods as prepupae and pupae before early spring emergence. *Philocasca antennata* likely has a similar life cycle.

The limnephilid species occurring in more general lotic conditions in the Gallatin drainage occur on inorganic substrates. These species are usually smaller in body size and are frequently much more numerous than the shredder species discussed above. These species are much better known and all are known as both adults and larvae. They usually feed as scrapers or collectors, but sometimes as herbivores or carnivores.

Apatania is represented by two, mostly allopatric species. *Apatania shoshone* occurs abundantly in the majority of the mainstem and *A. chasica* occurs in small, cold mountain streams. *Apatania chasica* emerges much earlier in the season than does *A. shoshone* and adults are often found crawling on snow. *Apatania chasica* pupates over the winter and so might well be better described as emerging later than *A. shoshone*. *Allomyia* is ecologically similar to *Apatania*, but occurs only in higher streams usually near springs. *Allomyia* is represented by two known species, but more are suspected based on larval collections.

Dicosmoecus atripes is the largest caddisfly in the Gallatin drainage and one of the few species known to be semivoltine. It occurs most abundantly in small streams with considerable spring influence, and is very common in the mainstem of the river just within Yellowstone National Park. Sub-ultimate instars construct cases of vegetation debris very unlike those of the fifth instar larvae. The final instar is reached by the end of the first summer. At this time, these larvae are actively feeding from the upper surface and sides of rocks, while the 2 year old individuals are inactive or pupating on the lower side of the same rocks. The large, dark adults are in flight mostly during September. Larvae feed on coarse detritus and take a large number of animal prey, mostly other caddis larvae and pupae.

Two species of *Ecclisiomyia* occur sympatrically in many of the smaller, alpine streams of the drainage. The two species are very different in body size and morphology. *Ecclisiomyia conspersa*, the larger species, pupates during the late winter and emerges in early spring, while *E. maculosa* pupates in the late spring or early summer and emerges in midsummer. Both species are rather general feeders and are best categorized as collector-gatherers, but include also some shredded debris and bryophytes.

Two species of *Oligophlebodes* are represented in the drainage. *Oligophlebodes minutus* is one of the most abundant insect species in medium mountain streams and in the upper mainstem. *Oligophlebodes ruthae* occurs in higher streams, emerges later in the season and is never as abundant as *O. minutus*. Both species feed on the closely attached algae, mostly diatoms and associated material on rocks. *Neophylax* is another genus represented by two allopatric species. *Neophylax rickeri* occurs abundantly across the

Gallatin Valley where it undergoes rapid growth in the summer, followed by a long period of inactivity before pupation and emergence in the fall. *Neophylax occidentis* occurs higher in the drainage, spends most of the winter as prepupae or as pupae, and emerges in the early summer. This is another example where the more upstream species of a longitudinal pair emerges earlier in the season because it overwinters as full grown larva or pupa rather than emerging in the very late fall.

The genus *Hesperophylax* is represented in the drainage by *H. occidentalis* and *H. designatus*. These species were not properly sorted or named until Parker and Wiggins (1985) revised the genus. Earlier keys failed to account for variation in tibial spur counts and in the shape of the fused intermediate appendages, often resulting in several names being applied to specimens from series of a single species. This of-course resulted in distributional and ecological data that made little sense. In the Gallatin drainage, *H. occidentalis* has the 1-2-2 spur count about twice as frequently as the 6% reported by Parker and Wiggins (1985). Adults of *H. designatus* are rather reliably identified by their larger size and more distinct wing markings when compared to *H. occidentalis*. In the Gallatin drainage, *H. occidentalis* is mostly restricted to springs. It may be found at almost any elevation, but is most common in small spring creeks in the Gallatin Valley and in the large spring near West Fork Creek. This species is further characterized by a highly asynchronous life cycle. Adults have been collected during nearly every month of the year. Active larvae of most instars as well as advanced pupae occur together throughout the year. *Hesperophylax designatus* is best known near Bozeman, from small side channels of the river with only limited spring influence. *Hesperophylax occidentalis* has never been taken in this situation. *Hesperophylax designatus*, at a single site, is much more synchronous in its development than *H. occidentalis*. Over the entire drainage, adults of *H. designatus* are present from late July through September. Young larvae appear soon after the adults, and reach the final instar by winter. They remain active and continue to grow through the next spring. Larvae of the two species cannot yet be distinguished. Larvae of both species occur mostly on rocks in areas of limited current, feeding primarily on diatoms, but include also filamentous green algae and fine detritus in their diet.

Family Brachycentridae: This family is represented in Montana and in the Gallatin drainage by four species (Table 22). *Amiocentrus aspilus* is largely restricted to the lower, warmer sections of the mainstem and is present in the benthos in appreciable numbers only during the late spring and summer months. This species is much more abundant in the warmer more vegetated waters of the East Gallatin drainage. In the lower parts of the mainstem, a very few specimens are taken during the winter, but these disappear before spring. In warmer streams outside the Gallatin drainage, the larvae may be found throughout the winter. In the upper parts of the drainage *Amiocentrus* is found most commonly in side channels which develop stands of *Ranunculus aquaticus* L. It also occurs on rocks with substantial growth of *Cladophora*, but it is rare on clean rock surfaces.

Micrasema bactro occurs in colder parts of the drainage than *Amiocentrus*. These two species are well separated in longitudinal distribution. Only *M. bactro* was taken as adults or metamorphotypes, but these collections are insufficient in number to rule out additional species being present in the drainage. Adults are relatively rarely taken probably because of a short emergence period. This species is most abundant in upper parts of the mainstem in association with bryophytes. It also occurs in some very alpine situations, but is never so abundant there.

Two species of *Brachycentrus* occur in the drainage. These two species are very similar and occur together in many areas. West of Bozeman where both are common, a clear seasonal separation is indicated. Although the emergence of the adults is separated by only 1.5 months, the growth of the larvae is grossly different (Figure 17). *Brachycentrus occidentalis* at this site shows strongly seasonal growth with the eggs hatching in July after being laid in May. The first four instars are passed quickly during the warmest period of the year. The fifth instar larvae are fully grown by mid-winter, and begin closing the case for pupation in March. By mid April only pupae are taken, and the adults appear very early in May. Emergence is also very synchronized with the bulk of the population emerging over a few days, but living for a couple weeks. In contrast, *Brachycentrus americanus* appears as first instar larvae in September, while some of the adults are still in flight, but after *B. occidentalis* has reached the final instar. The growth of this species is much slower, progressing through the instars over the course of the winter months. The final instar is not achieved until mid-April, by which time *B. occidentalis* is pupating. Pupation of *B. americanus* is less synchronous and adult flight period is much longer than that of *B. occidentalis*.

Table 22. Smaller families of Limnephiloidea known from the Gallatin River drainage. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) general trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Brachycentridae					
Amiocentrus aspilus (Ross)	4420000	Us	G	Cg-Cb	CG
Brachycentrus americanus (Banks)	4444320	Uw-S	G	Cg	CF
B. occidentalis Banks	4443200	Uw	G	Cg	CF
Micrasema bactro Ross	0134343	Uw	G	Cg	CG
Helicopsychidae					
Helicopsyche borealis (Hagen)	3133000	Aws	S	Cg	CG
Lepidostomatidae					
Lepidostoma cascadense (Milne)	0001222	Uw	G	Cg	CG
L. pluviale (Milne)	4432000	Uw	G	Cg	CG
L. spicatum Denning	0000022	Uw	G	Cg	CG
L. podagerum (McLachlan)	3200022	Uw	S	Cb	SD
L. unicolor (Banks)	3230000	Aws	S	Cg-Cb	SD-SH
Phryganeidae					
Phryganea cinerea Walker	2200000	U?	LM	Cb	SD
Agrypnia colorata Hagen	2000000	?	L	Cb?	SD?
Agrypnia improba (Hagen)	0000022	?	L	Cb?	SD?
Leptoceridae					
Ceraclea annulicornis (Stephens)	3320000	Uw	M	Cg	CG
Oecetis avara (Banks)	3200000	Uw	G	Cg	Pr
Uenoidae					
Neothremma alicia Dodds & Hisaw	0000234	Uw	G	Cg	CG

In the mainstem of the river directly west of Bozeman, a large, final instar of *B. americanus* was rarely found at times when the vast majority of individuals are in early instars. From the Gallatin Canyon upstream, these large individuals are abundant. In this area of the mainstem as well as in all tributaries where it occurs, *Brachycentrus americanus* takes 2 years to complete its growth. In the mainstem just below Yellowstone National Park where both *Brachycentrus* species are abundant, the pattern is similar to that found west of Bozeman, but with the following modification. Here *B. occidentalis* undergoes the same annual pattern of development, but is slightly delayed seasonally. *Brachycentrus americanus* is delayed more strongly, so that the larvae of that species do not emerge before the onset of winter. The eggs that were laid during that summer hatch in the fall so that 2 generations are present in the stream during most of the year. The mostly full grown larvae of *B. americanus* probably do not feed extensively over the late fall and winter. They emerge the next summer at about the same time as those with the univoltine life cycle in the river west of Bozeman. This pattern is the same in still higher parts of the mainstem and in tributaries where *B. occidentalis* does not occur.

Family Helicopsychidae: This largely tropical family is represented in Montana and the Gallatin drainage by a single species, *Helicopsyche borealis*. Within the Gallatin drainage this species is often abundant in the spring creeks of the Gallatin Valley and in parts of the East Gallatin, but it is usually rare in the mainstem of the Gallatin River. Isolated populations of this species occur in large springs, even at high elevations.

Family Lepidostomatidae: The family Lepidostomatidae is represented in the Gallatin drainage by five species (Table 22). Only *Lepidostoma pluviale* occurs in the mainstem of the river. This species is largely restricted to the middle and lower reaches of the river, but occurs higher in the drainage in large springs. The upper limit of its longitudinal range on the mainstem of the river, the mouth of the canyon, is very sharply defined compared to most other species. Within its range, *L. pluviale* is one of the most abundant insects in the river. It frequently makes up the bulk of the gut contents of mountain whitefish. *Lepidostoma unicolor* occurs in modest numbers in spring creeks in the Gallatin Valley, but may have large populations near the source of large springs. This species is strongly associated with aquatic vegetation, especially watercress. The adults emerge over much of the year. *Lepidostoma podagerum* is known from some springs in the Gallatin Valley, as well as springs at much higher elevations. The larvae are usually associated with wood. Two species, *L. spicatum* and *L. cascadense*, while never very common, occur together in many small and medium mountain streams. They appear ecologically very similar.

Family Leptoceridae: This is another family better represented in warmer, less torrential waters. In the Gallatin drainage only two species are known (Table 22). Both species are confined to the mainstem, and are most common in the lower parts of the drainage. Several additional species have been taken from the lower Madison river drainage and may also have limited occurrence in the lower Gallatin drainage. *Ceraclea annulicornis* occurs as far upstream as the lower parts of the Gallatin Canyon and it occupies a habitat apparently identical to the limnephilid *Apatania shoshone*. They are frequently taken in mixed aggregations from the same rock and can be identified in the field only with difficulty. The case of *C. annulicornis* is slightly finer and more tapered than that of *A. shoshone*. The larvae of these two species are easily identified in the field if pulled from the case. *Oecetis avara* is more strongly restricted to the lower parts of the river and is rare as far upstream as Bozeman. Larvae are most abundant in spring creeks in the Gallatin Valley. The adults are frequently attracted to lights far from where the larvae occur.

Family Uenoidae: This family, as redefined by Wiggins, Weaver and Unzicker (1985) is represented in the Gallatin drainage by a single species, *Neothremma alicia* (Table 22). This species is characteristic of very small, cold mountain streams. *Neothremma alicia* is frequently abundant and emerges primarily in mid-summer. *Sericostriata surdickae* Wiggins, Weaver and Unzicker, was recently described as a new uenoid species and genus from southwest Montana and adjacent Idaho. This species was reported to occur with *N. alicia* (Wiggins, Weaver and Unzicker, 1985), but it does not appear to occur within the Gallatin drainage.

Diptera

Only six species of Diptera are treated here (Table 23). These were the only species that were both specifically recognized and important in the quantitative data sets. This is a very small fraction of the total number of aquatic Diptera species which occur within the Gallatin drainage. These six species, however, constitute the vast majority of all dipterans, taken from large boulders in swift current with the exception of Chironomidae and Simulidae. These two families were very important in the quantitative data sets, but were not identified beyond the family level. Achieving species recognition for all stages of all of the species of these two families occurring in the Gallatin drainage was not feasible. These two families together are often about as numerous as all other taxa combined, but are generally much smaller in body size. They are also the most frequently taken prey item by most lotic predators. The simulids encountered are ecologically rather uniform, preferring clean substrates exposed to strong currents where they filter feed. Data for simulids are sometimes presented in the community ecology section. Chironomids occupy all habitats and have diverse feeding mechanisms. They are not included in the analysis of the community ecology data sets.

The Athericidae are represented in Montana by a single species *Atherix pachypus*. This species is most abundant in the warmer, less torrential streams of the Gallatin Valley, and is more common still downstream of the Gallatin drainage and in the rivers adjacent to it. This species favors highly cluttered substrate in moderate current. Dead adult females frequently accumulate in large numbers on the undersurfaces of bridges where they place their eggs.

Table 23. Diptera known from the Gallatin River drainage, which are thought to be recognizable to species and occurred in the quantitative data sets. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Athericidae					
Atherix pachypus Bigot	3222200	Uw	G	Cb	Pr?
Blephariceridae					
Bibiocephala grandis Osten Sacken	3443000	Uw	T	Cg	Sc
Agathon comstocki (Kellogg)	0000032	Uw	T	Cg	Sc
Deuterophlebiidae					
Deuterophlebia nielsoni Kennedy	3443300	As	T	Cg	Sc
Psychodidae					
Pericoma sp.	2222432	?	G	Cb	CG?
Tipulidae					
Antocha monticola Alexander	2222200	?	G	Cg	CG?

The family Blephariceridae, or net-winged midges is represented by two largely allopatric species. Both are restricted to clean rock surfaces in very fast current where they cling very strongly by way of ventral suckers. *Bibiocephala grandis* occurs on moderate sized boulders throughout most of the mainstem of the river and in the lower reaches of the larger tributaries. *Agathon comstocki* occurs mostly on larger rock faces of small mountain streams. The latter species is difficult to collect in numbers as it adheres very strongly and its preferred substrate can seldom be removed from the stream for examination. The two species have been taken together only where a small mountain stream enters the mainstem in the Gallatin Canyon. In that case, it is *Bibiocephala* that invades a short distance up the tributary stream.

In the mainstem west of Bozeman, *Bibiocephala* takes nearly a full year to complete its growth through four instars (Figure 18). The width of the first body segment, which consists

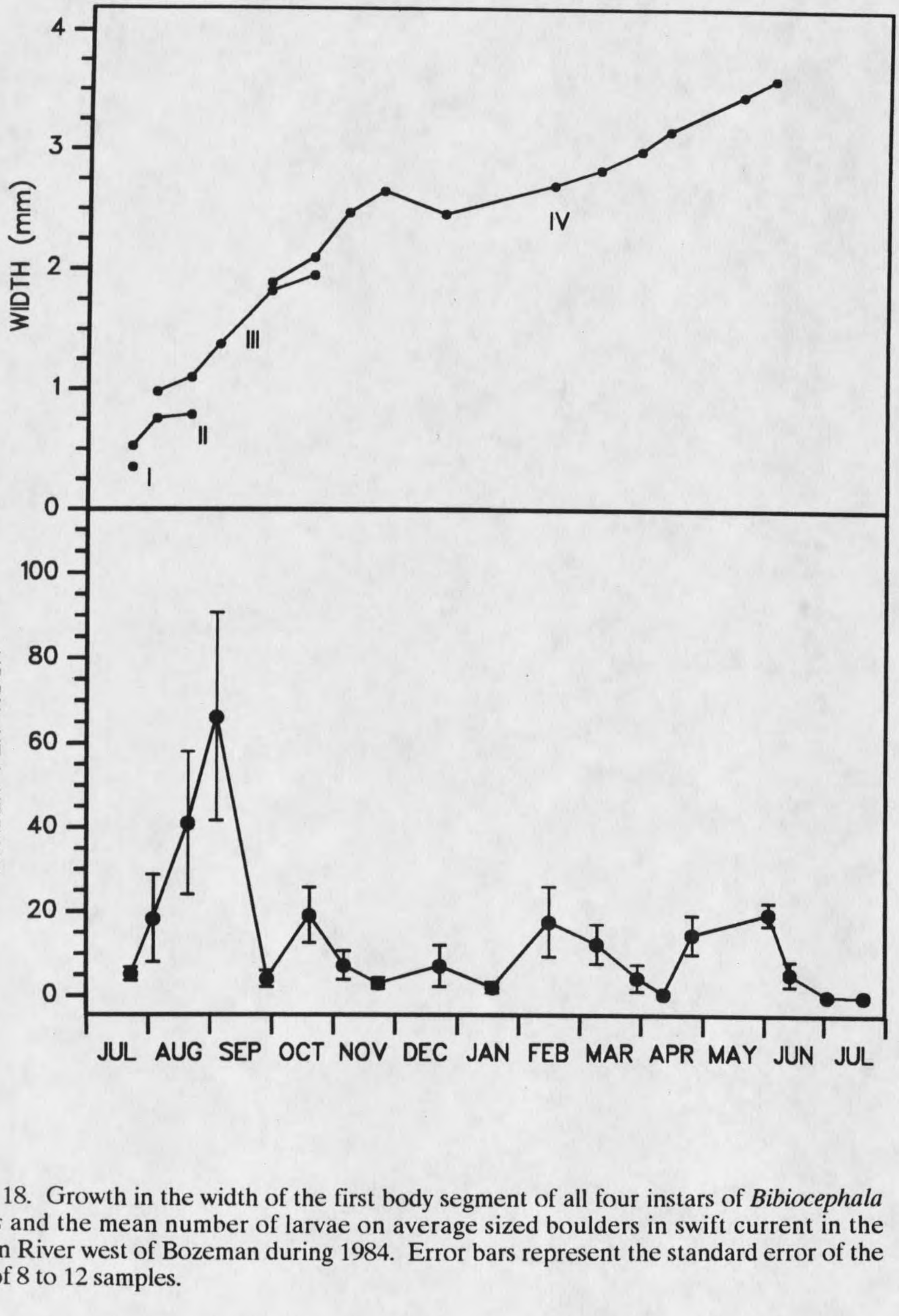

Figure 18. Growth in the width of the first body segment of all four instars of *Bibiocephala grandis* and the mean number of larvae on average sized boulders in swift current in the Gallatin River west of Bozeman during 1984. Error bars represent the standard error of the mean of 8 to 12 samples.

of the head, thorax and first abdominal segment combined, was measured in the absence of a more suitable sclerotized body part. Larval instar is easily determined using the number of gills, antenna segments and the size and shape of the sclerites associated with the pseudopods. The instars are likely to be taken for different species. Pupation occurs from mid June to mid July with the adults in flight during mid July. The first instar appears soon after the adults, and grows and molts quickly. The final instar larvae overwinter with little or no growth. This phenology is only slightly delayed in the highest parts of its range, where adults may be taken in early August. *Agathon comstocki* exhibits much more staggered larval growth over the winter and spring than does *Bibiocephala grandis*.

The larvae of *Bibiocephala* are highly aggregated, making quantitative sampling difficult. As many as 236 small larvae have been taken from a single rock and it is rare to have less than 8 to 10 larvae on a rock that has any at all. Larval densities are highest soon after the eggs hatch, and fall sharply when the final instar is achieved (Figure 18). The larval density is then relatively constant until emergence the next summer. The larvae are only rarely encountered in fish stomachs. *Bibiocephala* is ecologically very similar to the mayfly *Drunella doddsi*, but does not extend as far upstream. The longitudinal range of both species contracts upstream in years of low flow, primarily due to increased rock cluttering.

A single species of Deuterophlebiidae, *Deuterophlebia nielsoni* Kennedy occurs in the Gallatin drainage. This species may well be a junior synonym of *D. coloradensis* Pennak. It is present only during the summer months where it occurs on clean boulders or rock faces in very fast current. Its longitudinal range includes most of the mainstem and all but highest tributaries. It is uncommon in the East Gallatin drainage, and does not occur in the spring creeks of the Gallatin Valley. In the lower parts of its range, larvae of all instars, pupae and adults may be taken from late June through September. Their small size and very tight attachment undoubtedly cause them to be under represented in many samples. Pupae attach even more tightly. They are sometimes better counted on the rock without being removed.

The running waters of the Gallatin drainage contained what is presumed to be a single species of *Pericoma*, a psychodid. It is abundant in gravel riffles of cold mountain streams. It may be taken in small numbers far downstream.

The Tipulidae or crane flies are represented by many species, but most of these occur buried in fine substrates, water saturated soil or in springs. A single species of *Antocha*, probably *A. monticola*, occurs on large rocks in moderate current. It is never very common, but occurs in all parts of the drainage except cold mountain streams.

Coleoptera

A very large number of aquatic and semiaquatic beetles have now been recognized from the Gallatin River drainage. The number of these species occurring in the drainage may well outnumber those of Ephemeroptera, Plecoptera and Trichoptera combined. A complete faunal inventory and ecological characterization of the beetle species from the drainage are under-way, but they are very incomplete at this time. Most beetle species from the drainage occur in lentic waters, or along stream shorelines. Many species are nocturnal and highly congregated and secretive during the day. Beetle species are frequently of sporadic occurrence, but may be taken in very large numbers when found. Just 13 species are regularly taken in routine lotic samples (Table 24). They are numerically unimportant in the community data sets.

The Coleoptera species taken in the lotic samples are not very representative of aquatic beetles in several ways. Most species of aquatic beetles are aquatic as both larvae and adults. *Helichus striatus*, which has terrestrial larvae and *Lara avara*, which has terrestrial adults are the only exceptions known from the drainage. Most species of aquatic beetles known from the drainage can live more than 1 year as adults. *Narpus concolor* and *Lara avara* are the only known exceptions. Both of these species occur as adults for only a short time in the summer. Most aquatic and semiaquatic beetles within the Gallatin drainage have the larvae present only for a short time during the summer. Both species of *Amphizoa*, however, take nearly a full year to complete larval growth. The larvae of *Brychius horni* are most abundant from October to May and they are very rare during the summer. *Lara avara* is unique in taking more than 1 year and probably more than 4 years to complete its growth. The four remaining species of elmids have larvae, at various stages of development, as well as the adults, present throughout the year. The life cycle of these cannot be determined with the data available.

Table 24. Coleoptera known from the Gallatin River drainage, which are thought to be recognizable to species and occurred in the quantitative data sets. Columns one through five give for each species; 1) the status of the species at seven longitudinal zones, 2) the life cycle type, 3) habitat preference, 4) habits and 5) trophic group. Definitions and abbreviations are given in Tables 4 and 5.

Species	(1) abcdefg	(2)	(3)	(4)	(5)
Family Amphizoidae					
Amphizoa insolens LeConte	0000022	Uw	M	Cb	Pr?
A. lecontei Matthews	1111222	Uw	M	Cb	Pr?
Family Dryopidae					
Helichus striatus LeConte	2220000	?	−GM	Cb	?
Family Dytiscidae					
Oreodytes sp.	3322000	Us	M	Sw	Pr
Family Haliplidae					
Brychius horni Crotch	3322000	A	G	Sw	SH
Family Hydrophilidae					
Ametor latus (Horn)	3223200	U?	M	Cb	?
A. scabrosus (Horn)	0000233	U?	M	Cb	?
Family Elmidae					
Lara avara LeConte	3112310	S	G	Cb	SD
Cleptelmis ornata (Schaeffer)	3000300	A	G	Cb	CG
Heterlimnius corpulentus (LeConte)	0010332	A	G	Cb	CG
Narpus concolor (LeConte)	0000220	Uw	G	Cb	CG
Optioservus quadrimaculatus (Horn)	4320000	A	G	Cb	CG
Zaitzevia parvula (Horn)	3220000	A	G	Cb	CG

Pupation of all aquatic beetles known from the drainage apparently always occurs above water during warm seasons. Pupation may sometimes occur as much as 100 meters from water based on pitfall collections of larvae and teneral adults.

Community Ecology

The previous section characterized 241 species of aquatic insects known from the Gallatin River drainage with regards to their trophic preferences, life cycles, habitats, habits and longitudinal zonation. Quantitative data addressing community organization cannot be fully interpreted without this information on the species. The previous section also indicated that most taxonomically related species are ecologically separated longitudinally along the river, spatially in different habitats, or seasonally. Many of these species appear to be ecological equivalents, that is doing the same thing in the same way, but in a different place or at a different time or in another part of the drainage. The extent to which many species follow similar patterns of abundances with regards to spatial distribution, longitudinal distribution and seasonal distribution is examined in this section.

Spatial Community Structure

Seventy-two taxa and approximately 265,000 individual invertebrates were taken in the two data sets addressing spatial organization, 62 taxa and 133,000 individual invertebrates in the 93 samples of the summer data set and 50 taxa and 132,000 individuals in the 76 samples of the spring data set. Forty taxa were shared between the two collections, though most of these were at very different sizes at these two times. The spring and summer collections combined, contained only 57% of the species known to occur at this site.

As the Ephemeroptera, Plecoptera and Trichoptera are thought to be very nearly completely known at this site, it is worth examining the breakdown of species missing from the two spatial data sets. Sixty-seven percent of the 37 species of mayflies known from this site appeared in the quantitative samples. Of the 12 species not represented, one is unknown as nymphs and was not recognized during this study. Five species were restricted to organic substrates and thus not taken in single-rock samples. A single species of mayfly, *Cinygmula gartrelli* completed its life cycle between the times of the two spatial samples. The remaining five species are simply rare at this site, being more abundant either upstream or downstream.

Only 35% of the 37 stonefly species known from the site appeared in the two quantitative spatial samples. Again a single species, *Taenionema pacifica* completed its life cycle in between the time of the two sets of samples. Eight stonefly species were very rare at this site being more common in other parts of the drainage. The remaining 15 species which were not represented included most species of the families Capniidae and Leuctridae as well as *Alloperla severa* and *Paraperla frontalis*, all of which are hyporheic and do not appear in benthic samples until just before emergence.

Trichoptera species were represented similarly to the mayfly species in the spatial samples with 66% of the 29 species known from the area being present in one or both of the two sets of samples. Of the 10 species missing from the samples, five are generally restricted to organic substrates at the margins of the river and not expected in single rock samples. The remaining five species of caddisflies are simply very rare at this site. No caddisfly species completed its life cycle in between the two sampling dates.

Both data sets were characterized by many rare species and by a few very abundant species (Figure 19). Singleton species constituted the mode in both samples. More species were taken in August than in April, but these were mostly rather rare, numbering less than 40 individuals each in the entire sample. These usually represented species occurring at the stream margins, with summer life cycles. Otherwise the curves for the two collection dates are very similar and correspond well with the log-normal distribution. This distribution is expected for any species whose abundance is determined by the product of a number of independent environmental variables. That is, with products there are many ways to

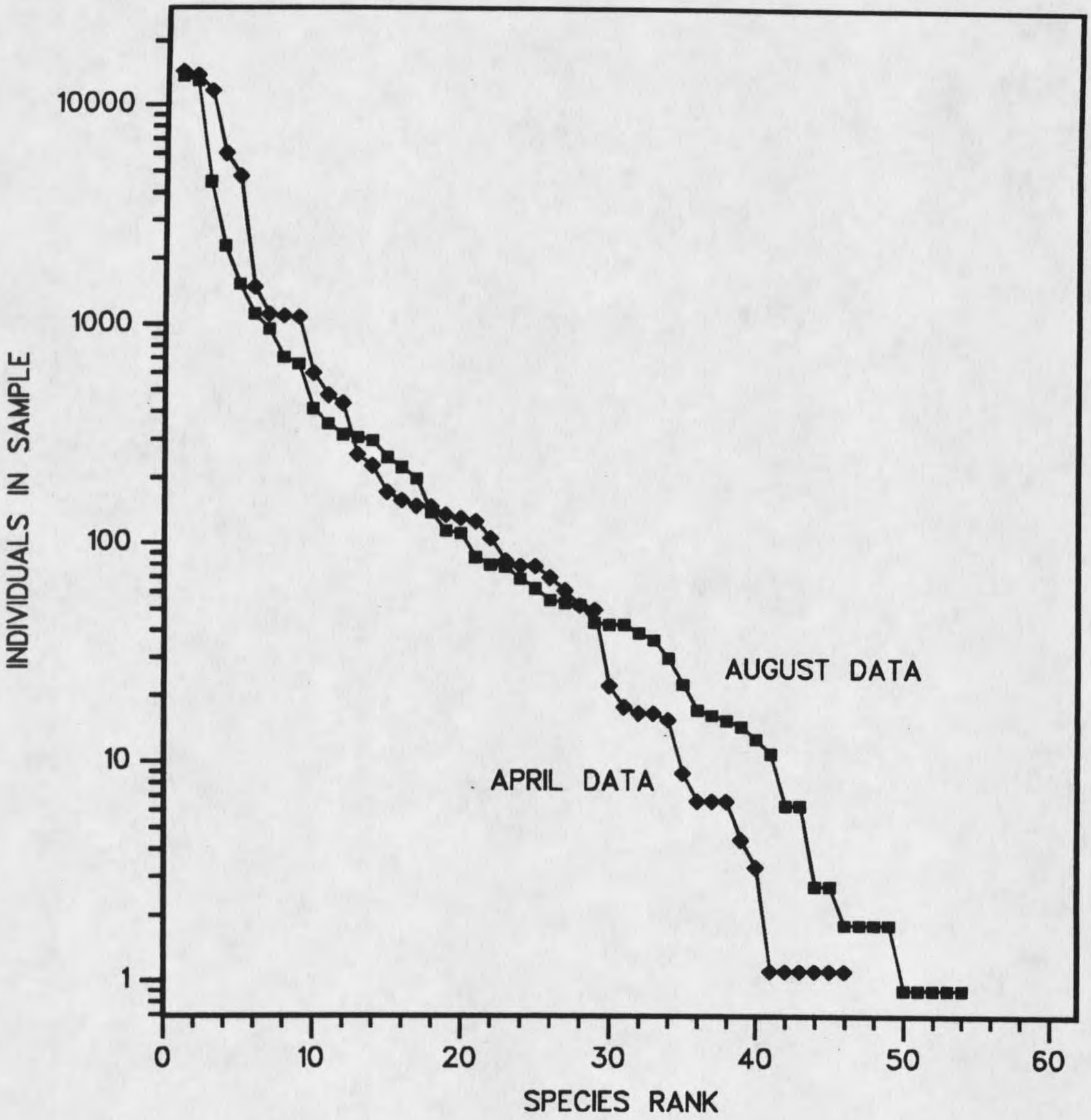

Figure 19. Total individuals per species in the August (N = 93) and in the April (N = 76) spatial data sets, Both are corrected to the mean sample size (N= 84.5). Only taxa thought to represent single species are shown.

produce zero or very small numbers, but very few ways to produce very large numbers. This is apparent in all of the data sets. The same distribution is expected also for communities made up of a large number of diverse species, which is definitely the case for the aquatic invertebrates treated here. This is also observed in all the data sets.

The log-normal distribution for both the population sizes of the species and the species abundances in the community at any one time means that the logarithm of the population density is a more natural variable for analysis than is the raw population densities. Consequently, the data were log transformed using the natural logarithm of the already area-normalized data augmented by one. This transformation is further justified to control variance, as the standard deviation of the raw species abundances is closely proportional to the mean. The log transformation also prevents the few, very abundant species, which are usually also small in body size, from dominating the analysis.

Bootstrap samples from both data sets (Figure 20) indicates that many, single rock samples are needed to take most of the species present. More samples were needed in August than in April to achieve the same percentage of the total. This is due to the presence of species with summer life cycles and the young of species with winter life cycles, both of which tend to be highly aggregated.

The number of species in the two data sets is so great relative to the number of observations that the number of species was greatly reduced before subjecting the data to multivariate statistical analysis. This reduces the impact of chance variation on the outcome and simplifies the interpretations of the eigenvectors. Since the objective of this part of the study is to examine spatial structuring of lotic communities, the multivariate analysis was performed for both data sets using the species with the greatest variance. That is those species which vary greatly over the spatially organized samples. This automatically excludes very rare species and thus avoids having these rare species contribute unduly to the results due to chance variation.

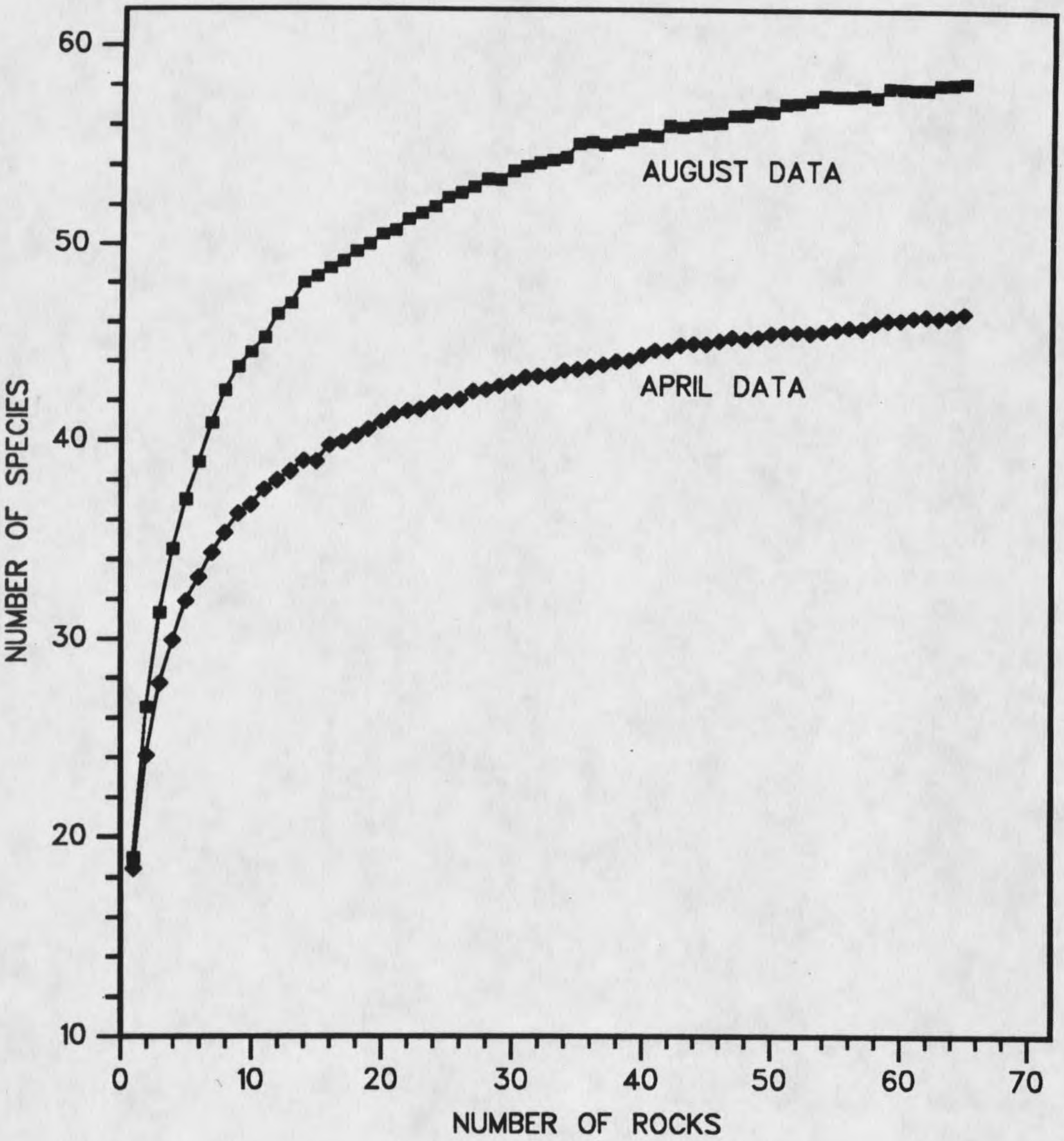

Figure 20. The mean number of species occurring in 300 bootstrap samples from the April (N = 76) and from the August (N = 93) spatial data sets. The bootstrap sample size ranges from 1 to 65.

The inclusion of species in the analyses was also subject to the constraint that they be more than a third grown at the time of sampling. This avoids both identification problems and possible complications of the species not having dispersed from egg-deposition sites. The number of species used in the analyses, subject to the above constraints, ranged from six to 30, and made little difference to the results. The results presented here for both data sets, were based on 12 species.

Spatial organization at this site, given single-rock sampling, seems restricted to few dimensions. For the April data, the first principal component accounts for 58% of the total variance (Table 25). Based on 1000 Monte Carlo simulations, the first principal component accounts for 2.9 times as much of the total variance as expected for variables with the observed variances, but with random covariance. An eigenvalue as large as the first is not expected in 1000 trials. The second eigenvalue is well within the range of values expected for variables with the observed variances, but with random covariance. The second eigenvalue is, however, rather large compared to the remaining eigenvalues. The second eigenvector is stable to jackknife validation indicating that the associated eigenvalue is distinct. Re-examination of the Monte Carlo results, this time with respect to the percentage of the remaining variance that is accounted for by each eigenvector, indicates that the second eigenvalue is larger than expected in 1000 trials.

For the August spatial data, the first principal component accounts for only 45% of the variance, but the first two principal components account for over 65% (Table 26). Based on 1000 Monte Carlo simulations, the first two principal components together account for just over twice as much of the total variance as expected for variables with the observed variances, but with random covariance. Eigenvalues as large as the first two are not expected in 1000 trials. The remaining eigenvalues are similar in size and the remaining eigenvectors account for no more of the variance than would the species alone and are thus not worth interpreting. For both of the spatial data sets the observations in the principal component space assumed an inverted U shape, with more breadth than height (Figure 21).

Table 25. Eigenvectors defining the first four principal components for the April spatial data set based on the covariance matrix of the log transformed abundances of the 12 species with the greatest variance.

Species	I	II	III	IV
Hydropsyche tana	.537	-.020	.036	-.113
Drunella flavilinea	.384	.220	-.504	-.391
Hydropsyche cockerelli	.368	-.169	.027	-.099
Arctopsyche grandis	.286	-.088	-.065	-.048
Ephemerella infrequens	.279	.015	.214	.102
Antocha monticola	.256	-.160	.179	.663
Isoperla quinquepunctata	.221	-.135	.624	-.185
Baetis tricaudatus	.193	.127	-.073	.179
Epeorus longimanus	.183	.314	.182	-.006
Brachycentrus americanus	.174	.545	-.211	.469
Cinygmula tarda	-.074	.640	.432	-.259
Cinygmula kootenai	-.219	.223	.051	.140
Eigenvalues	11.44	2.14	1.33	1.03
Percent variance	58.23	10.87	6.78	5.23
Cumulative percent	58.23	69.10	75.88	81.12

The correlations of the principal component with the number of species, number of individuals, water depth, rock weight and water velocity of each sample (Table 27) in conjunction with the known biology of the species make interpretation of the principal components fairly straightforward. For both data sets, the first principal component correlates strongly with velocity and thus helps separate fast water species from slow water species. The weighting applied to the species by the eigenvectors of both data sets support this simple interpretation. Species occurring in fast current are weighted positively while species occurring at the stream margins with little current are weighted negatively.

The first principal component is also correlated with the total number of invertebrates for both data sets. Rocks in fast currents generally contain more total invertebrates than rocks in little current. Access to moving water for filter feeders, and to non-silted rock

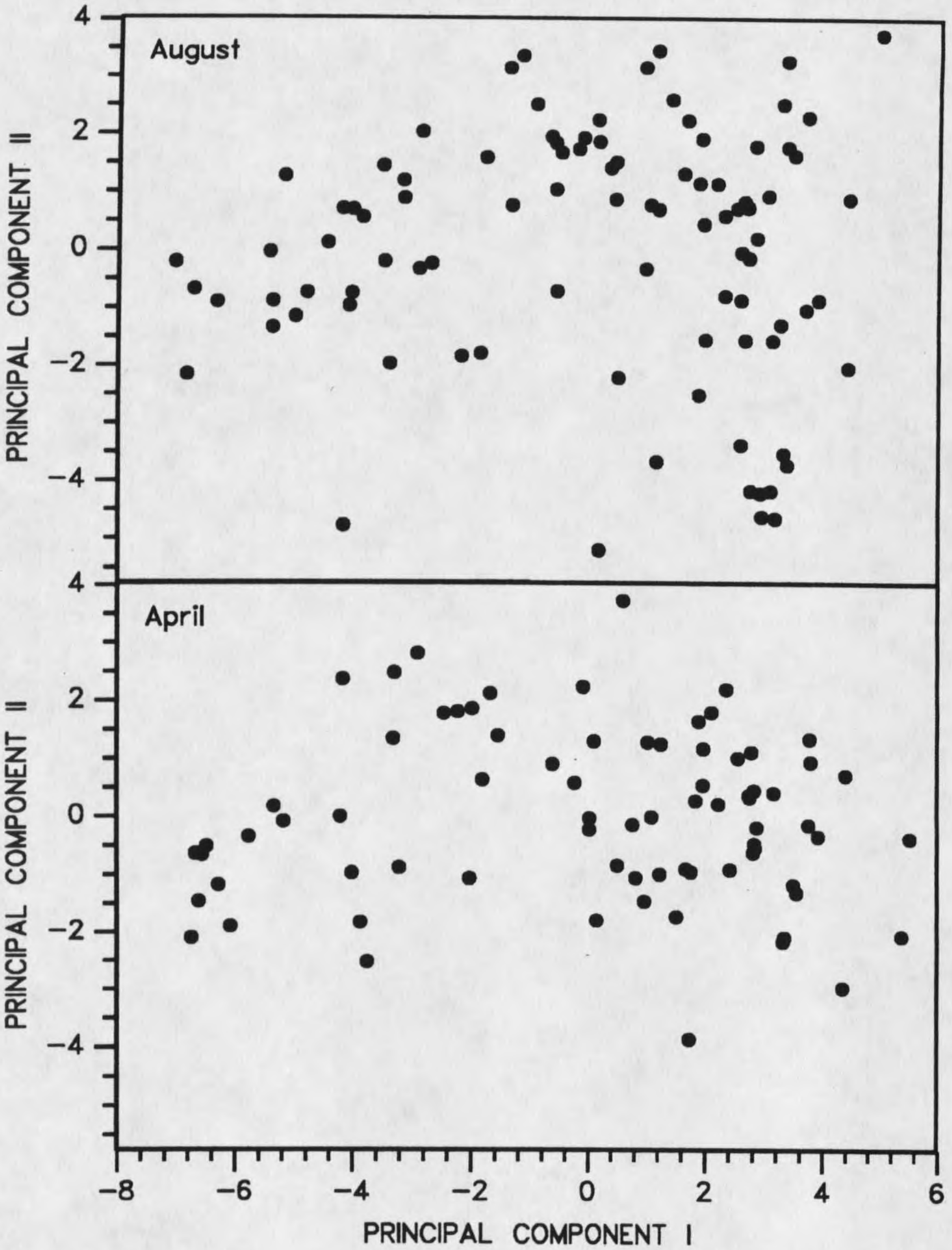

Figure 21. The 93 samples of the August spatial sample and the 76 samples of the April scored on the first two principal components.

surfaces for scrapers and clingers, is the most obvious explanations. The first component is not a pure measure of biomass in either data, but approaches it more closely in the April data.

Table 26. Eigenvectors defining the first four principal components for the August spatial data set based on the covariance matrix of the log transformed abundances of the 12 species with the greatest variance.

Species	I	II	III	IV
Baetis tricaudatus	.483	.165	.053	.172
Hydropsyche cockerelli	.393	.137	-.119	.099
Acentrella turbida	.349	.137	.565	-.041
Arctopsyche grandis	.347	.090	-.398	-.054
Bibiocephala grandis	.177	-.440	-.288	.384
Isoperla fulva	.160	.438	-.344	.152
Rhithrogena futilis	.159	.057	.491	.293
Drunella grandis	.045	.370	-.228	-.192
Ephemerella infrequens	-.177	.206	-.005	.739
Oreodytes sp.	-.245	-.072	-.070	.065
Paraleptophlebia bicornuta	-.285	.046	-.023	.329
Lepidostoma pluviale	-.336	.593	.073	-.062
Eigenvalues	9.99	4.45	1.33	1.25
Percent of variance	45.11	20.08	6.01	5.63
Cumulative percent	45.11	65.19	71.20	76.83

While the first component is correlated with total invertebrate density for both data sets, the correlation with species number is very different. In the August data species number is not correlated with the first principal component, while in the April data, species number is strongly and positively correlated with the first component. That is, during August there are more species occurring in areas with little current. These species are not abundant enough to affect the previous correlation with total invertebrate density. In April, there are relatively few species occurring in slow water. This difference is also manifest in the correlations with sample depth. Slow current velocities almost always occur in shallow water for rocks which are not strongly cemented into the substrate. Thus in

August, depth is not correlated with species number or with total number, but in April it is positively correlated with both.

Table 27. Correlations among the first three principal components based on the log transformed species abundances, the number of species, the total number of invertebrates, and rock depth, weight and overhead current velocity for the August and for the April spatial data sets. The upper triangular matrix indicates simple significance levels as ns for P > 0.05, * for P < 0.05 and ** for P < 0.01.

August (N = 93)	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]
[1] PC I	--	ns	ns	ns	**	ns	*	**
[2] PC II	.00	--	ns	**	*	ns	*	**
[3] PC III	.00	.00	--	ns	**	ns	ns	ns
[4] Species number	-.02	.52	-.19	--	**	ns	ns	ns
[5] Total number	.60	.23	-.29	.32	--	ns	**	**
[6] Depth	.05	-.15	-.07	-.07	-.16	--	**	**
[7] Weight	.21	-.23	-.11	.12	.41	.30	--	**
[8] Velocity	.72	-.30	-.01	-.14	.36	.40	.28	--

April (N = 76)	[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]
[1] PC I	--	ns	ns	**	**	**	ns	**
[2] PC II	.00	--	ns	ns	ns	**	ns	ns
[3] PC III	.00	.00	--	ns	ns	*	**	*
[4] Species number	.76	.13	.14	--	**	**	ns	**
[5] Total number	.63	.00	-.22	.54	--	ns	**	**
[6] Depth	.47	-.33	.24	.41	.22	--	ns	**
[7] Weight	-.04	-.17	-.32	.13	.34	.07	--	**
[8] Velocity	.65	-.11	-.25	.58	.55	.43	.33	--

In both of the spatial data sets, rock size is only very weakly correlated with the number of species, but is significantly and positively correlated with the total number of invertebrates. This may be due to a gross failure of the assumption that the rocks were spherical, which was used to correct the raw densities. It could also indicate that large rocks support a number of invertebrates disproportionally large for their surface area. The latter is quite reasonable, as large rocks are more stable and they frequently have a larger fraction of their lower surface available for invertebrate use. A possible complication arises because in the August data rock depth and weight are positively correlated and in April they are not.

The difference in this correlation is due to the configuration of the stream bed and to the water level. At the low water level of April, large rocks are to be found in all parts of the channel, while at the higher water levels in August only relatively small rocks are found in shallow water near shore.

Unlike the first principal component, the interpretation of the second principal component for the two data sets is rather dissimilar. In the August data, the second principal component is quite important capturing 20% of the total variance and is interpreted as a measure of rock clutter. The species that are characteristic of cluttered rocks are weighted positively and the species that are characteristic of clean rocks are weighted negatively. Scores on the second principal component are more variable for rocks that score high on the first principal component (Figure 21). Rocks in slow current are seldom very cluttered nor very clean. Species number correlates strongly with this component in this data set.

For the April data, the second principal component is hardly worth interpreting as it accounts for only 11% of the variance. It seems to separate shallow water species from deep water species. Species restricted to shallow water, either along the shores or on rocks in shallow turbulence, are weighted positively, while those more generally distributed are weighted negatively or just weakly. None of the species are thought to be restricted to deep water, which may account for the weakness of both the negative weights and correlations.

Tables 28 and 29 summarize all species occurring in more that 10% of the samples of the two spatial data sets. For the August data, the correlations with the first two principal components provide a concise, quantitative summary of the habitat preferences of the species. Species with rather different correlations with either the first or with the second principal component are unlikely to have substantial contacts with one-another. Correlations with the first principal component are very similar to those with water velocity alone and can serve to identify the velocity preferences of the species. The correlations with the second principal component are not very similar to those of any of the physical measures. It identifies two biological assemblages. One assemblage consists of many species that tend to occur together on highly cluttered rocks and the other assemblage consists of species that occurs on clean rocks. These species are not associated with many other species.

Table 28. Invertebrate taxa present in more than 10 percent of the samples (FP) from the August spatial data (N=93) ranked according to the mean of their log transformed abundances. Also shown for each taxon is its standard deviation (STD), and the correlations with the first two principal components (F1,F2), the total number of species (SN), the total number of individuals (TN), the depth (D), weight (WT) and velocity (V).

Taxon	mean	STD	FP	F1	F2	SN	TN	D	WT	V
Baetis tricaudatus	3.93	1.78	.95	.86	.20	.17	.69	-.18	.12	.52
Lepidostoma pluviale	3.02	1.75	.85	-.61	.71	.32	-.22	-.13	-.30	-.59
Hydropsyche cockerelli	2.60	1.43	.88	.87	.20	.12	.57	.03	.14	.57
Simulidae	2.42	2.51	.63	.68	-.30	-.00	.62	-.07	.26	.67
Acentrella turbida	2.18	1.44	.80	.77	.20	-.02	.35	-.05	.06	.49
Arctopsyche grandis	1.95	1.31	.81	.84	.15	.10	.62	.04	.21	.51
Drunella grandis	1.73	1.08	.84	.13	.72	.41	.35	.06	-.07	-.05
Isoperla fulva	1.52	1.31	.68	.39	.71	.48	.40	-.06	-.09	.08
Rhithrogena futilis	1.15	1.10	.62	.46	.11	.10	.12	.05	.00	.35
Attenella margarita	1.13	1.01	.67	-.61	.42	.36	-.20	-.21	-.24	-.62
Ephemerella infrequens	1.01	1.20	.47	-.46	.36	.43	-.07	-.27	-.21	-.45
Serratella tibialis	.93	.89	.60	.48	.30	.11	.34	-.13	-.06	.25
Atherix pachypus	.88	.97	.57	.42	.40	.38	.47	-.02	-.05	.15
Paraleptophlebia bicornuta	.76	1.17	.37	-.77	.08	.30	-.39	-.23	-.18	-.62
Pteronarcella badia	.72	1.00	.46	.38	.26	.31	.60	.04	.16	.28
Bibiocephala grandis	.66	1.39	.24	.40	-.67	-.22	.19	.10	.23	.63
Drunella doddsi	.56	.81	.40	.41	-.31	-.07	.23	-.07	.09	.45
Oreodytes sp.	.54	1.12	.24	-.69	-.14	.06	-.36	-.25	-.10	-.56
Brachycentrus occidentalis	.51	.72	.42	.42	.18	.30	.43	-.06	.13	.19
Ameletus sp. A	.50	.99	.25	-.55	.08	.38	-.25	-.18	-.14	-.49
Nixe criddlei	.42	.62	.38	-.48	.25	.37	-.18	-.21	-.19	-.51
Timpanoga hecuba	.39	.73	.29	-.67	-.12	-.14	-.37	-.37	-.24	-.57
Deuterophlebia nielsoni	.36	.74	.23	.40	-.65	-.20	.15	.21	.29	.68
Antocha monticola	.36	.67	.26	.00	.19	.36	.28	-.08	.11	-.06
Skwala parallela	.36	.56	.34	-.11	.43	.51	.00	-.21	-.25	-.32
Optioservus quadrimaculatus	.33	.70	.25	-.48	.03	.24	-.20	-.19	-.14	-.39
Neophylax rickeri	.31	.65	.22	-.40	.16	.26	-.24	-.26	-.24	-.39
Triznaka signata	.26	.62	.16	-.19	.26	.24	-.11	-.08	-.16	-.20
Ceraclea annulicornis	.26	.63	.18	-.55	.06	.18	-.25	-.19	-.28	-.44
Ochrotrichia logana	.23	.51	.22	-.08	.30	.42	.22	-.13	-.19	-.16
Tricorythodes minutus	.22	.52	.17	-.49	.07	.17	-.12	-.22	-.02	-.39
Rhyacophila bifila	.22	.56	.17	.30	.19	.12	.30	.08	-.04	.23

Table 28. *Continued*

Taxon	mean	STD	FP	F1	F2	SN	TN	D	WT	V
Epeorus longimanus	.18	.47	.16	-.13	-.07	.28	-.09	.08	.06	-.05
Paraleptophlebia heteronea	.17	.54	.10	-.18	.11	.29	-.16	.04	-.02	-.20
Zapada cintipes	.15	.50	.10	.17	.10	.12	.23	-.24	-.19	-.06
Baetis hageni	.15	.38	.15	.00	.08	.08	-.06	.03	-.02	-.03
Hesperoperla pacifica	.11	.29	.14	.13	.04	.25	.14	.27	.13	.22
Brachycentrus americanus	.10	.29	.12	.19	-.13	.15	.29	-.07	.03	.19

For the April data, the correlations with the first principal component are less well recapitulated by water velocity alone. Water velocity and depth are both involved and most species correlate positively. In this data set, the first principal component accounts for almost as much of the total variance as do the first two components of the August data set. In April relatively few species occur in shallow water with little current and the distinction of clean and cluttered rocks is largely lost.

Table 29. Invertebrate taxa present in more than 10 percent of the samples (FP) from the April spatial data (N=76) ranked according to the mean of their log transformed abundances. Also shown for each taxon is its standard deviation (STD), and the correlations with the first two principal components (F1,F2), the total number of species (SN), the total number of individuals (TN), the depth (D), weight (WT) and velocity (V).

Taxon	mean	STD	FP	F1	F2	SN	TN	D	WT	V
Lepidostoma pluviale	4.96	.98	.99	.23	.32	.19	-.03	-.06	-.39	-.34
Baetis tricaudatus	4.47	1.00	1.00	.65	.19	.54	.71	.02	-.06	.47
Hydropsyche tana	4.10	1.88	.93	.97	-.02	.72	.57	.53	-.06	.65
Ephemerella infrequens	3.84	1.14	.99	.83	.02	.68	.56	.38	-.14	.35
Drunella flavilinea	3.36	1.57	.88	.82	.20	.57	.51	.20	-.03	.56
Simulidae	3.17	2.42	.76	.58	-.05	.54	.63	.09	.27	.78
Cinygmula tarda	2.50	1.20	.89	-.21	.78	.02	-.27	-.25	-.29	-.23
Epeorus longimanus	2.22	1.11	.89	.56	.41	.50	.24	.22	-.14	.26
Hydropsyche cockerelli	1.99	1.35	.78	.92	-.18	.71	.53	.57	.00	.68
Brachycentrus americanus	1.93	1.24	.86	.48	.64	.41	.41	-.03	.05	.25
Arctopsyche grandis	1.52	1.14	.72	.85	-.11	.67	.63	.43	.17	.70
Antocha monticola	1.17	1.24	.58	.70	-.19	.47	.42	.38	-.15	.33
Isoperla quinquepunctata	1.09	1.19	.55	.63	-.17	.51	.24	.44	-.15	.25
Isoperla fulva	.83	.68	.70	.40	.06	.34	.18	.15	-.14	.14
Drunella grandis	.77	.66	.66	.37	.00	.35	.22	.00	-.16	.17
Cinygmula kootenai	.73	1.02	.39	-.73	.32	-.54	-.43	-.35	-.12	-.67
Atherix pachypus	.61	.88	.41	.49	-.00	.45	.45	.34	.01	.21

Table 29. *Continued*

Taxon	mean	STD	FP	F1	F2	SN	TN	D	WT	V
Rhyacophila bifila	.57	.76	.43	.43	-.15	.51	.53	.09	.32	.68
Serratella tibialis	.52	.89	.28	.22	-.05	.29	.22	.15	.12	.09
Bibiocephala grandis	.49	.99	.26	.13	-.16	.22	.19	.12	.26	.66
Drunella doddsi	.48	.77	.32	.16	-.15	.24	.27	-.05	.32	.64
Brachycentrus occidentalis	.41	.77	.28	.53	-.13	.43	.48	.32	-.04	.23
Paraleptophlebia heteronea	.39	.65	.30	-.15	.10	.02	-.16	.20	-.16	-.34
Ameletus sp. C	.37	.85	.20	-.61	-.15	-.41	-.41	-.32	-.10	-.59
Caudatella heterocaudata	.37	.70	.25	.35	-.05	.32	.25	-.02	-.06	.36
Apatania shoshone	.35	.67	.28	-.20	.19	.04	-.13	.02	-.12	-.25
Pteronarcella badia	.29	.58	.24	.15	.06	.18	.05	.05	-.08	.00
Ceraclea annulicornis	.28	.66	.20	-.22	.03	.03	-.29	.15	-.14	-.29
Ochrotrichia logana	.25	.65	.14	.12	.00	.16	-.07	.28	-.04	.02
Micrasema bactro	.21	.57	.14	.22	-.00	.34	.15	.35	.00	.09
Rhyacophila brunnea	.12	.39	.11	.23	.04	.15	-.02	.21	-.27	-.01
Rhithrogena futilis	.11	.31	.12	-.14	.20	.03	-.08	-.24	.18	.04
Hesperoperla pacifica	.10	.31	.12	.18	.06	.30	.13	.13	.11	.20

Canonical correlation analysis of the species used in the principal components analysis and sample depth, weight and velocity indicates that current velocity is of paramount importance. For both data sets the first canonical variate formed from the physical variables is primarily velocity alone (Tables 30 and 31). The corresponding canonical variates formed from the species largely recapitulates the principal components (Figures 22 and 23). This is most striking, as the principal components were based on covariance and the canonical correlation is based only on correlation. The linear combinations of log transformed species abundances which correlate best with the physical variables are only slightly better correlated than are the principal component scores themselves which were entirely blind to the physical data.

Discriminant analysis was used with the two spatial data sets to determine if any set of species could be used to differentiate between rocks above and below the large pool which occupied the center of the sample area. The scores on the first canonical variate based on the physical variables were used to select a subset of rocks that were most comparable in terms of the physical measures. Jackknife validation of all the discriminant analyses

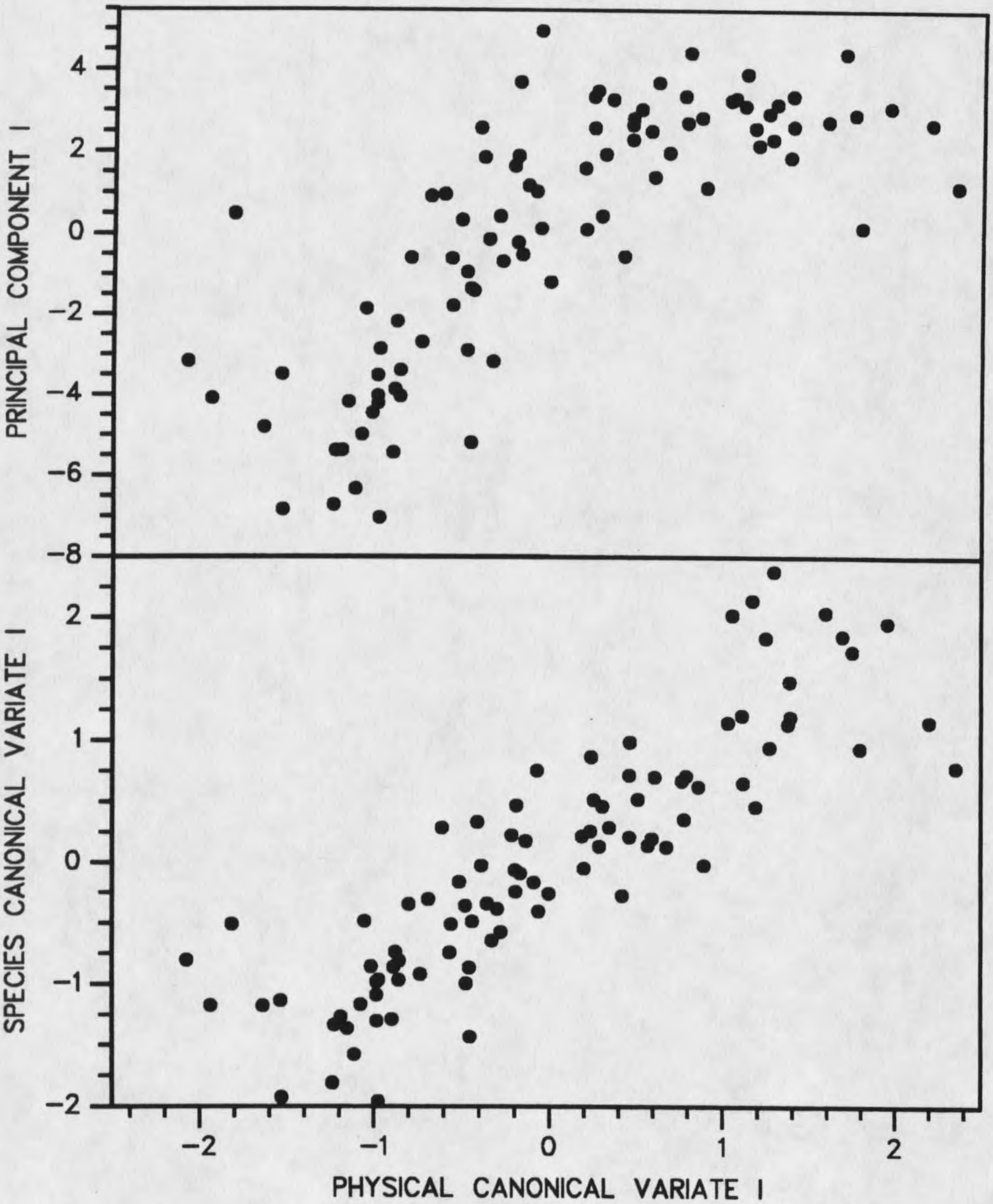

Figure 22. The 93 samples of the August spatial sample scored on the first principal component and on the first pair of canonical variates.

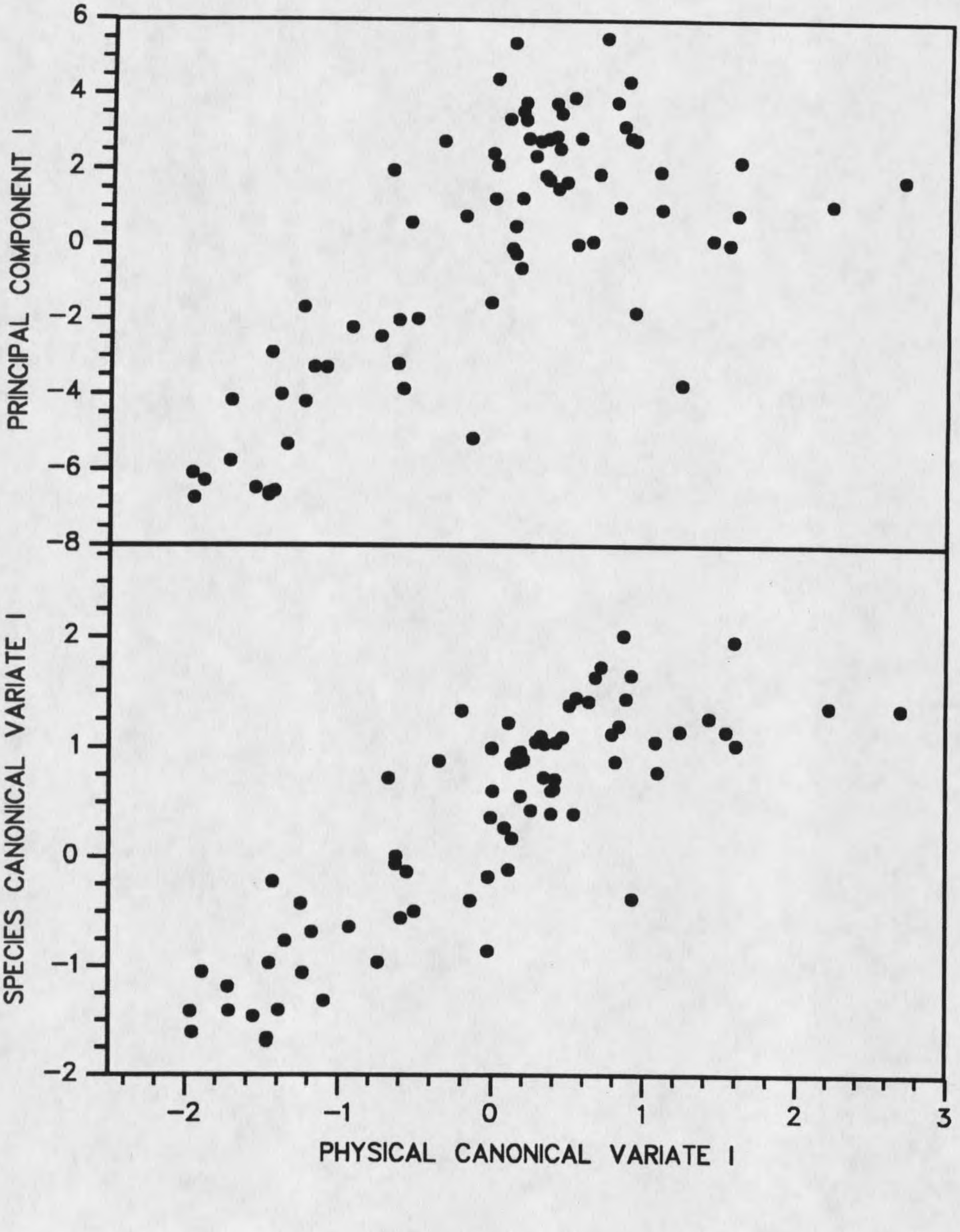

Figure 23. The 76 samples of the April spatial sample scored on the first principal component and on the first pair of canonical variates.

indicated only very weak, if any biological response to the presence of the pool. Rocks seem populated according to water depth and velocity quite independent of position in the pool riffle sequence.

Table 30. Eigenvectors defining the three canonical variates based on the log transformed abundances of the 12 species with highest variance and the three physical measures for the 93 samples of the August spatial data set.

Variable	I	II	III
Species			
Bibiocephala grandis	.546	.068	-.255
Baetis tricaudatus	.344	-.911	-.202
Hydropsyche cockerelli	.156	-.273	-.050
Rhithrogena futilis	.116	.244	-.408
Acentrella turbida	.082	-.273	-.146
Drunella grandis	.032	.384	.003
Ephemerella infrequens	-.053	-.409	-.096
Isoperla fulva	-.059	.160	-.484
Lepidostoma pluviale	-.065	-.198	-.517
Arctopsyche grandis	-.068	-.104	.921
Oreodytes sp.	-.070	-.600	.206
Paraleptophlebia bicornuta	-.103	-.423	.259
Fraction of structure	.339	.051	.090
Physical variables			
Water depth	-.383	1.050	-.013
Rock weight	.094	-.193	1.043
Water velocity	1.067	-.027	-.304
Fraction of structure	.321	.365	.314
Eigenvalues	.758	.358	.065
Canonical correlations	.871	.599	.255
Wilks lambda	.145	.600	.935
Chi square values	164.150	43.409	5.706
Degrees of freedom	36	22	10

Table 31. Eigenvectors defining the three canonical variates based on the log transformed abundances of the 12 species with highest variance and the three physical measures for the 76 samples of the April spatial data set.

Variable	I	II	III
Species			
Hydropsyche tana	.701	.744	.577
Baetis tricaudatus	.173	-.556	-.474
Hydropsyche cockerelli	.149	.546	-.590
Epeorus longimanus	.090	.058	.023
Cinygmula tarda	.020	-.092	-.669
Drunella flavilinea	-.107	-.565	-.604
Antocha monticola	-.109	.077	-.359
Brachycentrus americanus	-.119	.199	.329
Isoperla quinquepunctata	-.188	.290	-.051
Cinygmula kootenai	-.269	.529	-.032
Ephemerella infrequens	-.512	.371	-.354
Fraction of structure	.372	.076	.089
Physical variables			
Water depth	.124	1.058	.316
Rock weight	-.139	-.196	1.037
Water velocity	.977	-.536	-.375
Fraction of structure	.430	.259	.311
Eigenvalues	.709	.525	.278
Canonical correlations	.842	.725	.528
Wilks lambda	.100	.343	.722
Chi square values	156.878	72.820	22.177
Degrees of freedom	36	22	10

Longitudinal Community Structure

Two data sets are presented in this section. The mainstem longitudinal data set with 16 stations and 125 single rock samples had 59 taxa and approximately 135,000 individuals. The tributary longitudinal data set with 45 stations, each with a single larger sample using an aquatic net had 97 taxa and approximately 114,000 individuals. The tributary longitudinal sample excluded many small invertebrates, especially elongate ones which readily burrowed through the net. These two data sets, unlike the two spatial data sets, cannot be directly compared to each other and are treated largely separately below. In both cases, multivariate analysis was based on the log transformed data using the species with greatest variance for the same reasons as for the spatial data sets.

The two longitudinal data sets together included 57 stations. The means, standard deviations and correlations of five common measures of stream size are presented in the upper part of Table 32. All these measures are highly correlated. The correlations between headwater distance, link magnitude and drainage area are essentially perfect. Station elevation is negatively correlated with all of the other measures. Principal component analysis of this correlation matrix accounts for over 85 percent of the structure in the first axis (Table 32). This axis represents the simple sum of all the physical measures accounting for the negative correlation with elevation. The second component captures most of the residual variation, which is almost entirely due to stream order and elevation. Stream order changes more and more slowly as stream size increases. Much of the mainstem of the river is sixth order even where the other measures of stream size vary greatly. Elevation describes stream size only very loosely. Small streams may occur at any elevation, but very large streams cannot occur at the highest elevations.

The mainstem longitudinal data: In the mainstem data the number of species and total number of invertebrates per sample is highest in the headwaters within, or very near, Yellowstone National Park (Figure 24). Both species number and total invertebrate density, however, appear to drop at the uppermost station and they both drop very sharply below the park. The downstream drop in species number and total density is very likely due to the inflow of Taylor Creek, which is heavily silted during spring run-off and also during summer storms. This unusual silt load is due to soil type within the drainage, aggravated by logging and grazing. Species number and invertebrate density partially recover downstream and display another depression around Cascade Creek, the narrowest part of the Gallatin Canyon. Another small peak in both occurs at the mouth of the Gallatin Valley, followed by a depression at the lowermost sites.

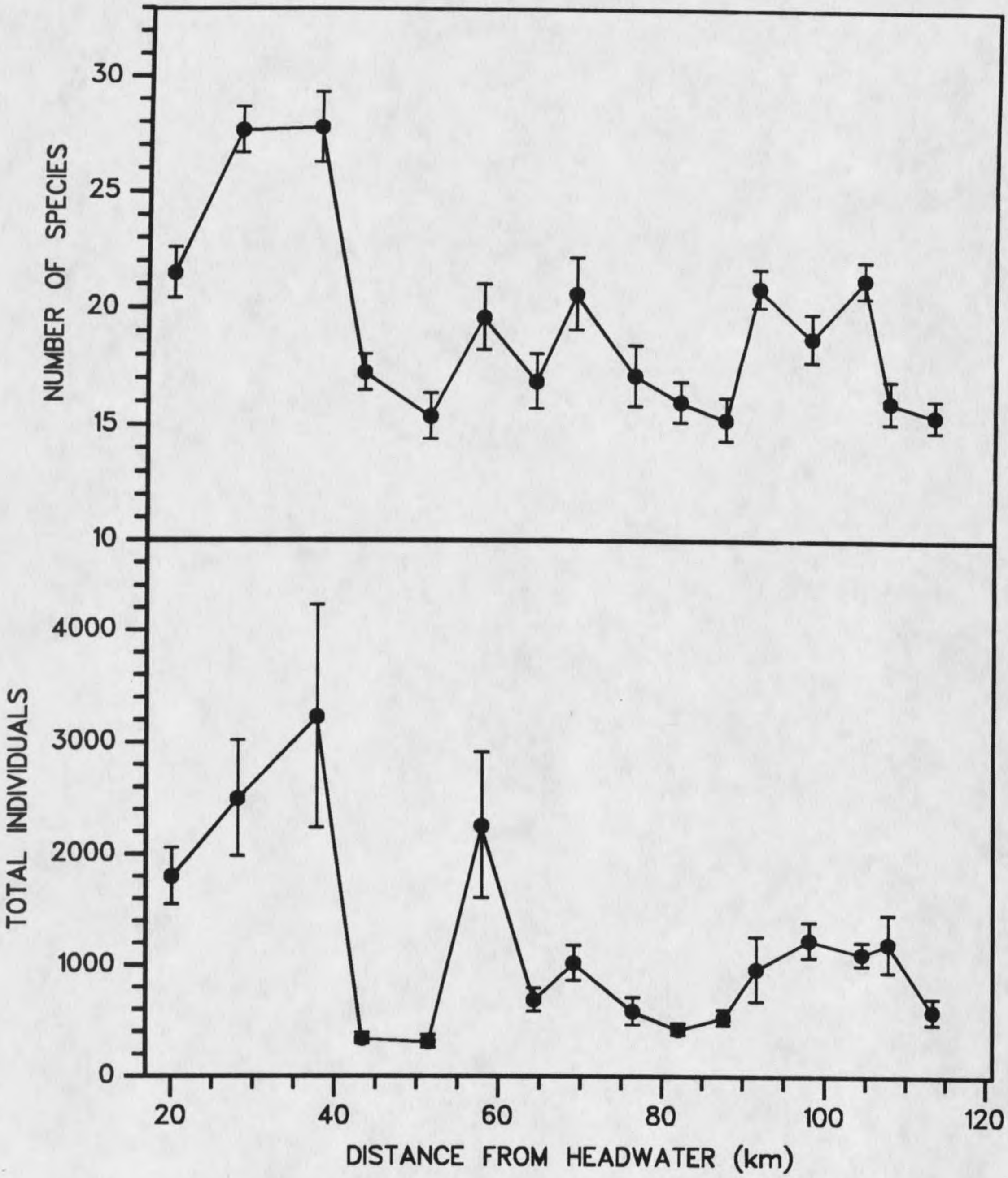

Figure 24. Mean number of species and of individual invertebrates at the 16 stations of the mainstem longitudinal study. Error bars represent the standard error of the mean of 6 to 12 samples.

Table 32. Means, standard deviations (STD) and correlations among five physical measures of stream size for the 57 stations used in the mainstem and in the tributary longitudinal data sets. Also shown are the first three eigenvectors (I-III) defining the first three principal components based on the correlation matrix.

Variable	mean	STD	Correlations [1]	[2]	[3]	[4]	[5]
[1] Stream order	3.63	1.71	1.00	.82	.80	-.55	.76
[2] Headwater distance (km)	31.63	37.69	.82	1.00	.99	-.75	.98
[3] Link magnitude	104.11	163.03	.80	.99	1.00	-.73	.98
[4] Elevation (m)	1878.91	240.91	-.55	-.75	-.73	1.00	-.74
[5] Drainage area (km^2)	571.70	965.81	.76	.98	.98	-.74	1.00

	I	II	III
Stream order	.412	.592	-.679
Distance	.479	.073	.221
Link magnitude	.475	.069	.311
Elevation	-.392	.800	.453
Drainage area	.470	.004	.433
Eigenvalues	4.26	.46	.25
Percent variance	85.28	9.16	5.00
Cumulative percent	85.28	94.43	99.43

Principal component analysis revealed three axes which account for greater variance than would the species with random covariance (Table 33). A Monte Carlo simulation using the observed variances for the species, but random covariance indicated that eigenvalues as large as the first three are not expected in 1000 trials. These three components together capture 1.7 times more variance than expected with random covariance. The first and second components account for a very similar fraction of the total variance, 28% and 27% respectively. The third component accounts for 17% of the total variance and brings the total variance captured by the first three components to 71%. The remaining eigenvalues are much smaller and decline only gradually indicating little further pattern in the data.

The first two principal components define a plane through the data without well defined axes. Jackknife analysis indicated that while the eigenvalues are very stable, the first two eigenvectors are quite unstable and therefore not subject to easy, direct interpretation. The scores on the first two eigenvectors are, however, easily interpreted. These always clearly separate the upper three stations and the lower three stations from the remaining stations. The shape of the data in the space of the first two principal components always has a "L" or "V" shape with the uppermost three and the lowermost three stations out in the arms (Figure 25).

Table 33. Eigenvectors defining the first four principal components for the mainstem longitudinal data set based on the covariance matrix of the log transformed abundances.

Species	I	II	III	IV
Brachycentrus americanus	.513	.225	-.377	.117
Ephemerella infrequens	.463	.112	.241	-.117
Micrasema bactro	.423	-.153	-.099	-.178
Arctopsyche grandis	.300	.001	.068	-.031
Antocha monticola	.290	.166	-.108	.169
Baetis tricaudatus	.279	-.134	.074	-.212
Caudatella heterocaudata	.238	-.299	.531	-.104
Apatania shoshone	.097	.015	.277	.863
Drunella flavilinea	.061	.244	.269	.163
Hydropsyche tana	-.047	.452	.496	-.279
Lepidostoma pluviale	-.083	.694	-.016	-.078
Serratella tibialis	-.112	-.181	.300	-.002
Eigenvalues	6.54	6.29	3.96	1.61
Percent variance	27.67	26.64	16.75	6.83
Cumulative percent	27.67	54.31	71.06	77.89

The first two principal components thus identify three distinct sections of the river; the valley, the canyon and the upper meadow sections. Some of the samples from Station 11 appear quite similar to those from the uppermost three stations. Most of the samples from Station 4 appear intermediate to the lowermost three stations and the stations of the Gallatin Canyon. This pattern is retained with bootstrap sampling even with greatly reduced sample sizes, as long as all stations are represented. Thirty-two observations revealed this dominant pattern nearly as well as all 125 observations.

The first principal component seems best interpreted as a measure of total invertebrate density or the nearly equivalent species number. The scores on the first component (Figure

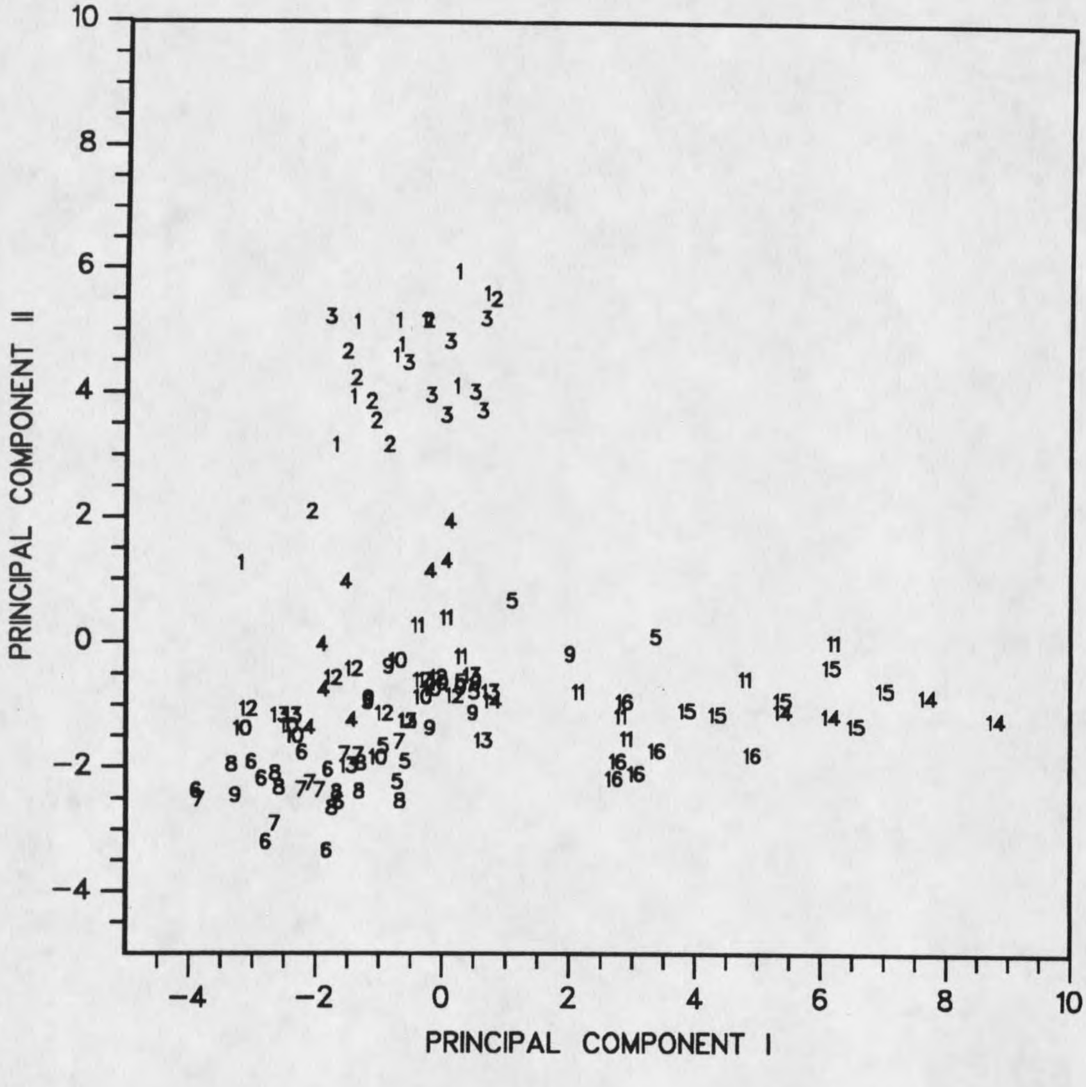

Figure 25. The 125 samples of the mainstem longitudinal data set scored on the first two principal components. The numbers plotted give the station numbers as identified in Table 3.

26) closely approximate the curves of total invertebrate density and species number and they are highly correlated with these measures (Table 34). The first eigenvector obtained from jackknife validation or bootstrap samples, always had a number of large positive weights and no large negative weights. Even though the first and second eigenvalues are very similar, the two axes were not observed to switch their order on any of the validation analyses.

Table 34. Correlations among five simple measures of stream size, the first principal component scores based on the same physical measures of stream size for all sites, the first three principal component scores based on the log transformed species abundances (Fauna PC), the number of species, and the total number of invertebrates for the mainstem longitudinal data set (N = 125). Some correlations were rounded down to 0.99. The upper triangular matrix indicates simple significance levels as ns for $P > 0.05$, * for $P < 0.05$ and ** for $P < 0.01$.

		[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]
[1]	Stream order	--	**	**	**	**	**	**	*	**	**	**
[2]	Link magnitude	.63	--	**	**	**	**	**	**	**	**	**
[3]	Elevation	-.62	-.99	--	**	**	**	**	**	**	**	**
[4]	Drainage area	.64	.99	-.99	--	**	**	**	**	**	**	**
[5]	Divide distance	.61	.99	-.99	.99	--	**	**	**	**	**	**
[6]	Physical PC I	.72	.99	-.99	.99	.99	--	**	**	**	**	**
[7]	Fauna PC I	-.56	-.59	.54	-.58	-.54	-.59	--	ns	ns	**	**
[8]	Fauna PC II	.20	.56	-.62	.61	.62	.57	.00	--	ns	ns	ns
[9]	Fauna PC III	.29	.33	-.30	.29	.30	.32	.00	.00	--	**	ns
[10]	Species number	-.39	-.42	.39	-.42	-.39	-.42	.82	-.04	.33	--	**
[11]	Total number	-.36	-.34	.30	-.34	-.30	-.34	.80	-.00	.07	.63	--

The second principal component, as obtained from jackknife validation or bootstrap sampling, normally gives strong positive weights to a few species which are largely restricted to the lowermost stations. This component gives only weak weights to the more widespread species or those species which are more common at the upper stations. The second principal component has near zero correlation with both species number and total invertebrate density. This helps substantiate the interpretation of the first principal component.

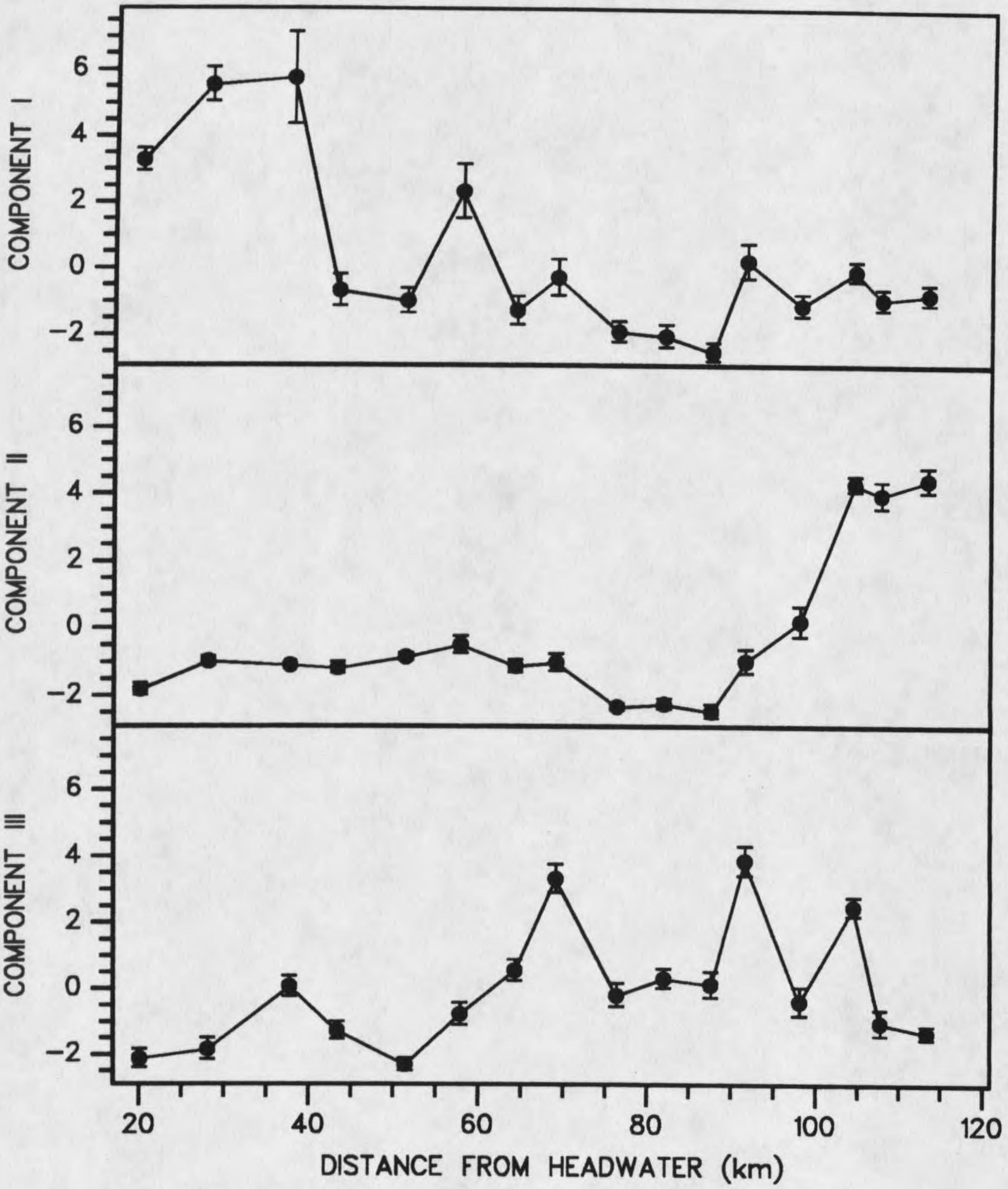

Figure 26. Mean scores on the first three principal components at the 16 stations of the mainstem longitudinal study. Error bars represent the standard error of the mean of 6 to 12 samples.

The eigenvector defining the third principal component, unlike the first two, is extremely stable to jackknife validation and bootstrap sampling. It accounts for 16.8% of the total variance which is quite distant from the 26.6% explained by the second and the 6.8% explained by the fourth. It is interpreted as identifying an assemblage of species which occur at greatest abundance on stable substrates, usually in association with aquatic bryophytes in the lower half of the river. These species display a pattern of abundance unrelated to the first two principal components (Figure 26). The third component shows moderately strong, positive correlation with species number, but essentially no correlation with total density (Table 34). Mainstem stations 3, 5, 9, 14 and 15 all had heavy bryophyte growth, which is normally associated with stability of the substrate. Stability of the substrate is in turn a function of local channel morphology. Several species occurring in the lower half of the river have population peaks at these same stations.

Principal component analysis was repeated, as above, using the data remaining after removing the observations for the uppermost three and the lowermost three stations. The goal was to examine finer structure within the Gallatin Canyon, which might have been hidden by the extreme range of the stations in the previous analysis. This analysis resulted in the first principal component being a clean measure of total invertebrate density with all species weighted positively and accounting for 33% of the total variation. The remaining components accounted for little or no covariance and failed to separate the stations into meaningful groups. The entirety of the Gallatin Canyon area may be viewed as a relatively homogeneous stretch of the river.

Table 35 gives, for all species that occur in more than 10 percent of the samples, the overall mean, the standard deviation and the correlations with the first principal component based on the five physical measures of stream size, the first three principal components based on the fauna, the number of species and with total invertebrate density. The near equivalence of the first faunal component with total density is readily apparent. The

Table 35. Invertebrate taxa present in more than 10 percent of the samples (FP) from the main-stem longitudinal data (N= 125) ranked according to the mean of their log transformed abundances. Also shown for each taxon is its standard deviation (STD), and its correlations with the first principal component from the physical data (P1), the first three principal components from the faunal data (F1, F2,F3), the number of species present (SN) and the total number of individuals in the sample (TN).

Taxon	mean	STD	FP	P1	F1	F2	F3	SN	TN
Baetis tricaudatus	5.53	1.07	1.00	-.46	.66	-.31	.14	.55	.62
Epeorus longimanus	3.58	1.07	.96	.27	-.24	-.06	.35	-.06	-.13
Brachycentrus americanus	2.76	1.70	.90	-.40	.77	.33	-.44	.48	.62
Drunella flavilinea	2.61	1.13	.94	.44	.14	.54	.48	.20	.26
Caudatella heterocaudata	2.57	1.58	.88	-.25	.38	-.47	.67	.55	.50
Rhithrogena futilis	2.44	1.04	.93	-.30	.31	-.10	.06	.42	.36
Ephemerella infrequens	2.34	1.51	.90	-.27	.79	.19	.32	.75	.82
Hydropsyche tana	1.55	1.66	.61	.56	-.07	.69	.10	.13	.10
Arctopsyche grandis	1.46	1.11	.78	-.45	.69	.00	.12	.70	.70
Lepidostoma pluviale	1.07	1.83	.30	.65	-.12	.95	-.02	-.16	-.02
Drunella doddsi	.99	.88	.65	.06	-.11	-.18	.32	.11	.05
Antocha monticola	.96	1.26	.50	-.15	.59	.33	-.17	.40	.55
Apatania shoshone	.94	1.30	.45	.03	.19	.03	.42	.27	.26
Pteronarcella badia	.84	1.03	.52	-.56	.64	-.13	-.05	.63	.64
Micrasema bactro	.81	1.30	.38	-.73	.83	-.30	-.15	.61	.68
Hydropsyche cockerelli	.71	.93	.44	.38	-.07	.29	.75	.22	.15
Hesperoperla pacifica	.71	1.04	.46	-.67	.78	-.24	-.01	.68	.77
Serratella tibialis	.64	1.10	.29	.18	-.26	-.41	.54	.00	-.12
Simulidae	.63	.96	.38	-.08	.26	.14	-.09	.18	.29
Rhyacophila bifila	.53	.80	.41	-.22	.48	-.16	.25	.58	.63
Glossosoma spp.	.52	1.30	.19	-.55	.67	-.14	-.20	.59	.67
Drunella grandis	.50	.68	.45	-.20	.60	.06	.07	.57	.63
Isoperla fulva	.47	.64	.42	-.08	.42	.02	.21	.47	.49
Prostoia besametsa	.44	.90	.26	-.59	.78	-.19	-.19	.61	.71
Bibiocephala grandis	.43	.95	.24	-.31	.22	-.08	-.10	.27	.24
Caudatella hystrix	.39	1.05	.18	-.59	.74	-.17	-.20	.65	.75
Brachycentrus occidentalis	.32	.90	.16	-.23	.46	-.06	.16	.45	.53
Rhyacophila brunnea	.26	.82	.11	-.67	.58	-.19	-.28	.38	.51
Optioservus quadrimaculatus	.25	.75	.12	-.58	.53	-.10	-.24	.36	.46
Rhyacophila vaccua	.25	.53	.25	-.37	.41	-.21	-.06	.44	.38
Kogotus nonus	.15	.44	.12	-.65	.71	-.18	-.22	.56	.69
Atherix pachypus	.15	.41	.14	-.03	.26	.07	.21	.26	.23
Isoperla quinquepunctata	.14	.40	.12	.37	-.03	.61	.14	.03	.06
Rhithrogena robusta	.13	.34	.14	.18	-.22	-.15	.09	-.06	-.16

correlation with the physical component allows easy identification of headwater species, which have strong negative correlations; lower river species which have strong positive correlations; and widespread species with have only weak correlations. Most species occur in association with many other species, but a few are weakly or even negatively correlated with species number and with total density.

To facilitate the interpretation of the correlations in Table 35 a few species are examined individually. Figure 27 gives the densities for three Trichoptera species. *Arctopsyche grandis* occurs at all stations along the mainstem, but is most abundant near the border of Yellowstone National Park. *Lepidostoma pluviale* is restricted to the lower part of the mainstem. *Apatania shoshone* is widespread, but very patchy occurring in areas with stable substrate.

The mayfly genus *Caudatella* has three species which occur in the mainstem of the river (Figure 28). *Caudatella hystrix* is restricted to a narrow stretch of the upper river and can be quite abundant. *Caudatella edmundsi* is restricted to a narrow portion of the canyon, but is rare in all the samples. This species can be abundant in the appropriate habitat, but only from the same reach of the river. *Caudatella heterocaudata* occurs throughout the mainstem in association with stable substrates similar to the caddisfly *Apatania shoshone*. It is not abundant in the lowermost or uppermost parts of the river.

Examination of the species according to their general trophic group indicates that all trophic groups correlate with total density rather closely (Figure 29). Scrapers, mostly *Drunella doddsi*, *Bibiocephala grandis*, *Apatania shoshone* and two species of *Glossosoma*, are unusually rare at the uppermost station. The upper two stations both have solid surface ice throughout the winter, have stable substrate with abundant bryophytes and are in open meadows. The absence of scrapers from the uppermost station is not easily explained.

The tributary longitudinal data: The sixteen stations used in the previous data set could be easily described in terms of any of the five measures of stream size. All these measures of stream size are monotonic functions when confined to the course of a single stream. This is not true for the stations used in the tributary data set. When a single measure of stream size is needed, stream order is used as it is the most widely used measure

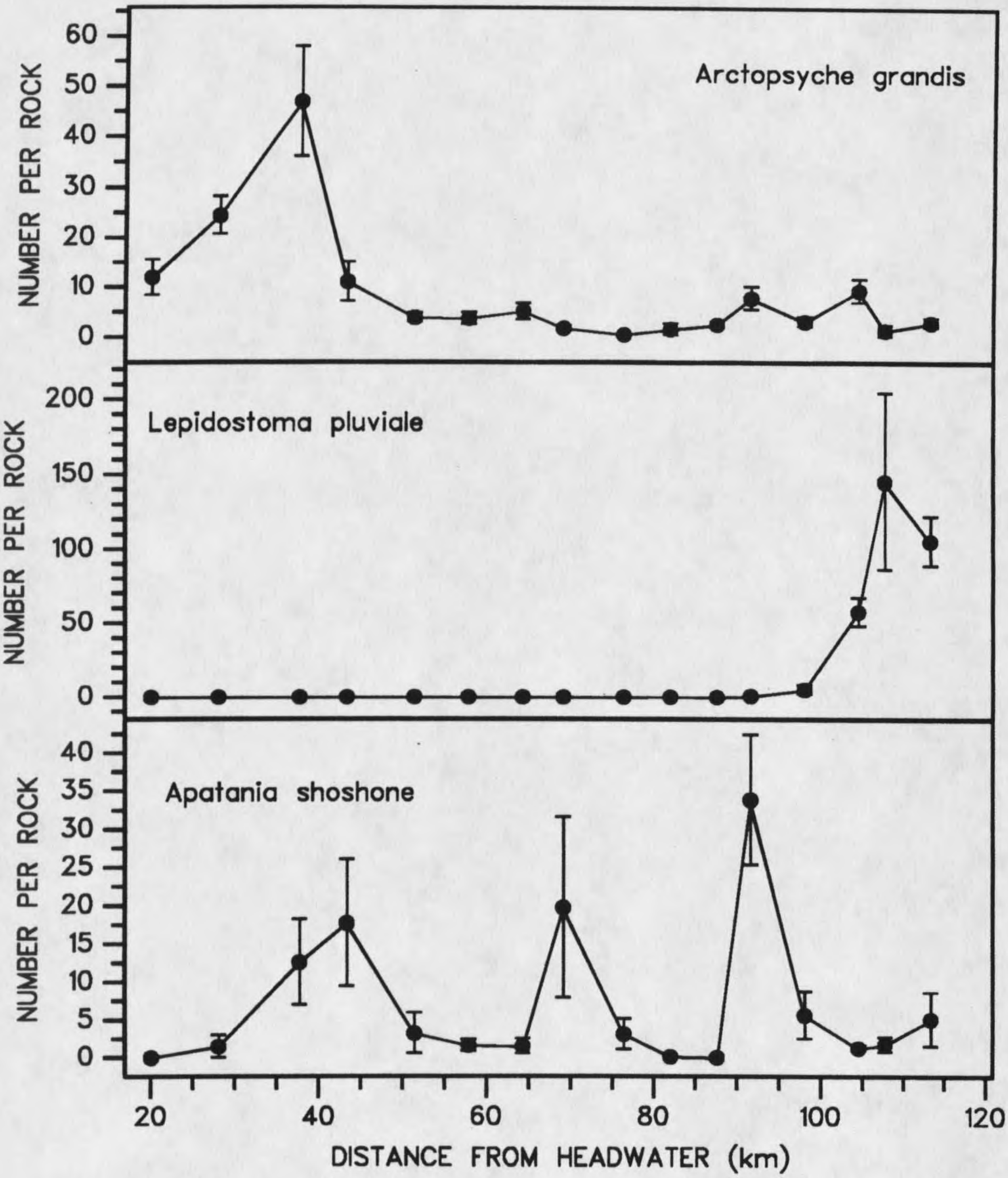

Figure 27. Mean density of three caddis species at the 16 stations of the mainstem longitudinal study. Error bars represent the standard error of the mean of 6 to 12 samples.

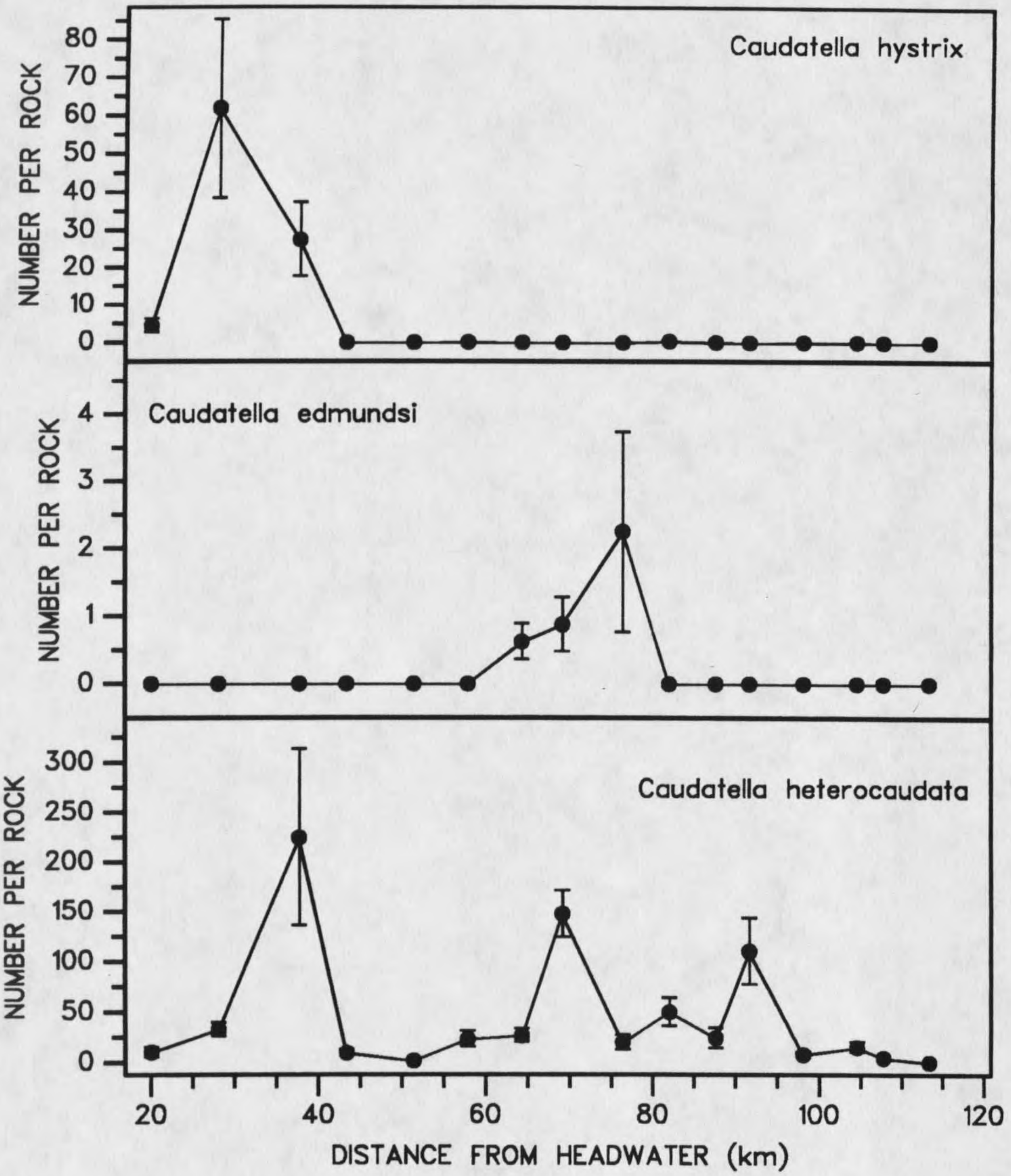

Figure 28. Mean density of three *Caudatella* species at the 16 stations of the mainstem longitudinal study. Error bars represent the standard error of the mean of 6 to 12 samples.

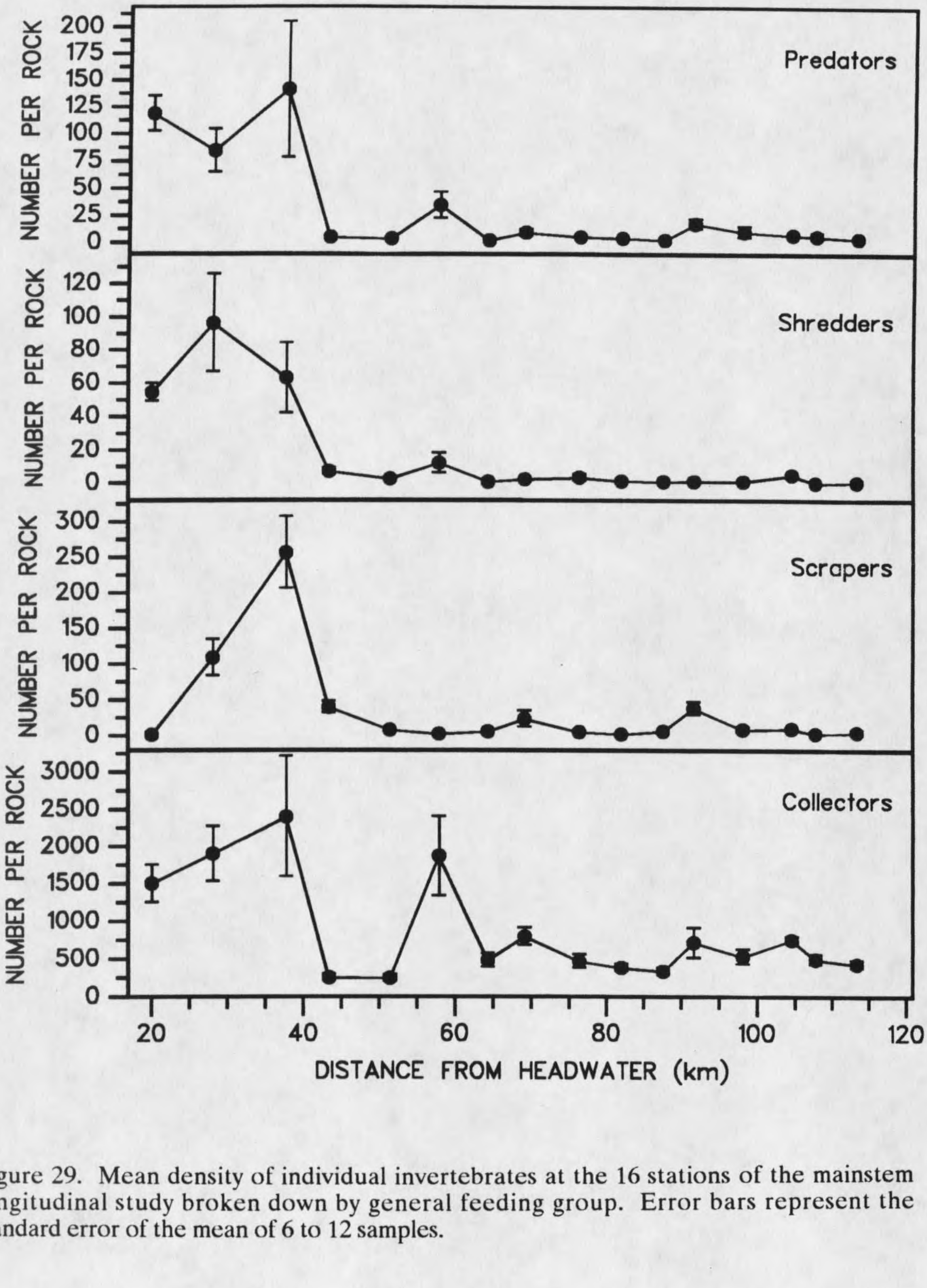

Figure 29. Mean density of individual invertebrates at the 16 stations of the mainstem longitudinal study broken down by general feeding group. Error bars represent the standard error of the mean of 6 to 12 samples.

and also serves to describe the faunal response to stream size better than any of the other measures. The relationship between stream order, elevation, drainage area and the first principal component, based on all five measures of stream size, for the 45 stations used in the tributary data set, is shown in Figure 30. Link magnitude and distance to the headwater are nearly identical to drainage area. The unusual relationship between stream order and elevation is due to the elongate shape of the drainage.

In the tributary data, species number is highest in streams of intermediate size and total invertebrate density is highest in the largest streams (Figure 31). Only two of the 45 stations occur at fifth order streams. These two streams, the lower parts of Taylor Creek and the mainstem of the river above Taylor Creek are at the same elevation, but Taylor Creek is smaller and normally carries a heavy load of silt. They are often very different with regard to biological variables.

Principal component analysis of these data indicates that only two components account for greater variance than would the species with random covariance (Table 36). A Monte Carlo simulation using the observed variances for the species, but random covariance indicated that eigenvalues as large as the first two are not expected in 1000 trials. These two components together capture 2.3 times more variance than expected with random covariance.

The first two principal components are quite distinct, with regards to the magnitude of the eigenvalue. Together they account for 62% of the total variance. The number of species that were used in this analysis was increased to 20 because for these data, the eigenvectors are more clearly interpreted with more species. The main nature of the results of this analysis was not sensitive to the number of species used over the range of 10 to 50 species. The remaining eigenvalues are much smaller and decline only gradually indicating little further pattern in the data.

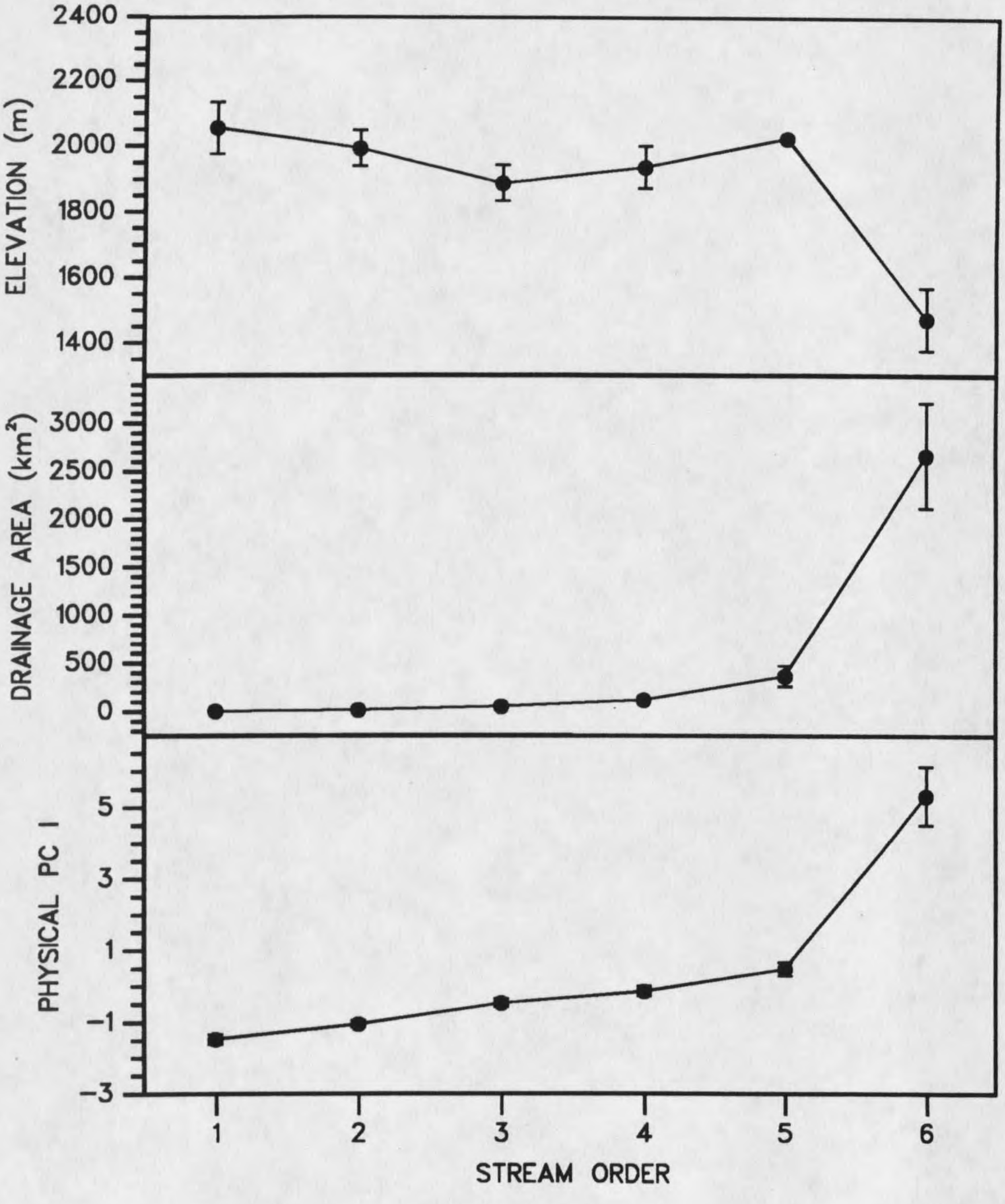

Figure 30. Mean elevation, drainage area, and score on the first principal component based on the correlation matrix of five physical measures of stream size using the 57 stations used in the two longitudinal studies. Error bars represent the standard error of the means. Sample size for orders 1 through 6 is; 6, 11, 13, 8, 2, and 5 respectively.

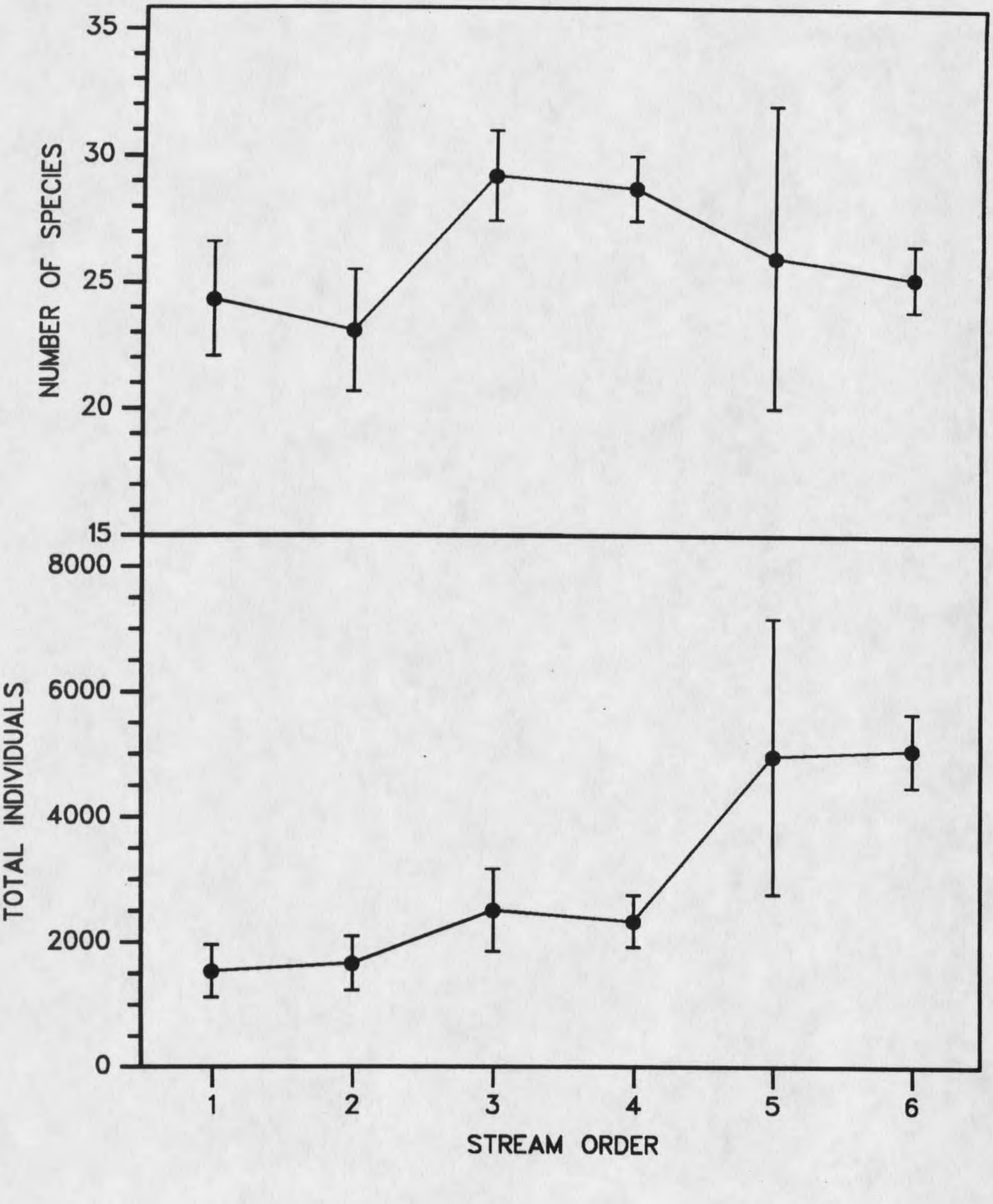

Figure 31. Mean number of species and of individual invertebrates at each stream order based on the 45 stations of the tributary longitudinal study. Error bars represent the standard error of the means. Sample size for orders 1 through 6 is; 6, 11, 13, 8, 2, and 5 respectively.

Table 36. Eigenvectors defining the first four principal components for the tributary data set based on the covariance matrix of the log transformed abundances.

Species	I	II	III	IV
Baetis tricaudatus	.411	.108	.294	.361
Ephemerella infrequens	.381	.128	.235	-.137
Brachycentrus americanus	.320	.150	.040	-.216
Drunella grandis	.230	.105	.034	-.213
Rhithrogena futilis	.215	.316	.027	.125
Isoperla fulva	.208	-.035	.037	.389
Arctopsyche grandis	.174	.220	.031	-.035
Lepidostoma pluviale	.123	-.098	.015	.432
Caudatella hystrix	.031	.321	.170	-.150
Micrasema bactro	.092	.105	.182	-.209
Drunella doddsi	.007	.363	.040	-.091
Doddsia occidentalis	-.121	.370	-.365	.034
Neothremma alicia	-.156	-.014	.557	.138
Yoraperla brevis	-.171	-.176	.306	-.076
Rhithrogena robusta	-.178	.313	-.073	.253
Oligophlebodes minutus	-.192	.383	.029	-.077
Parapsyche elsis	-.206	.107	.025	.191
Epeorus grandis	-.210	.290	-.041	.358
Drunella coloradensis	-.272	.013	.423	.089
Baetis bicaudatus	-.297	.157	.252	-.247
Eigenvalues	40.13	16.68	6.87	5.18
Percent variance	44.02	18.30	7.53	5.68
Cumulative percent	44.02	62.32	69.85	75.53

The first principal component accounts for 44 percent of the total variance and is interpreted as representing a contrast between lower river species and headwater species. Headwater species are weighted negatively. Species that are characteristic of the mid-reaches of the river, or that are very widespread in the drainage are not strongly weighted in this component. The second principal component accounts for 18 percent of the variance and is interpreted as a measure of species diversity. Species which normally occur in association with many species are weighted positively, while those which occur in more species poor sites are weighted negatively. Most species naturally occur in species rich sites. These are streams of intermediate size.

The first and second principal components have similar and moderate positive correlation with total invertebrate density (Table 37). This indicates that total density does not dominate either of the first two components, as is commonly observed with this type of data. The first principal component is strongly correlated with all measures of stream size, but not with the number of species. The second component is not correlated with any of the measures of stream size, but is quite strongly correlated with species number. These correlations support the direct interpretation of the eigenvectors given above.

Table 37. Correlations among five simple measures of stream size, the first principal component scores based on the same physical measures of stream size for all sites, the first two principal component scores based on the log transformed species abundances (Fauna PC), the faunal zones, the number of species, and the total number of invertebrates for the tributary longitudinal data set (N = 45). The upper triangular matrix indicates simple significance levels as ns for P > 0.05, * for P < 0.05 and ** for P < 0.01.

		[1]	[2]	[3]	[4]	[5]	[6]	[7]	[8]	[9]	[10]	[11]
[1]	Stream order	--	**	**	**	**	**	**	ns	**	ns	**
[2]	Link magnitude	.74	--	**	**	**	**	**	ns	**	ns	**
[3]	Elevation	-.54	-.69	--	**	**	**	**	ns	**	*	**
[4]	Drainage area	.69	.98	-.68	--	**	**	**	ns	**	ns	**
[5]	Divide distance	.77	.99	-.72	.98	--	**	**	ns	**	ns	**
[6]	Physical PC I	.82	.98	-.79	.96	.99	--	**	ns	**	ns	**
[7]	Fauna PC I	.74	.61	-.41	.57	.65	.66	--	ns	**	ns	**
[8]	Fauna PC II	.17	-.20	-.20	-.23	-.14	-.06	.00	--	**	**	*
[9]	Fauna zone	-.73	-.51	.56	-.48	-.57	-.62	-.75	-.52	--	**	**
[10]	Species number	.15	-.05	-.30	-.07	-.00	.06	-.03	.73	-.45	--	**
[11]	Total number	.52	.49	-.44	.45	.53	.53	.40	.37	-.56	.51	--

The first principal component is thus a biological index of stream size. Of the five physical measures of stream size, the first principal component correlates most strongly with stream order and least strongly with elevation (Table 37). This supports the widespread use of stream order as a biologically important index of stream size. The decelerating rate of change in stream order when progressing downstream corresponds to a deceleration in the rate of change in community structure.

The first principal component is a steadily increasing function when examined in context of stream order (Figure 32). The close agreement between the two fifth order streams is noteworthy. These two sites differed greatly in total invertebrate density and species number. The species that are most characteristic of that stream size were, however, correctly represented at both sites. The difference in total density is due to other species and is reflected in the second principal component. Taylor Creek is relatively species poor similar to sixth order streams while the mainstem above Taylor Creek is species rich similar to fourth order streams. The second principal component varies somewhat more smoothly with regard to stream order than does species number, possibly due to orthogonality constraints.

The first two principal components can be used to characterize the 45 stations in terms of these two dominate axes of variation in the benthic communities. Cluster analysis was used to describe the distances between the stations in the principal component space and to group similar sites together. Six groups of stations seem interpretable as identified in Figure 33. The raw principal component scores, as well as group identification, or faunal zone, are presented in Figure 34 to allow better evaluation of the cluster analysis result.

The 45 stations in the space of the first two principal components occupy an inverted U shape with the lowest elevation stations at the lower right and the most alpine stations on the lower left. The lower and middle sections of Taylor Creek, as well as Spanish Creek, appear similar to the mainstem sites. These constitute the first faunal zone. The mainstem of the river above Taylor Creek, or just below Yellowstone National park, is distant from all other stations. Its score is similar to the mainstem stations on the first principal component, but similar to much smaller mountain streams on the second principal component. This station contains the species that are characteristic of the mainstem of the river, but also many species that are characteristic of smaller streams. It is a very productive site, based on standing densities and also very rich in species.

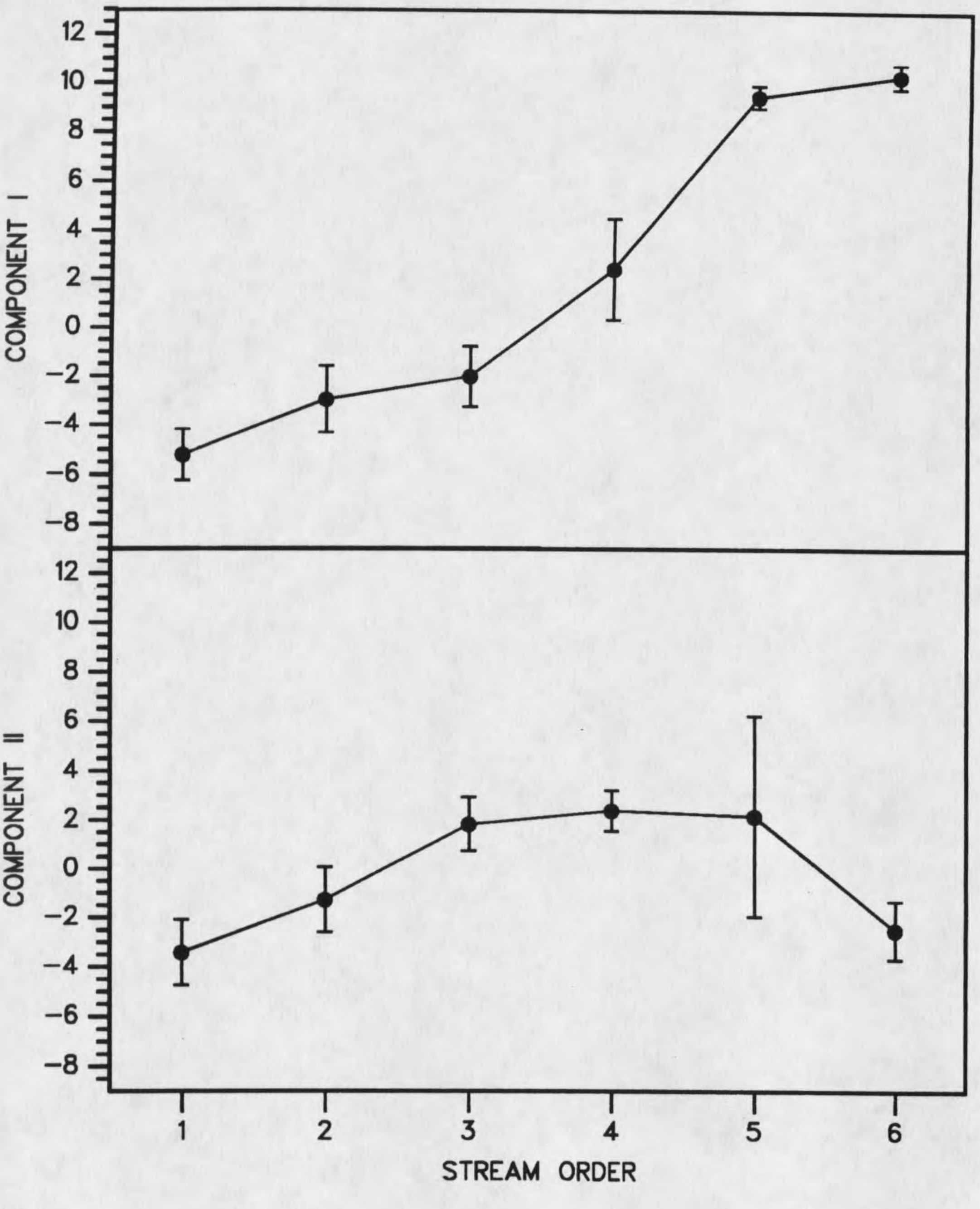

Figure 32. Mean score on the first two principal components based on the log transformed species abundances at each stream order for the 45 stations of the tributary longitudinal study. Error bars represent the standard error of the means. Sample size for orders 1 through 6 is; 6, 11, 13, 8, 2, and 5 respectively.

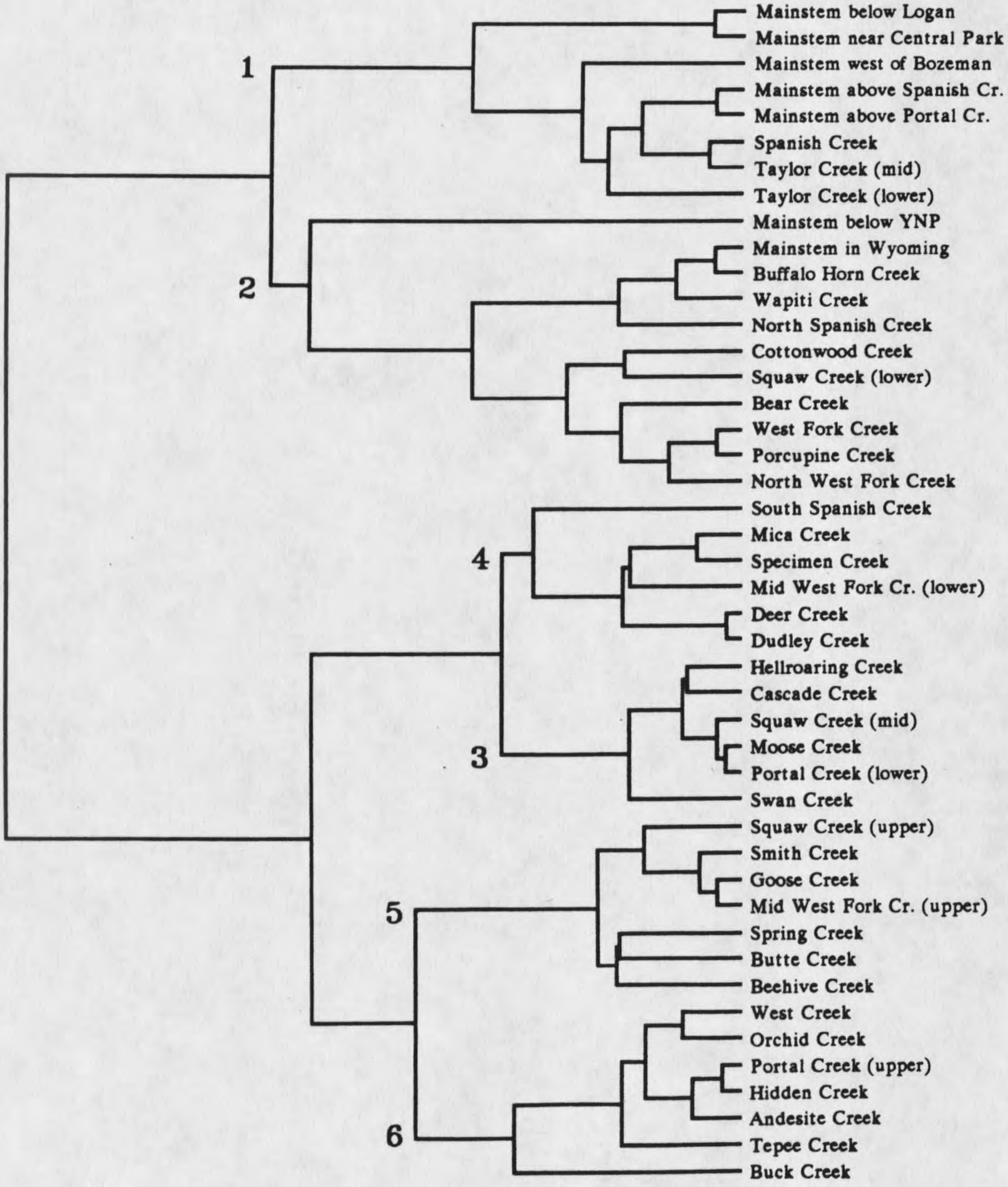

Figure 33. Dendrogram showing the similarity of the 45 stations of the tributary longitudinal study based on the first two principal components and agglomerative clustering using medians. Six groups are identified for reference elsewhere.

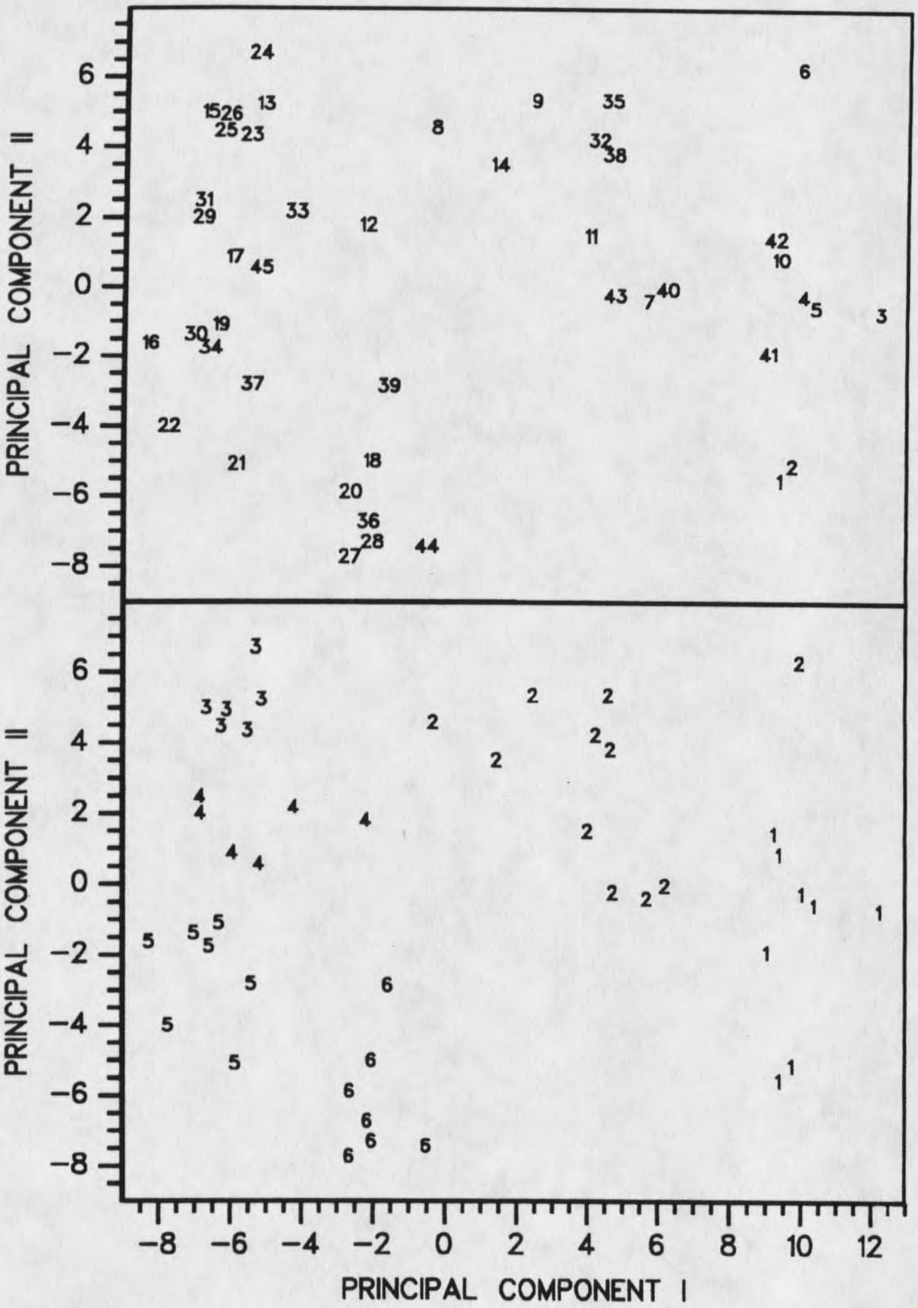

Figure 34. The 45 stations of the tributary longitudinal study scored on the first two principal components. The upper division shows the stations numbers identified in Table 3, while the lower division shows the group number identified in Figure 33.

The stations of faunal zone 2 contain the upper mainstem and the larger, open (unforested) mountain streams. Zones 3 through 6 describe increasingly alpine streams. The differences between faunal zones 3 and 4 as well as 5 and 6 are more quantitative than qualitative. Zones 3 and 4 together represent the cooler mountain streams recognized as longitudinal zone "f" in the species summary tables. These streams are of similar physical size, but the streams of faunal zone 3 have more species with greater average density than the streams in zone 4 (Table 38). Likewise, the streams of faunal zone 5 and 6 are physically similar in size with zone 6 streams averaging slightly larger. These represent the most alpine sites in the drainage, longitudinal zone "g" of the species summary tables. The streams of the zone 6 are characterized by rather species-poor communities of low total density compared to those of zone 5.

Table 38. Mean values of five physical measures of stream size and of species number and total invertebrate density for each of the six faunal zones.

Variable	Faunal Zone					
	1	2	3	4	5	6
Sample size	8	11	6	6	7	7
Stream order	5.4	3.3	3.0	2.7	1.7	2.0
Link magnitude	286.9	20.5	16.0	9.8	2.6	4.9
Elevation (m)	1638.0	1898.6	1858.7	1904.5	2094.1	2068.8
Drainage area (km^2)	1744.9	109.3	51.4	40.4	5.7	14.8
Headwater distance (km)	76.9	16.4	11.7	8.9	3.1	5.6
Species number	25.4	29.7	32.5	27.5	25.1	17.4
Total density	4273.8	3120.6	2969.5	1611.2	1922.3	667.0

There is little indication that location within a common drainage predisposes stations toward being similar. Even stations along a single water course are not necessarily similar in terms of the fauna. For example the middle station on Taylor Creek is much more similar to Spanish Creek than to the lower station on the same stream. Faunal differences occur over shorter linear distances in smaller streams than in larger ones. For example, the three stations along Squaw Creek are each placed in different faunal zones as are stations along all other smaller streams.

Faunal zonation is most interesting when examined in terms of physical stream size (Figure 35). Drainage area, or the nearly equivalent link magnitude or linear distance from the headwater and elevation, provide the greatest separation of the stations for plotting purposes. Log transforming drainage area prevents small differences on small streams being obscured by the much larger streams. The faunal zones show reasonably good separation in terms of drainage area and elevation, except for faunal zones 5 and 6. This separation occurs in transverse bands across drainage area and elevation. That is, small streams at lower elevations appear similar to larger streams at higher elevations.

All stations of faunal zones 5 and 6, except one appear in the upper left corner of Figure 35. Buck Creek was placed in faunal zone 6 based on the fauna, but appears closer to faunal zone 3 streams in terms of stream size and elevation. Re-examination of the data for Buck Creek indicates that the species present are not at all characteristic of alpine streams. This site is however, the most depauperate of all the stations in both species number and total density. Its correct place was not revealed in the space of the first two principal components because of its extremely low invertebrate numbers. The reason for this depauperate fauna is uncertain, but may involve ice. The sample site occupies a cold draw and had much more ice and snow remaining when sampled than other similar sites.

The remaining zone 5 and 6 streams are not at all separated in terms of drainage area and elevation. These are all extreme headwater streams and contain typical headwater species. The streams of faunal zone 6 tend to be slightly larger that those of faunal zone 5, but are very depauperate in both species and individuals. The explanation for this is not to be found in drainage area or elevation. Water chemistry may offer an explanation.

At the other extreme, all of the faunal zone 1 stations fall in the lower right of Figure 35 except two. These are the lower and middle reaches of Taylor Creek. This drainage is

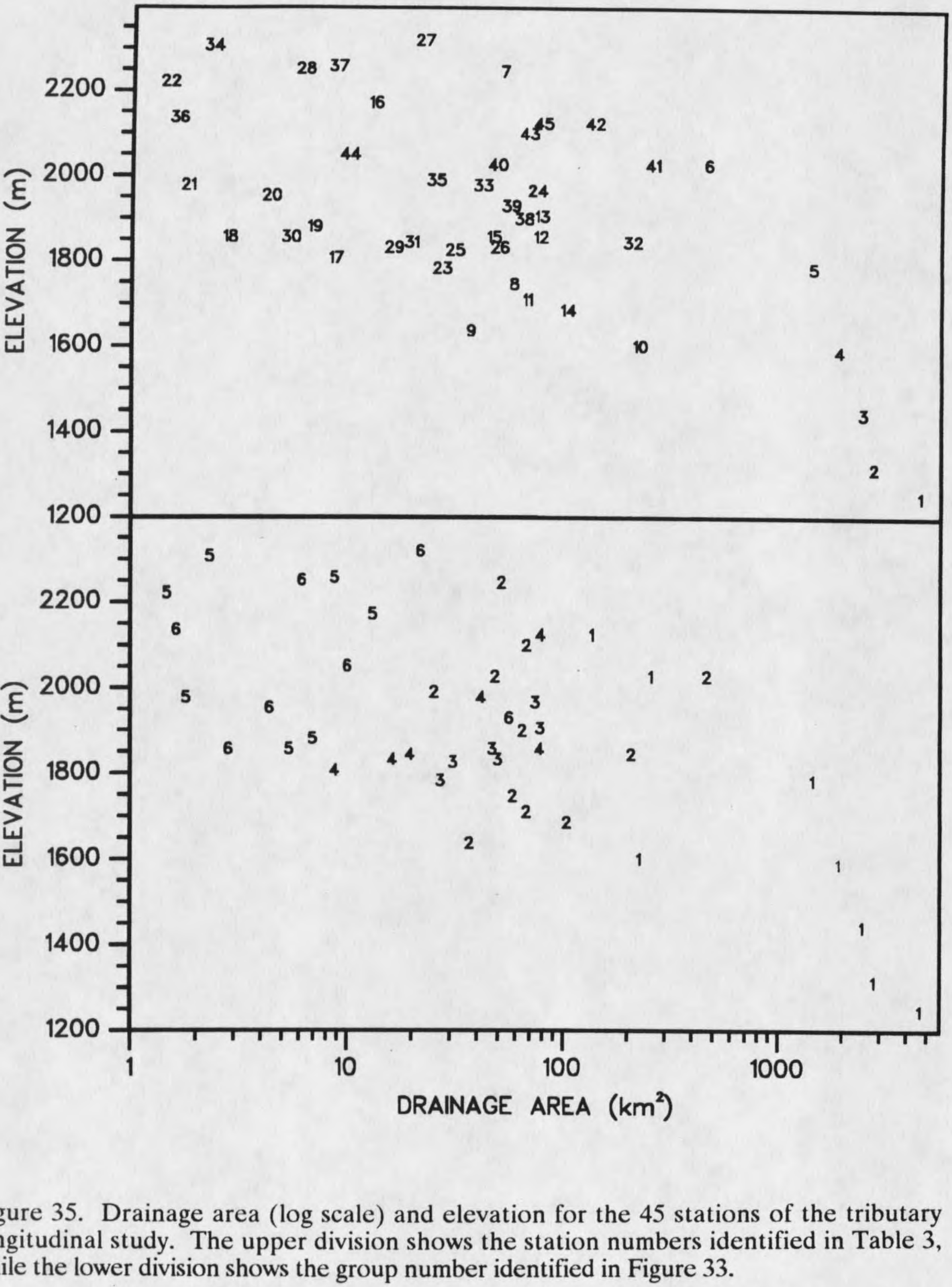

Figure 35. Drainage area (log scale) and elevation for the 45 stations of the tributary longitudinal study. The upper division shows the station numbers identified in Table 3, while the lower division shows the group number identified in Figure 33.

more unforested, more silty and more disturbed than other parts of the drainage. These sites appear as though they should have faunas similar to zone 2 or zone 3 streams.

Faunal zones 3 and 4 form rather tight bands in terms of drainage area and elevation except for one station. South Spanish Creek has a zone 4 fauna, but appears to be closer to the zone 3 band in terms of elevation and drainage area. This is a small difference, but could be due to most of the drainage being exceptionably high and cold. The drainage is also entirely within a primitive area, so it is undisturbed by logging or grazing.

The zone 2 streams are rather widespread in terms of drainage area and elevation. Six of these occur where expected, in a band between the zone 1 and the zone 3 stations. The remaining five of these stations occur where the fauna would be expected to be more similar to that of faunal zones 3 or 4. One of these sites is on the mainstem of the river, well within Yellowstone Park, and so cannot be due to human disturbance. This site is however in open range heavily used by wildlife. The station just below Yellowstone National Park could as well have been assigned to faunal zone 1. It is actually quite unique (Figure 33). Porcupine Creek, North West Fork Creek and Buffalo Horn Creek are likewise undisturbed drainages with faunas more characteristic of larger streams at lower elevations. Buffalo Horn Creek and especially Porcupine Creek have partially unforested drainages. The final zone 2 site that is apparently out of place is Wapiti Creek, which is within the unforested Taylor Creek drainage.

Canonical correlation analysis was used to further examine the relationships between the physical measures of stream size and the species. These analyses provided no further insight on the nature of these relationships. The failure is probably due to the very high correlations between the measures of stream size and to the small number of physical measures. If additional physical variables involving water chemistry, geology, temperature and discharge were incorporated, the results of canonical correlation would likely prove more interesting. These types of variables, however, are often difficult to measure meaningfully in stream systems where the important variables (means, minima, maxima, and duration times at various levels) are very poorly related to any reasonable number of point measurements. This is undoubtedly much of the reason that streams are usually characterized in physical terms while lakes are better characterized chemically.

The species that occurred in more than 10 percent of the samples are characterized with regard to their overall mean, standard deviation and correlations with the first principal component based on the physical measures of stream size, the first two principal components based on the fauna, the number of species and with total invertebrate density in Table 39. Interpretation is straightforward.

Table 39. Invertebrate taxa present at more than 10 percent of the 45 tributary stations (FP) ranked according to the mean of their log transformed abundances. Also shown for each taxon is its standard deviation (STD), and its correlations with the first principal component from the physical data (P1), the first two principal components from the faunal data (F1, F2), the number of species present (SN) and the total number of individuals in the sample (TN).

Taxon	mean	STD	FP	P1	F1	F2	SN	TN
Baetis bicaudatus	3.72	2.54	.73	-.51	-.74	.25	.30	-.02
Drunella doddsi	3.68	1.93	.89	-.07	.02	.77	.55	.28
Ephemerella infrequens	3.05	2.76	.71	.58	.88	.19	.26	.55
Oligophlebodes minutus	2.92	2.50	.73	-.35	-.49	.62	.50	.08
Rhithrogena futilis	2.66	2.18	.64	.44	.63	.59	.48	.54
Rhithrogena robusta	2.62	2.04	.71	-.21	-.56	.63	.47	.11
Drunella coloradensis	2.42	2.25	.60	-.46	-.77	.02	.21	.01
Baetis tricaudatus	2.28	2.98	.42	.68	.87	.15	.17	.61
Epeorus grandis	2.25	2.26	.62	-.29	-.59	.52	.40	-.04
Doddsia occidentalis	2.16	2.16	.58	-.23	-.36	.70	.40	-.11
Rhyacophila 'brunnea'	2.14	1.44	.84	-.43	-.39	.46	.44	.00
Pericoma sp.	1.82	2.22	.53	-.17	.17	.32	.34	.11
Brachycentrus americanus	1.78	2.36	.44	.35	.86	.26	.16	.36
Parapsyche elsis	1.70	1.66	.58	-.40	-.79	.26	.34	-.11
Megarcys spp.	1.66	1.40	.69	-.45	-.81	.14	.22	-.15
Caudatella hystrix	1.61	1.77	.58	-.12	.11	.74	.56	.32
Arctopsyche grandis	1.41	1.81	.47	.30	.61	.50	.31	.41
Drunella grandis	1.37	1.83	.42	.45	.80	.24	.16	.47
Neothremma alicia	1.33	2.01	.38	-.28	-.49	-.03	.30	.12
Doroneuria theodora	1.28	1.34	.60	-.27	-.21	.24	.30	-.33
Rhyacophila narvae	1.28	1.45	.49	-.31	-.60	.20	.44	.00
Micrasema bactro	1.22	1.54	.53	.00	.38	.28	.25	.13
Yoraperla brevis	1.19	1.95	.33	-.37	-.56	-.37	-.02	-.20

Table 39. *Continued.*

Taxon	mean	STD	FP	P1	F1	F2	SN	TN
Kogotus nonus	1.13	1.40	.53	-.12	.06	.61	.62	.33
Drunella spinifera	1.09	1.39	.44	-.24	-.38	.25	.47	.04
Atherix pachypus	.98	1.21	.53	.33	.27	.23	.27	.54
Ameletus sp. D	.97	1.36	.47	-.33	-.51	-.25	-.00	-.13
Rhyacophila vaccua	.94	1.28	.44	-.26	-.56	.35	.35	.14
Glossosoma spp.	.87	1.19	.47	-.29	-.46	.18	.12	-.18
Isoperla fulva	.85	1.85	.22	.87	.71	-.08	.03	.52
Ephemerella alleni	.83	1.20	.42	-.33	-.58	-.18	-.05	-.21
Rhyacophila hyalinata	.78	1.15	.42	-.19	-.50	.45	.41	.21
Epeorus deceptivus	.67	1.49	.24	-.19	-.32	-.08	.12	.04
Pteronarcella badia	.63	1.50	.20	.57	.67	-.09	-.08	.44
Paraleptophlebia vaciva	.61	1.22	.29	-.27	-.26	-.46	-.12	-.24
Hesperoperla pacifica	.60	1.28	.22	.35	.68	.13	.03	.38
Anagapetus debilis	.55	1.12	.22	-.19	-.39	.07	.23	-.07
Rhyacophila vofixa	.52	1.06	.24	-.10	-.29	.38	.32	.04
Epeorus longimanus	.51	1.23	.18	.37	.39	.19	.28	.64
Lepidostoma cascadense	.47	.98	.24	-.10	.01	.10	.24	-.10
Isoperla petersoni	.45	1.10	.22	-.10	-.01	.22	.35	.33
Pictetiella expansa	.43	.98	.20	-.03	-.14	.43	.50	.28
Drunella flavilinea	.41	.98	.18	.30	.60	.10	.06	.34
Chyranda centralis	.40	.71	.33	-.26	-.48	.11	.25	-.03
Hydropsyche tana	.40	1.26	.11	.61	.53	-.09	.05	.35
Ecclisiomyia maculosa	.38	.90	.20	-.21	-.16	.14	.18	.02
Skwala curvata	.36	.90	.18	-.03	.03	.35	.29	-.08
Rhyacophila bifila	.36	.90	.18	.48	.57	.12	.05	.34
Ecclisiomyia conspersa	.35	.81	.22	-.15	-.26	.20	.31	.05
Paraleptophlebia heteronea	.35	1.09	.11	.34	.32	.06	.08	.18
Bibiocephala grandis	.33	.94	.20	.21	.51	-.00	.05	.10
Ameletus sp. E	.32	.70	.24	-.23	-.42	.10	.19	.02
Apatania shoshone	.32	1.01	.13	.39	.48	.06	.02	.33
Isoperla fusca	.32	.89	.13	-.24	-.25	-.46	-.05	-.15
Rhyacophila angelita	.30	.70	.22	-.09	-.22	.27	.35	-.05
Hydropsyche cockerelli	.30	1.12	.11	.57	.46	-.08	.00	.34
Ameletus sp. B	.29	.80	.16	.20	.44	.13	-.03	.22
Ephemerella aurivillii	.25	.57	.22	-.05	.21	.25	.34	.11
Ameletus sp. F	.25	.79	.11	-.07	.11	.21	.29	.15
Skwala parallela	.25	.79	.11	.62	.52	-.04	.06	.57
Cryptochia sp.	.25	.41	.27	-.30	-.40	-.30	-.20	-.29
Rhyacophila verrula	.24	.68	.16	-.22	-.31	-.29	.10	.03
Diura knowltoni	.22	.68	.13	.02	.27	.27	.19	-.02
Pteronarcys californica	.15	.52	.11	.28	.46	-.02	-.10	.26
Neophylax occidentis	.15	.52	.11	-.04	-.16	.32	.38	.47
Cinygma integrum	.12	.31	.13	-.15	-.22	-.15	-.05	-.19
Isoperla sobria	.12	.31	.13	-.17	.02	-.03	.05	.21
Agathon comstocki	.12	.31	.13	-.09	-.26	.40	.27	.00
Dicosmoecus atripes	.10	.29	.11	-.16	.03	-.03	-.03	-.04

The average density in each of the faunal zones, based on this data set as well as the mainstem longitudinal data set and a much larger number of more qualitative collections from many other sites and dates, is described for 241 species in the species ecology section. For this purpose, faunal zones 5 and 6 as well as faunal zones 3 and 4 were pooled. The differences between the streams of the these zones are more quantitative than qualitative, as discussed previously. The zones are therefore difficult to distinguish with qualitative collections. The number of zones that were recognized for larger and lower elevation streams was increased because these sites are few in number, well collected and frequently distinctive.

When examined by trophic group (Figure 36), predators, shredders and collectors generally increase in density as stream order increases, while the density of scrapers peaks in the mid-order streams. Scrapers have high variance at all stream orders. This is most likely due to the highly aggregated nature of many of the scrapper species. With regard to predator and collector densities, Taylor Creek is similar to a sixth order stream, while the mainstem above Taylor Creek is similar to a fourth order stream.

Gradients in scraper and collector densities generally agree with the predictions of the river continuum concept (Vannote et al. 1980). The gradient of shredder density is mostly opposite that predicted by the river continuum concept. There is a small decrease in shredder density proceeding from the headwaters to second order streams, but thereafter shredder density increases downstream. The large variance associated with the sixth order sites is due to the scarcity of many shredder species in the upper mainstem and to the presence of other shredder species, some in huge densities, in the lowest sites on the mainstem. Headwater streams and the lowest part of the mainstem have more species of shredders than streams of intermediate size.

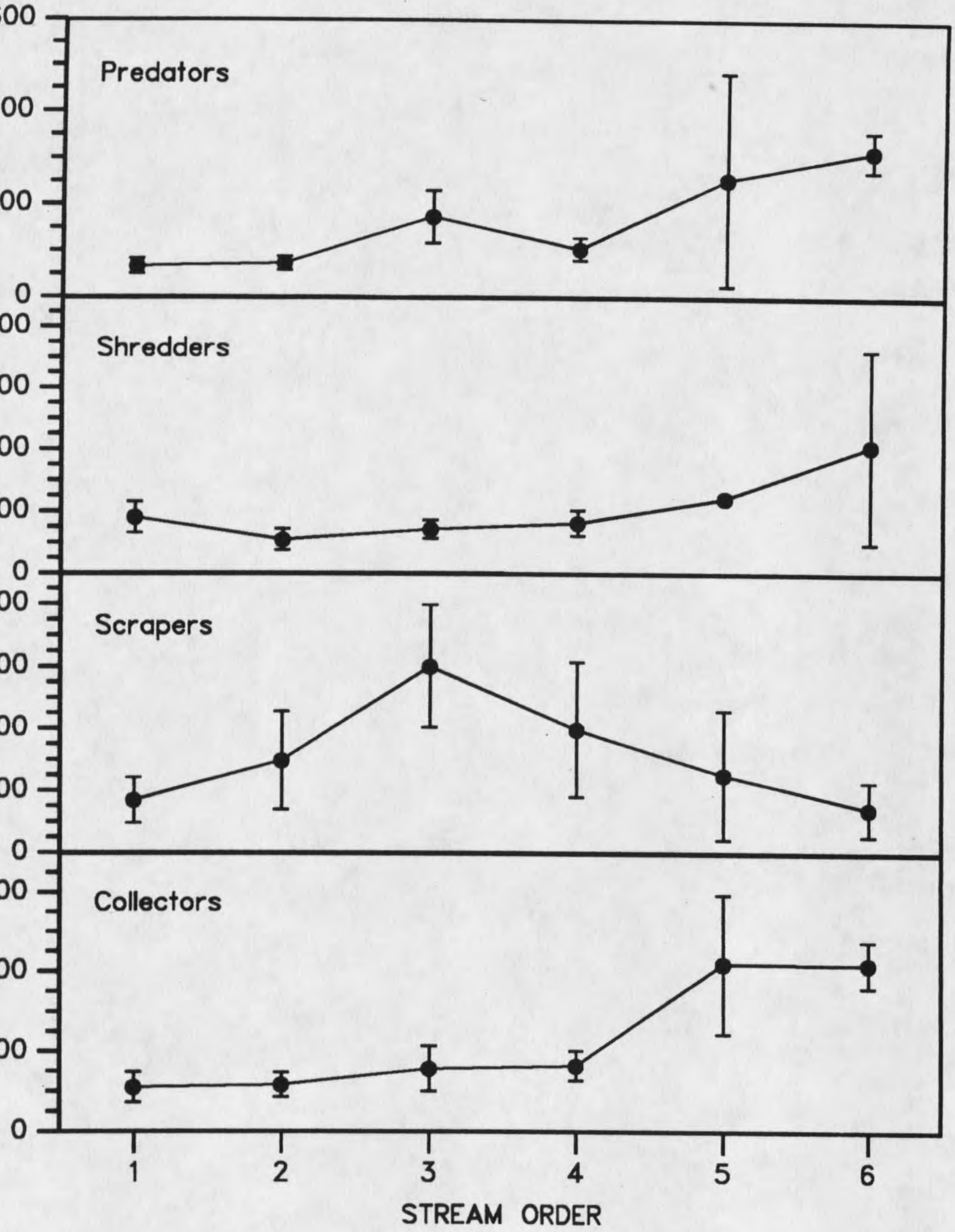

Figure 36. Mean density of individual invertebrates at each stream order based on the 45 stations of the tributary longitudinal study broken down by general feeding group. Error bars represent the standard error of the means. Sample size for orders 1 through 6 is; 6, 11, 13, 8, 2, and 5 respectively.

Temporal Community Structure

Sixty-seven taxa and approximately 416,000 individual invertebrates were taken in the 180 samples and 19 dates of the temporal data set. These data are more difficult to interpret than either the spatial data or the longitudinal data because of the confounded effects of life history, migration and seasonal changes in stream area. That is, there are three primary ways for invertebrate densities on rocks in shallow water with fast current to change. Life history, including egg hatching, mortality and emergence is the most obvious. Density changes may also be caused by seasonal differences in habitat use, which occur for some species. Changes in the total amount of suitable habitat, can also cause changes in density. The area occupied by the river at the site of the temporal samples fluctuates greatly over the course of a year.

The average number of species per rock and the average number of invertebrates per rock exhibit interesting patterns over the course of the year (Figure 37). The number of species per rock is highest during the late fall and early spring. The peak in species number during the fall is associated with the appearance in the benthos of species with winter life cycles. The winter depression in species number is not associated with life history or with river area changes, but with low total density caused by winter mortality or migration from shallow water. The peak in species number during the spring is associated with the appearance in the benthos of species with summer life cycles, which occurs before all species with winter cycles have emerged. The peak in species number during the spring occurs during a depression in total invertebrate density. The decline in the average number of species per rock after the spring peak is associated with increasing total density. At that time many of the species with winter life cycles are absent from the benthos and the species with summer life cycles become very abundant.

Total invertebrate density, unlike average species number, does not approximate a closed, annual loop (Figure 37). Total density was very low during the first July, but during

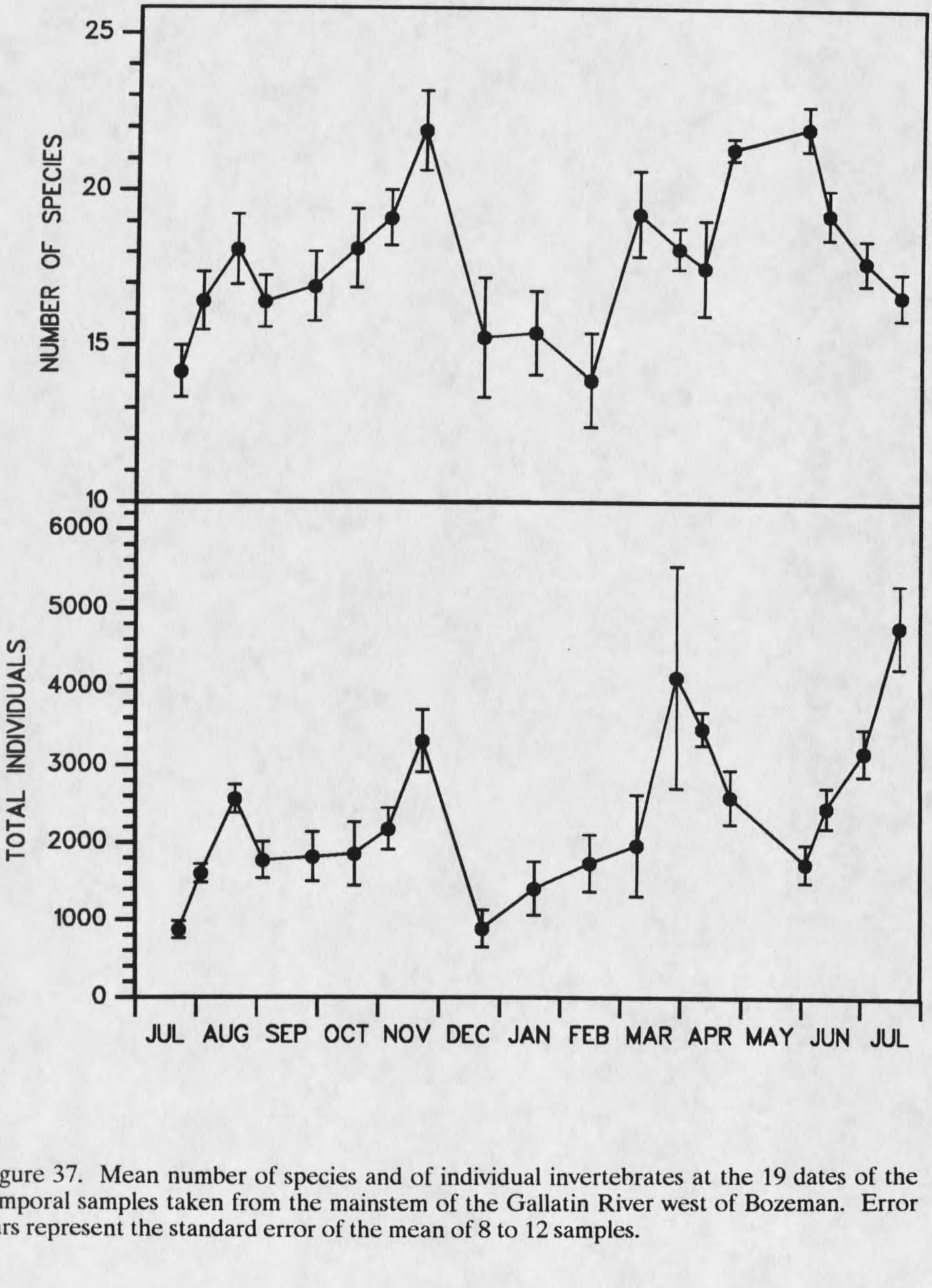

Figure 37. Mean number of species and of individual invertebrates at the 19 dates of the temporal samples taken from the mainstem of the Gallatin River west of Bozeman. Error bars represent the standard error of the mean of 8 to 12 samples.

the next July, density was at an all-time high. This appears to be due primarily to early spring run-off before the second summer, which was associated with early, warmer temperatures. Many species with summer cycles appeared earlier, and achieved higher total densities, the second summer than during the first summer. Some species, with winter cycles also emerged earlier, and then reappeared in the benthos earlier the second summer.

Principal component analysis was used to address the extent to which species follow similar trajectories in density, regardless of the cause. This analysis, using the covariance matrix of the 10 species with greatest variance, revealed three density trajectories which account for greater variance than would any of the individual species with random covariance (Table 40). A Monte Carlo simulation using the observed variances for the species, but random covariance indicated that eigenvalues as large as the first three are not expected in 1000 trials. The variance accounted for by the first three principal components is 1.6 times greater than expected with random covariance.

Table 40. Eigenvectors defining the first four principal components for the temporal data set based on the covariance matrix of the log transformed abundances.

Species	I	II	III	IV
Hydropsyche tana	.629	.151	.065	.084
Ephemerella infrequens	.585	-.079	-.086	-.232
Lepidostoma pluviale	.262	.389	-.353	.029
Hydropsyche cockerelli	.214	.148	.561	-.036
Arctopsyche grandis	.148	.216	.433	-.095
Bibiocephala grandis	.059	-.097	.192	.911
Drunella flavilinea	.040	.378	-.488	.159
Pteronarcella badia	-.038	.427	.153	.050
Serratella tibialis	-.167	.500	-.039	.156
Acentrella turbida	-.302	.408	.248	-.215
Eigenvalues	11.12	5.90	4.03	2.38
Percent variance	39.21	20.81	14.22	8.41
Cumulative percent	39.21	60.02	74.24	82.65

The first three components together account for 74 percent of the total variance and are associated with rather distinct eigenvalues. The eigenvectors associated with these eigenvalues are thus expected to be stable and proved to be stable to both jackknife validation and bootstrap sampling. The sample size of 8 to 12 replications on each of the nineteen dates could be reduced to at least half, as long as all dates were retained, without substantially altering these results.

The eigenvectors beyond the first three, each weighted heavily only a single species and accounted for little of the total variance. The eigenvalues associated with these differ little from one-another, so the eigen vectors define only a spherical hyperspace with only poorly defined major axes. These high order eigenvectors capture the individual or unique nature of the species, and so are of little interest here.

The three assemblage trajectories are most easily understood when the mean scores for all the dates are shown (Figure 38) and discussed in terms of positive participation of the species. The first principal component generally follows the density trajectory of species with typical winter life cycles. As most species at this site have winter life cycles and species with winter life cycles tend to be the most abundant, when sampled over an entire year, this result is expected. The pattern is one of low scores or densities in summer, which then increase over the autumn months, decline in the winter, increase briefly in the spring before declining again to the summer low.

The sharp decline at the start of winter and the increase during the spring are interesting. Life history events and river area changes cannot be responsible at that season. Migration from shallow areas during the winter seems the most likely explanation. Comparing the scores on the first principal component to total invertebrate density (Figure 37) is worthwhile. The agreement is generally good, except in the second summer. At that time the scores on the first principal component drop to complete an annual cycle, but total invertebrate density is rapidly increasing. The first principal component is not sensitive to the reduced flow and increased temperatures which occurred the second summer.

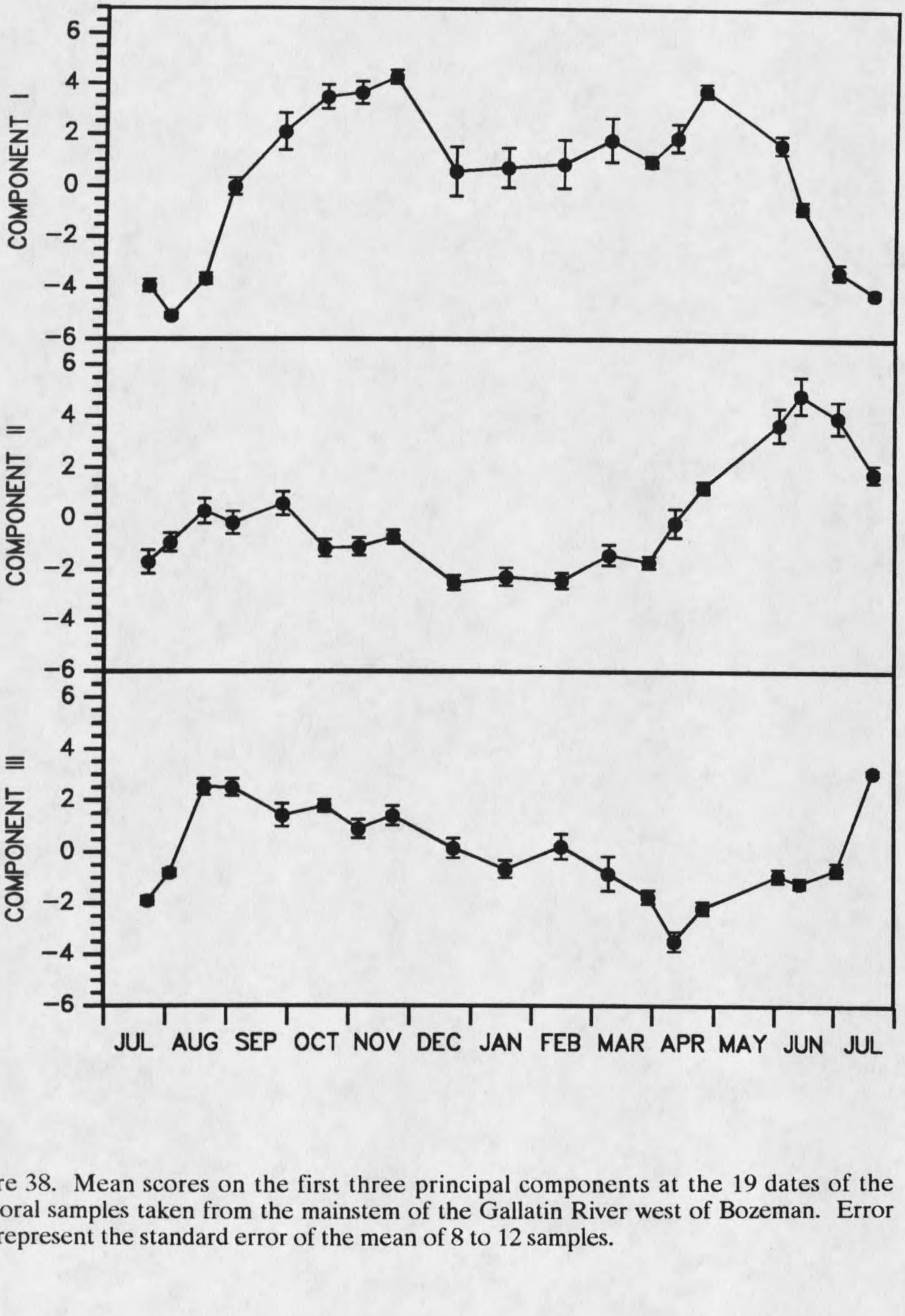

Figure 38. Mean scores on the first three principal components at the 19 dates of the temporal samples taken from the mainstem of the Gallatin River west of Bozeman. Error bars represent the standard error of the mean of 8 to 12 samples.

The scores on the second principal component follow a trajectory similar to most species with summer life cycles. The scores on this component show little variation over much of the year, but increase rapidly in the spring and peak in early summer.

The trajectory of the scores on the third principal component follows species with winter life cycles which peak earlier in the autumn, decrease more steadily through the winter and then rise again earlier in the spring, than do species identified by the first principal component. The scores on the third component, unlike those of the first two components, do not form a closed, annual loop. This component helps to identify the species with winter cycles which emerged earlier and then reappeared in the benthos earlier the second summer.

All species occurring in more than 10 percent of the 180 temporal samples are listed in Table 41 and characterized by their overall mean, standard deviation and correlations with the first three principal components and with species number and total invertebrate density. To facilitate interpretation of these correlations, the density trajectories of a few species are examined individually below.

The three hydropsychid caddisflies that occur at this site have rather similar seasonalities of density (Figure 39). For all three species, the second generation appeared earlier in the season than did the first. These species are pupating during the late spring and are rather sensitive to higher temperatures associated with the low spring flow that occurred the second spring. The small depression that occurred for all three species during late March and early April is most likely associated with mass movement of the larvae at that time.

The seasonalities of the benthic density of the two most abundant winter stoneflies are shown in Figure 40. These two species have an abbreviated winter life cycle, which includes a summer diapause of the eggs or early instar larvae. Species with short winter life cycles had no opportunity to participate in the dominant principal component axes because of

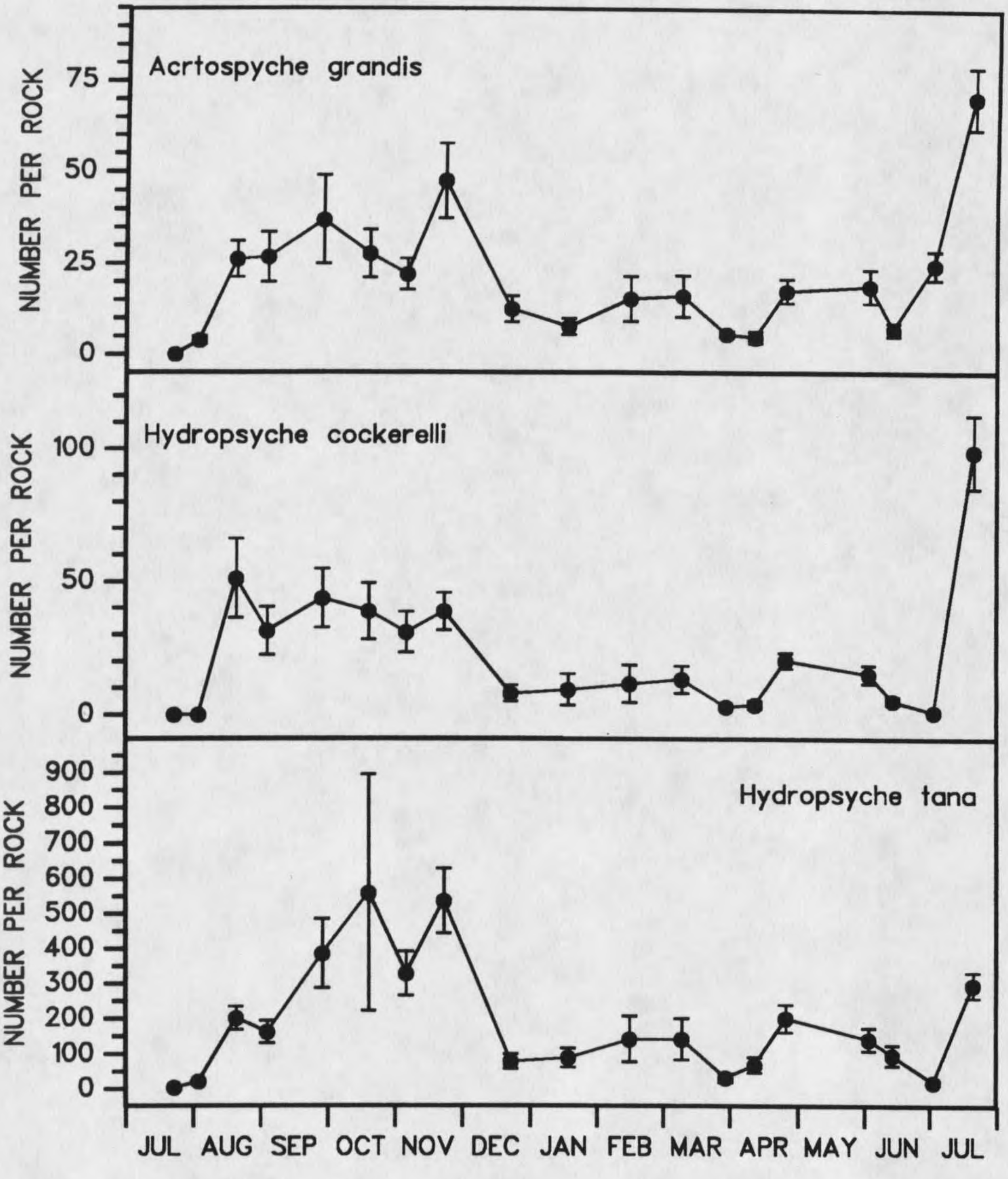

Figure 39. Mean number of three Trichoptera species at the 19 dates of the temporal samples taken from the mainstem of the Gallatin River west of Bozeman. Error bars represent the standard error of the mean of 8 to 12 samples.

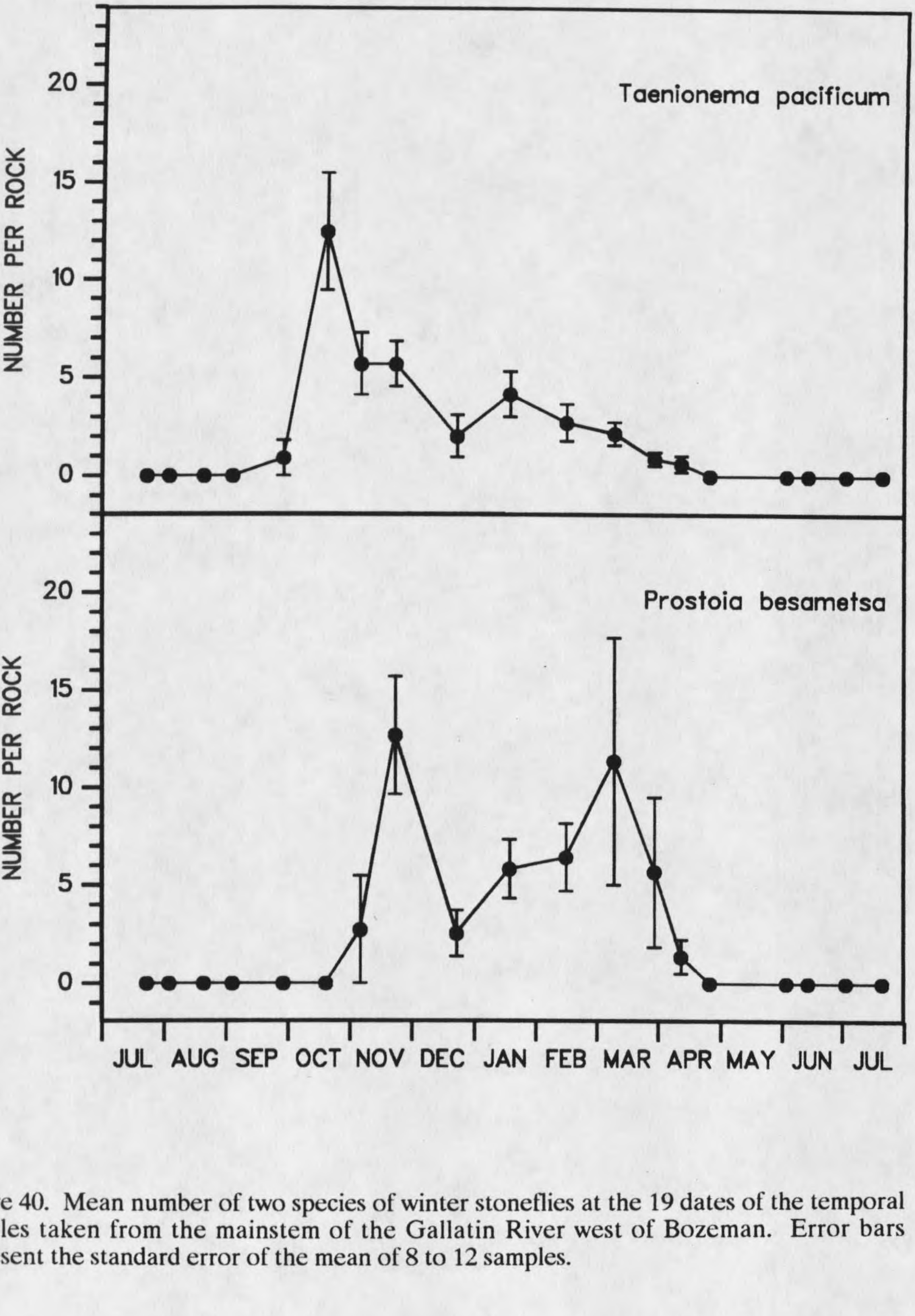

Figure 40. Mean number of two species of winter stoneflies at the 19 dates of the temporal samples taken from the mainstem of the Gallatin River west of Bozeman. Error bars represent the standard error of the mean of 8 to 12 samples.

their low densities, compared with species which have the more typical long-winter life cycle or summer life cycle.

Table 41. Invertebrate taxa present in more than 10 percent of the samples (FP) from the temporal data (N=180) ranked according to the mean of their log transformed abundances. Also shown for each taxon is its standard deviation (STD), and the correlations with the first three principal components (F1,F2,F3), with the total number of species (SN) and with the total number of individuals (TN).

Taxon	mean	STD	FP	F1	F2	F3	SN	TN
Simulidae	6.19	1.24	1.00	-.04	-.16	.34	-.10	.57
Baetis tricaudatus	4.91	1.17	1.00	.28	.08	.24	.41	.60
Hydropsyche tana	3.35	2.28	.77	.92	.16	.06	.46	.09
Ephemerella infrequens	2.55	2.10	.67	.93	-.09	-.08	.48	.15
Arctopsyche grandis	2.44	1.25	.90	.39	.42	.69	.46	.46
Hydropsyche cockerelli	2.15	1.57	.78	.45	.23	.72	.40	.37
Lepidostoma pluviale	1.61	1.68	.59	.52	.56	-.42	.59	.19
Bibiocephala grandis	1.42	1.52	.59	.13	-.15	.25	.03	-.15
Acentrella turbida	1.35	1.73	.46	-.58	.57	.29	-.04	.27
Drunella flavilinea	1.21	1.57	.48	.09	.59	-.62	.32	.25
Epeorus longimanus	1.18	1.21	.56	-.05	.33	-.56	.19	-.03
Pteronarcella badia	1.13	1.34	.56	-.10	.78	.23	.40	.30
Isoperla fulva	1.12	1.14	.59	.55	-.05	.34	.42	.19
Rhyacophila bifila	1.12	1.10	.66	.54	.14	.08	.44	.24
Brachycentrus americanus	1.11	1.10	.65	.40	.45	-.27	.58	.28
Drunella doddsi	1.07	.90	.68	.41	-.09	-.06	.31	-.02
Serratella tibialis	.98	1.51	.40	-.37	.80	-.05	.21	.16
Rhithrogena futilis	.87	.99	.52	.25	-.30	.24	.14	-.04
Drunella grandis	.77	1.00	.48	.14	.31	.33	.43	.42
Caudatella heterocaudata	.74	1.16	.35	-.25	.35	-.39	.09	-.11
Deuterophlebia nielsoni	.64	1.21	.27	-.59	-.21	-.05	-.32	-.21
Antocha monticola	.56	.84	.40	.19	.32	.16	.37	.33
Taenionema pacificum	.53	.85	.33	.52	-.35	.18	.15	-.00
Prostoia besametsa	.51	.95	.27	.37	-.30	-.07	.18	.03
Atherix pachypus	.47	.74	.37	.07	.49	.26	.34	.23
Brachycentrus occidentalis	.40	.63	.35	-.13	.25	.40	.24	.34
Cinygmula tarda	.25	.73	.13	.19	.14	-.37	.20	.01
Isoperla quinquepunctata	.23	.64	.14	.28	.18	-.22	.37	.03
Amiocentrus aspilus	.16	.50	.12	-.09	.50	-.05	.26	.17
Hesperoperla pacifica	.10	.31	.11	.09	.25	.02	.27	.01

Three species of mayflies with summer life cycles are shown in Figure 41. These species are not represented in the benthos during the winter and have very rapid increases in population densities when they first appear. They can easily complicate non-temporal

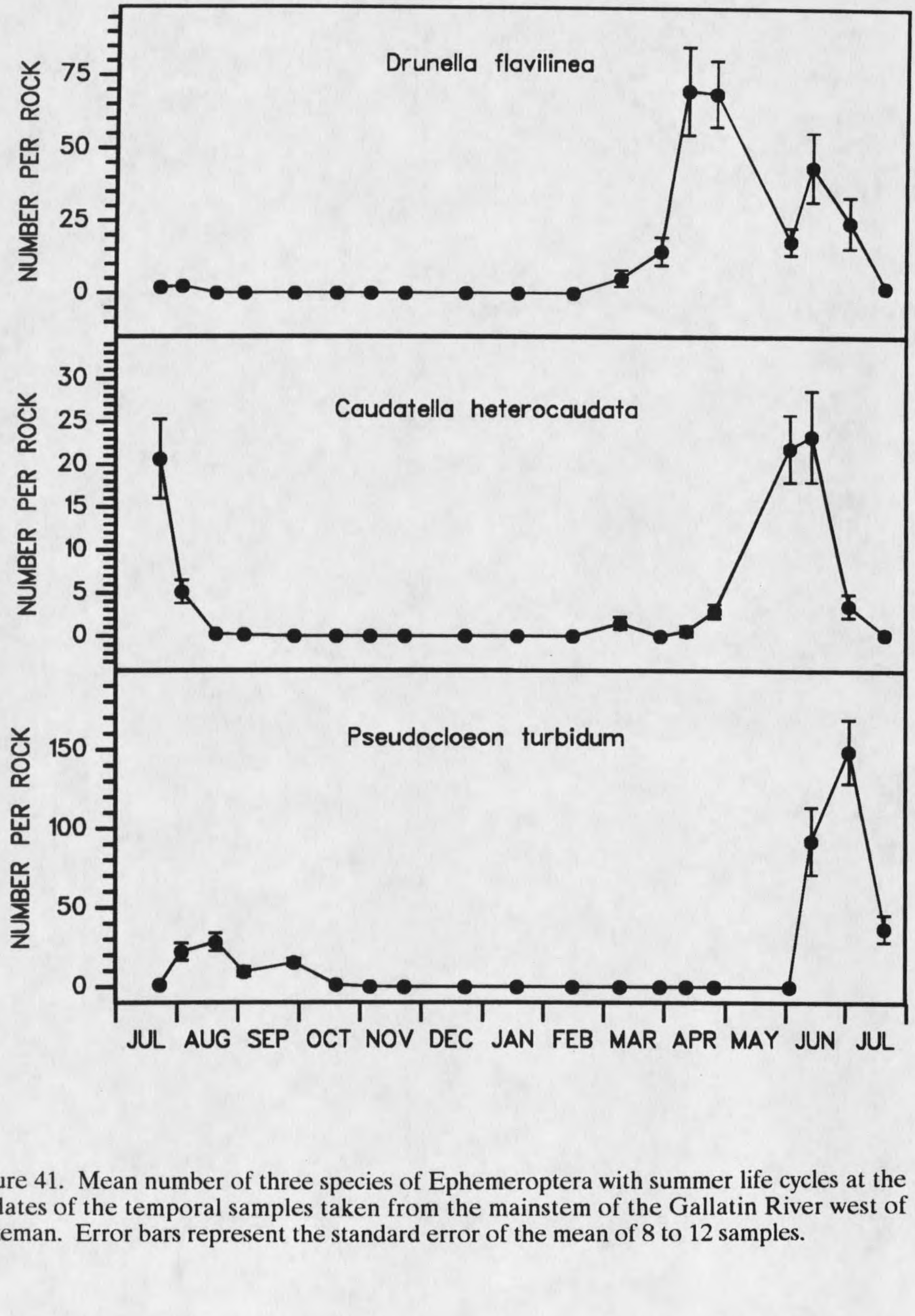

Figure 41. Mean number of three species of Ephemeroptera with summer life cycles at the 19 dates of the temporal samples taken from the mainstem of the Gallatin River west of Bozeman. Error bars represent the standard error of the mean of 8 to 12 samples.

studies. The seasonal density trajectory of *Drunella flavilinea* forms a simple closed annual cycle. *Caudatella heterocaudata* completed its growth and emergence earlier the second season than it did during the first, but achieved similar densities both years. *Pseudocloeon turbidum* was much more abundant the second summer than it was during the first. Two other mayfly species, *Ephemerella infrequens* and *Serratella tibialis* are thought to be ecologically identical at this site except for their seasonality (Figure 42).

There is little indication that the species of a trophic group show similar seasonalities (Figure 43). The peak in shredder density in the spring is due almost entirely to the appearance of young *Pteronarcella badia* from eggs laid the previous summer. Most shredder species at this site are normally rather rare in benthic samples. The density of scrappers declined over the year and seems associated with increased cluttering and siltation of the substrate due to low spring flows.

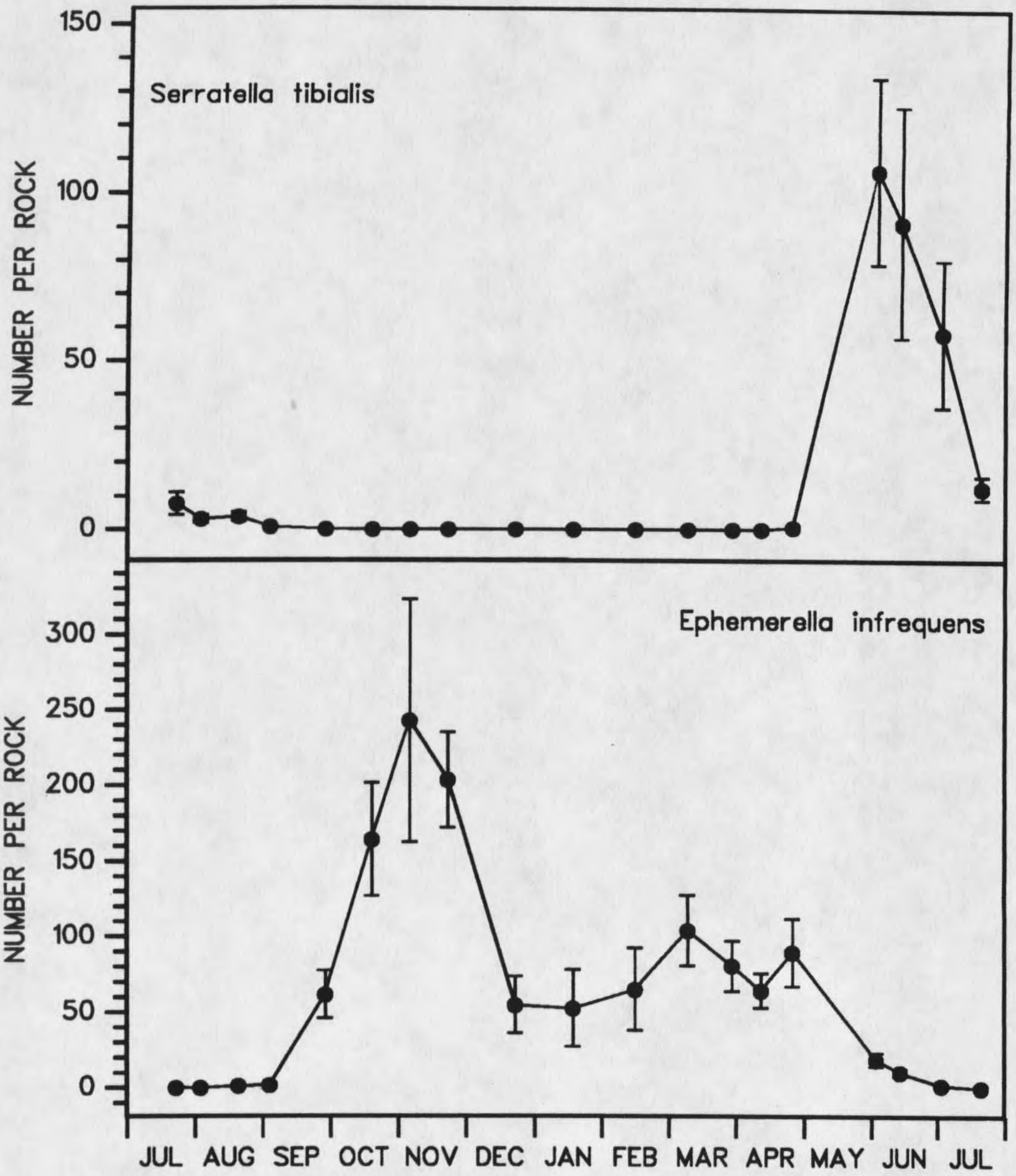

Figure 42. Mean number of two functionally equivalent species of Ephemeroptera at the 19 dates of the temporal samples taken from the mainstem of the Gallatin River west of Bozeman. Error bars represent the standard error of the mean of 8 to 12 samples.

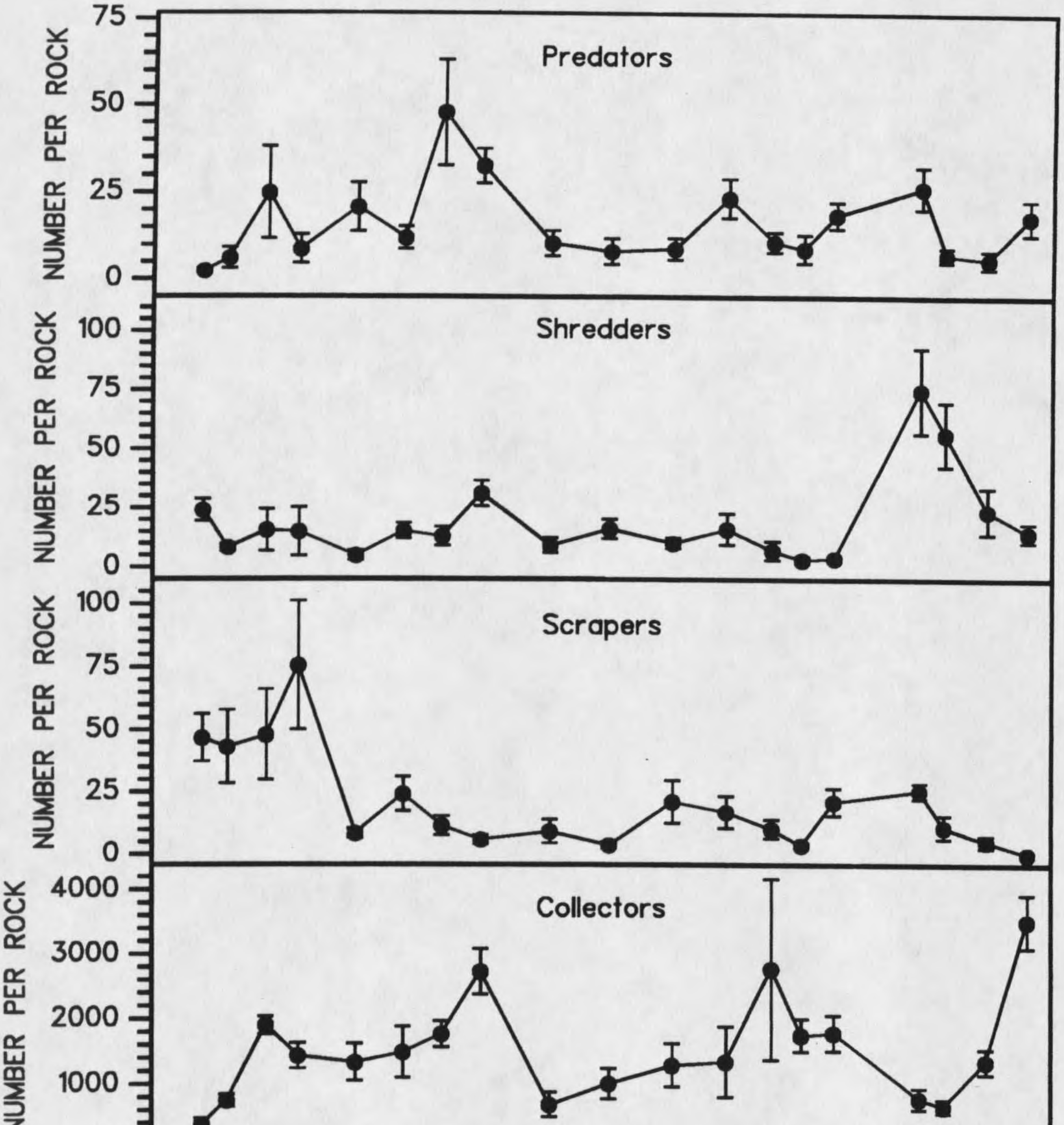

Figure 43. Mean density of individual invertebrates at the 19 dates of the temporal samples taken from the mainstem of the Gallatin River west of Bozeman, broken down by general feeding group. Error bars represent the standard error of the mean of 8 to 12 samples.

CONCLUSIONS

The aquatic insect community of the Gallatin River drainage is composed of a great many species, and is probably typical of relatively undisturbed drainages throughout much of the northern Rocky Mountains. A detailed faunal inventory provides a very basic and important characterization of invertebrate communities. A reasonably complete faunal inventory may require several years of collecting and requires detailed knowledge of the taxonomy, life histories and specialized habitats of the organisms. Quantitative benthic samples normally contain only a small fraction of the species present. Insect traps take far more species than benthic samples, and can serve as an important control of the quality of the faunal inventory. The collection of both the larvae and adults is far superior to collection of either one alone, and also provides a control of the quality of the inventory.

Life history studies of any type require a firm taxonomic basis. With many groups of aquatic invertebrates, this may require several years to achieve and is undoubtedly the limiting factor in our knowledge of these species. Community studies require a firm taxonomic base as well as knowledge of the species life histories. It is therefore not surprising that invertebrate communities in general are so poorly understood.

Life history data are strongly and variably organized taxonomically. Lower taxonomic categories are more predictive, but life history details are never fully predictable based on other species. Closely related species usually have an obvious difference in one aspect of their life history, which undoubtedly provides sufficient ecological separation. Less closely related species usually differ ecologically in many ways and are not easily compared.

The life histories of only a very few of species examined were variable within the Gallatin River drainage. This variability increases outside the drainage and is most pronounced in areas very different from the Gallatin drainage, especially where other elements of the fauna change substantially.

All types of invertebrate sampling have strong taxonomic bias, high variance, and seasonal confounding which make direct, quantitative comparisons of different data sets very difficult. Use of very fine capture nets in benthic sampling necessitates large amounts of laboratory time to process huge numbers of very small invertebrates, which can seldom be accurately identified, and about which little, if anything, is known. More useful environmental information may be obtained by focusing on species which can be identified and which have been ecologically characterized.

In the Gallatin drainage, single rock samples provide a convenient, natural sampling unit for quantitative studies. Dominant patterns of spatial, altitudinal and temporal community organization are revealed with reasonable sample sizes.

Principal component analysis provides a powerful tool for determining the dominant patterns of variation in large data sets. This analysis provides a concise summary of bulky covariance and correlation matrices as well as a transformation of the data which minimizes dimensionality. For the data examined during this study, one to three principal components extracted all of the interpretable pattern from the data. Stability and significance of principal component analysis are readily assessed by jackknife analysis and Monte Carlo simulations, but are usually rather obvious based on the eigenvalues themselves. The average principal component score for a set of replicated samples normally has a lower standard error than do the original variables or their sum. Species number and total invertebrate density frequently approximate two of the significant principal components in these analyses.

For the data analyzed for this study, canonical correlation analysis was useful only in substantiating the interpretation of the principal components for the spatial data sets. Lack of a sufficient number of non-redundant physical-chemical variables probably caused this failure. Discrimination analysis was much more useful than canonical correlation. This analysis provides powerful means of distinguishing between previously identified groups of observations based on the data. Jackknife cross-validation provides a direct measure of the success of this analysis. The lack of success at discriminating the observations is a powerful statement about the data which may be as ecologically interesting as very good discrimination.

Spatial community structure in the lower parts of the Gallatin River is strongly determined, throughout the year, by water velocity. Many species occupy areas with little current during the summer, while during the remainder of the year, few species occupy those areas. Community structure on rocks in rapid current is more variable during the summer when some individual rocks are rather clean and others are quite cluttered. These rocks and their communities become much more similar over time until the next spring flood occurs. The flooding river is important in cleaning rocks of accumulated debris. Reduced floods, when they occur, eliminate some of the species requiring clean rocks from the area. High floods, by clearing away organic debris near the stream edges when they occur, eliminate other species from the area.

Aquatic insect communities vary so greatly along the course of rivers and streams that the uppermost sites in the Gallatin River drainage have no species in common with the lowermost sites. Changes in community structure occur more rapidly along small streams than along similar distances of larger streams. The mainstem of the Gallatin River can be divided into three distinct faunal regions corresponding to the lower valley, middle canyon and upper meadow areas of the river. Sites along the tributary streams within the drainage represent several sets of replicated communities that are more strongly determined by stream size and elevation than by nearness or connectivity of the streams. Unforested drainages, whether natural or man made, have stream faunas more similar to those of larger streams. Taylor Creek, rather than the larger mainstem of the river, represents by far the more continuous upstream extension of the lower mainstem, based on the insect community.

Many species occur only in the lower parts of the mainstem of the river. These are the species that are most subject to being lost from the system due to human impacts.

In the lower parts of the Gallatin River, the dominant pattern of temporal community structure on boulders in shallow water with swift current is driven by species with long winter life cycles. This pattern has peak density in late autumn, is apparently insensitive to year-to-year variation in flow and temperature, and involves migration from shallow areas with rapid current during the mid-winter. The second strongest pattern of temporal community organization corresponds to the density pattern of species with summer life cycles. A third pattern of temporal community organization corresponds to species with long winter life cycles that exhibit peak density in late summer, decline evenly over the winter and exhibit signs of sensitivity to annual variation in flow and temperature. Species with short winter life cycles were too rare in the benthos to define patterns of community organization.

PERSPECTIVES FOR FURTHER WORK

As stated in the introduction, this study was undertaken in order to generate hypotheses more than to test them, in order to lay a foundation for future work. At the start of the study, very little was known of the species composition or the community structure within the drainage. Initial hypotheses were therefore limited to very general or vague statements. By the end of the study, a great deal of new information had been gathered, which allows many specific hypotheses to be stated. A hypothesis, however, is not properly generated and tested with the same data. Doing so would result in a strong bias for accepting the hypotheses that were so constructed. For that reason, most of the conclusions presented above should be regarded as hypotheses and subjected to testing with new data. The number of these hypotheses is very large, but a few examples are discussed below. These are arranged starting with narrowly focused hypotheses and ending with broader hypotheses.

Species specific hypotheses generated by this study are so numerous that only a few examples will be mentioned here. Many others can be easily constructed from the information presented above. For example: The mayfly *Ephemerella alleni* is hypothesized as being parthenogenetic, based on the absence of males at all sites. It is further hypothesized as being gynogenic, based on the synchrony of its emergence and its small population size. The caddisfly *Brachycentrus americanus* is hypothesized to switch from a one-year to a two-year life cycle in the upper parts of its range within the Gallatin drainage. Species of *Callibaetis* are hypothesized not to be ovoviviparous in the Gallatin drainage. The population size of *Pteronarcys californica* is hypothesized to be prematurely reduced in the lower Gallatin River due to the bedload movements and irrigation withdrawals that occur there.

Life cycle types are hypothesized for hundreds of species based solely on field observations over several years. Life cycles determined by such means must be subjected to further laboratory testing. This may take many lifetimes to achieve for so many species. Species designated as having asynchronous life cycles are most critically in need of further work. Life cycles hypothesized to contain periods of diapause are also in need of laboratory work.

A large number of stonefly species in the Gallatin River are hypothesized as being hyporheic. This is based on the scarcity of the nymphs in the benthos when compared to the adults, the concentration of the nymphs in areas of upwelling water before emergence, and the synchrony of emergence. The degree of synchrony and the degree of the restriction to areas of upwelling water are hypothesized to be indications of their occurrence deeper in the substrate. Testing this hypothesis may prove difficult. It is clear, however that certain areas of upwelling water are regularly used by hyporheic species, and that even normally rare species can be taken regularly in large numbers. These "hyporheic windows" may be useful in monitoring ground water conditions.

Other hypotheses refer to groups of species, for example: Body size is hypothesized to be of the utmost importance in resource partitioning of both predatory and detritivorous stoneflies. The head capsule widths of Trichoptera larval instars are hypothesized to be rather constant when expressed as a percentage of the final instar. Many sets of species are hypothesized to form guilds that are distributed according to altitudinal, seasonal, or habitat differences.

The following four hypotheses are proposed as examples of sampling methods that may help improve the usefulness of information gathered by more applied studies. The four perlid species of the upper Missouri River drainage are all easily identified (with experience) even when small, they are all semivoltine, and they all have obvious altitudinal preferences, but with considerable overlap. These four species were all observed to have marked shifts in their altitudinal range over the course of the study. Measuring the ratio of these species' densities, possibly separating different size classes, may provide a sensitive index to detect changes in temperature and flow conditions at a site, or for comparing different sites. Pursuing this hypothesis, by measuring ratios, may eliminate much of the large sampling variance associated with measuring benthic densities. Changing conditions might be detected with a single sample when the young perlids are observed to be mostly of a different species than the older ones. This was observed during this study, and was always followed by shifts in dominance of the older perlids in subsequent years.

Some species that are easily identified at any size, that have wide altitudinal range, that are univoltine, but occur in the benthos for most of the year, and that are reasonably well synchronized in growth and emergence may provide a useful measure of site productivity. The mean head-capsule width of a relatively small sample should provide an index of productivity to be used in comparing different sites, or in comparing changes at a single site over time. *Drunella doddsi* is the most obvious choice for use in testing this hypothesis in the Gallatin drainage. Separating the influence of temperature from chemical or physical factors might be partially achieved if temperature is also directly monitored.

Altitudinal shifting in habitat preference was discussed briefly with the heptageniid mayflies. This hypothesis suggests that species near the upper end of their altitudinal range become increasing restricted to areas of little current near shore, while near the lower end of their range they become increasing restricted to areas of faster water. This hypothesis has serious implications when comparing data from different streams. It may provide a measure for detecting habitat changes that is much more sensitive than looking for species replacements and not subject to the large sampling variance associated with measuring benthic densities.

Even with years of experience, predicting the species composition of an unfamiliar stream based on observing the physical conditions at the site seems very unreliable. Annual variation in temperature, discharge, and water quality does not so clearly mark the physical habitat as they do the species living there. A quick and very incomplete species inventory seems to provide much better information for predicting the remaining species that are present as well as those that are not expected to be present. Unusual combinations of species may indicate unusual conditions. Comparing the drainage area and elevation of the site to those of streams with similar species may provide a means of judging the relative degradation of the drainage. Testing these hypotheses awaits gathering more intensive species inventory data over a wide area to establish a calibration data base.

Some hypotheses are specific to streams of the Gallatin drainage. Taylor Creek is hypothesized to be the dominant influence on the benthic community in the Gallatin River below their confluence. The influence is pronouncedly negative in terms of species richness and total invertebrate density. Further work in this area may result in land management recommendations in the Taylor Creek drainage. West Fork Creek, on the other hand, is hypothesized as being unaffected by the development associated with the Big Sky ski resort. This situation could easily change in the future.

The following hypotheses are of a very general nature. The following mode of parapatric speciation is hypothesized to operate in river systems. Some individuals of a species move into a smaller tributary stream for even a short distance. In this new habitat they are immediately subjected to a colder thermal environment and selected for physiological adaptation. Their development and emergence are delayed, possibly until the next year, which results in immediate reproductive isolation. The adults are selected to maintain this reproductive isolation. The final result is two species whose immatures differ only with regard to their temperature preferences, and whose adults differ in terms of color, genitalia, or mating behavior. Possible examples are very numerous. Recently derived pairs of species would have little altitudinal overlap when compared to more ancient pairs of species. Species whose emergence is split between spring and autumn may represent an intermediate stage in this process. Testing this hypothesis waits only for better systematic data. It may be better tested in non-glaciated river systems where the sister species may both remain endemic.

Though inherently circular, it seems easy to hypothesize that many of the presently fashionable theories are distorted by sampling methods and taxonomic difficulties. For example, the River Continuum Concept hypothesizes highest species diversity in middle order streams because of the greater diurnal temperature fluctuation that occurs there. Quantitative data from this study, provide little support of this view. The data from the complete species inventory of three insect orders, suggests that streams of intermediate order have the lowest number of species. Mountain headwater streams and large rivers have many species that are difficult to sample in the benthos, and that are difficult to identify to species. Headwater streams have many species burrowing in wood, beneath under-cut banks, or deep in the substrate. Large rivers have many species that are very small, prefer deep water or shoreline areas, or occur in the benthos at low densities or for only a short time each year. Adult collections, over the course of a year, clearly indicate the presence and importance of these species. Diurnal temperature fluctuation may not be of paramount importance to species diversity. Annual temperature fluctuation and physical habitat complexity may be more important.

An alternate hypothesis, consistent with other premises of the River Continuum Concept is that streams of all orders have about the same number of species. Streams of all sizes are of about the same biological age, and they have similar physical predictability. Age and predictability may be more important in generating and maintaining large number of species than diurnal temperature fluctuation.

Other hypotheses may be distorted by phylogeny, or taxonomy. For example, the River Continuum Concept predicts altitudinal pattern in trophic group dominance. Again the quantitative data from this study provided only mixed support for the predicted patterns. The data from the complete species inventory of three insect orders, suggests that the number of collector species increases markedly downstream, that the number of predator species slowly declines downstream, that the number of shredder species is depressed in middle order streams, and that the number of scraper species is about constant. However, the increase in the number of collector species in larger rivers may be taxonomically complicated by the increased dominance of mayflies in large rivers. Likewise, the number of shredder species must decline in larger rivers as stoneflies decline in dominance, but in western Montana this occurs only in very large rivers. Life cycle strategies again may cause additional complications as stonefly shredder species in large rivers tend to have short winter life cycles and may thus go undetected. These taxonomic differences may explain much of the predicted pattern in trophic group dominance, but for reasons that cannot be generalized. Patterns in taxonomic composition, body size, habitat use, and life cycle should all be accounted for before more dynamical hypotheses are proposed.

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