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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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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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

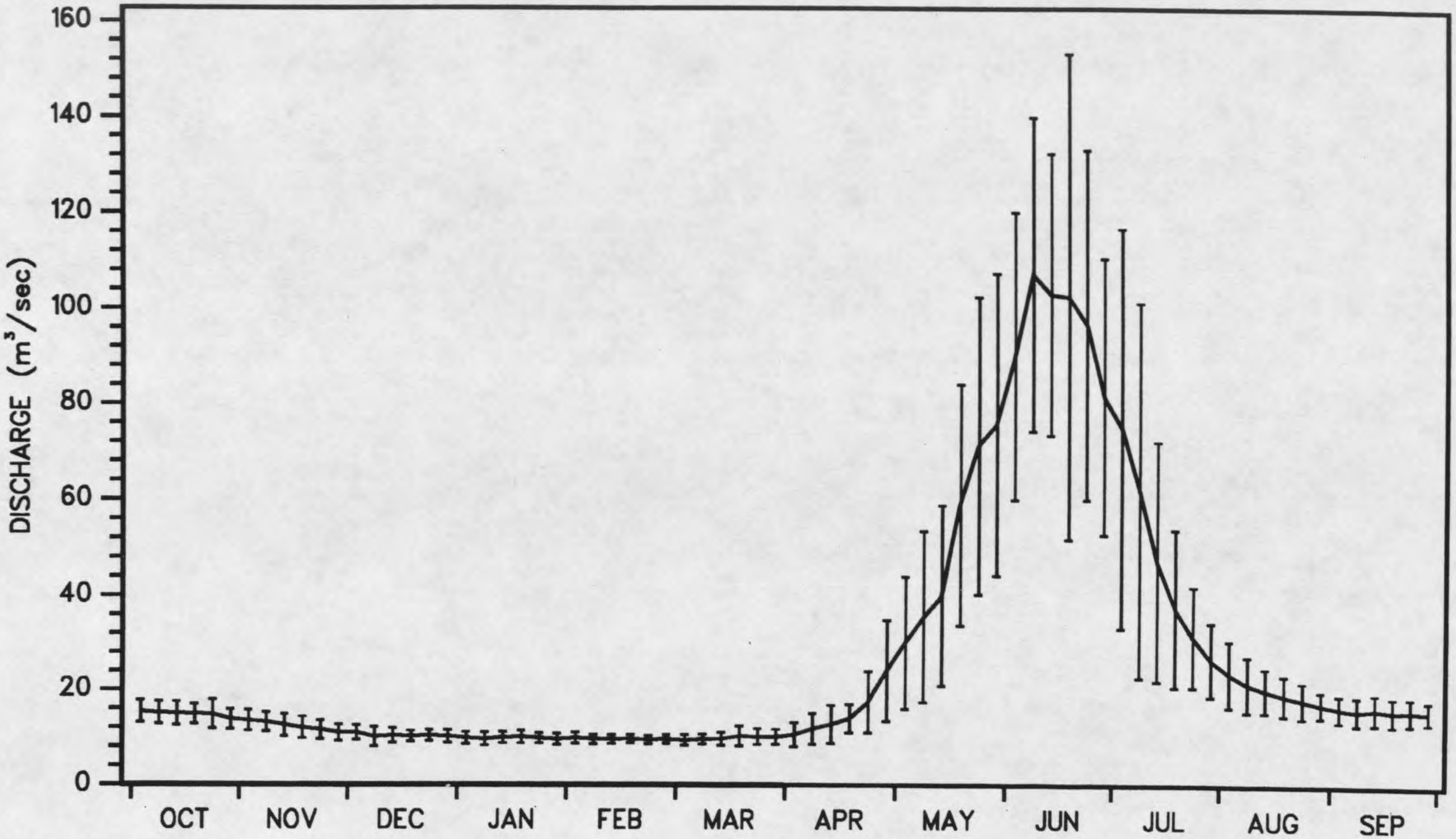

Figure 1. Average discharge of the mainstem of the Gallatin River near the forest boundary based on ten years beginning October 1971, based on U.S. Geological Survey water resources data. Error bars are standard deviations at five day intervals.

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

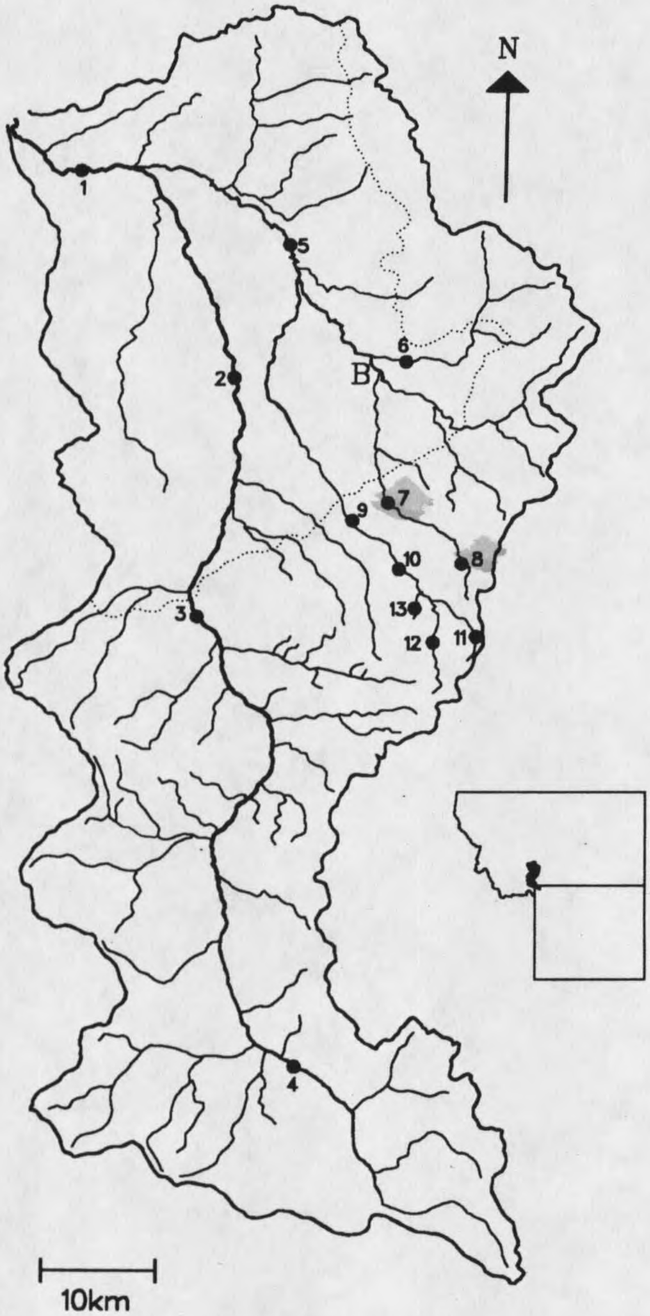

Figure 2. The Gallatin River drainage showing the locations of the 13 most important stations used in species life history studies. These are coded by the station number identified in Table 1. The dotted line indicates the approximate downstream limit of the forest. The letter "B" marks the location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