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Title: Ecological Relationships Among Western Ephemerellidae:

Growth, Life Cycles, Food Habits, and Habitat Relationships

Abstract approved: Redacted for privacy

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The purpose of this study was to describe the life cycles,
feeding ecology, and habitat use of western species in the mayfly
family Ephemerellidae. Data were used to compare the ecological
relationships and strategies among species and to examine patterns
of adaptive radiation within the family. Data were further used to
develop hypotheses describing the general importance of food,
temperature, habitat, and season in affecting the development and
organization of benthic invertebrate communities in stream
ecosystems.

Growth rate and length of growth period were examined in nine
species. Growth rates of most species were related to temperature,
but little evidence was found that implicated food as an important
factor affecting individual growth in the field. Growth period and
final size were most clearly related to specialization of different
species for habitats that differ in duration of stability.

Both food specialists and generalists were found among 20
species examined for gut contents. Proportion of detritus, diatoms,
animal matter, and moss ingested varied among species. Within a
species, diet varied with both locality and habitat, but these
differences were not sufficient to mask differences in diet among
species.

Among 14 species, taxa varied in their distribution along a stream continuum (2nd to 7th order) and in their preference for gravel, cobble, boulder, or moss substrates. Most species were habitat specialists and occurred on only one or two substrate types and at only a few stations.

When four niche dimensions were considered, overlap between species was found to be least for station, followed by substrate type, season, and food. Complementarity in niche overlaps between niche axes was found for species in the genus Drunella but not among species in the family as a whole.

From this study I inferred that stream insects show similar patterns of resource use as do animals in other ecosystems, although evidence for a discrete guild substructure was not strong. I conclude by stressing the need for further research that examines how the multiple and interacting factors in stream ecosystems have shaped both the ecology of single species and the structure of entire communities.

Ecological Relationships Among Western Ephemerellidae:

Growth, Life Cycles, Food Habits, and Habitat Relationships

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I would like to extend special thanks to a few of the many who deserve recognition. Warmest appreciation to Norm Anderson, my major advisor, for sage advice over five years and for the many gentle reminders that natural history is in the domain of the real world and not merely a simple-minded abstraction. Thanks also to my other committee members: to Ken Cummins for many valuable suggestions and for tolerating my seemingly perverse interpretations of data; to Jim Hall for pointing out a tendency or two for "arm-waving" explanations and for his thorough editing; to Pete McEvoy for reminding me that some insects live on land; to Ron Clarke for discussions on the metaphysics and ethics of what scientists do; and to Scott Overton for discussions on inference.

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INTRODUCTION

Patterns of structure in biological communities, the
mechanisms by which patterns arise, and the factors that influence
the functioning or productivity of populations and communities are
important areas of investigation for ecologists. Study of natural
communities is undertaken to advance general understanding of both
the range of structural and functional attributes found among
communities and the important intrinsic and extrinsic processes that
operate within them. Presently a comprehensive understanding of
community phenomena in stream ecosystems is poorly developed.

Hynes (1970) reviewed and synthesized most of the literature
on stream ecosystems published prior to 1966. He demonstrated a
number of broad relationships between environmental parameters and
the abundance or distribution of biota in streams, but his review
clearly showed that we have not succeeded in producing an holistic
understanding of stream communities. There are a number of reasons
for this. First, stream ecologists have often approached their
research from a single factor perspective (i.e. how does factor "X"
influence species "A" or community "Z"). Seldom have stream
ecologists attempted to integrate the varied effects of multiple
factors to produce a more coherent understanding of the ecology of
either single species or assemblages of species. Second, stream
ecologists have usually depended on empirical generalizations rather
than theoretical frameworks by which to explain patterns. Such an
approach has certain strengths (Macan 1963), but also has important
weaknesses. Third, until recently, little research of either an
empirical or theoretical nature has integrated population- and
community-level phenomena with broader views of ecosystem structure
and dynamics.

Since Hynes's review, a few researchers (Cummins 1974, Minshall 1978, Vannote et al. 1980) have developed conceptual models of "ecosystem structure and function". These models emphasize the origin and transfer of energy and matter among system compartments and usually treat biota as processors (Cummins 1973, Anderson and Sedell 1979). Conversely, a wealth of data on the natural history and autecology of specific stream organisms has been published, but only recently have researchers attempted to explain population and community level phenomena within the context of generalized models or ideas (Ross 1963, Allan 1975a, Patrick 1975, Friberg et al. 1977, Vannote 1978, Cummins and Klug 1979, Vannote et al. 1980, Vannote and Sweeney 1980, but see Theinemann 1954, Ide 1935). Development of models of community structure and organization for stream systems has lagged behind that for ecosystem models. Because of this we have a poor understanding of how symmetrical the relationships between structure and function are (i.e. does structure imply function and vice-versa?). Few studies have attempted to quantify both community and ecosystem properties in the same model (see McIntire and Colby 1978 for an important exception). Furthermore, interpretation of community phenomena within streams has often borrowed extensively from models and data from other systems (e.g. Patrick 1975, Friberg et al. 1977), frequently without adequate consideration of the unique features of stream systems that may compromise interpretations.

Problem, Goals, and Objectives

This study was directed toward determining the important features around which communities of benthic invertebrates in stream ecosystems are structured and organized. General goals toward which the research of this dissertation was addressed were:

1. What patterns of resource utilization are found in stream communities?

2. What environmental constraints are and have been important in producing observed patterns among populations and communities?

Specific objectives of the research and questions addressed were these:

1. Describe and compare basic aspects of the life cycles, feeding ecology, and habitat utilization of a number of species of Ephemerellidae from streams that differed in environmental characteristics.

    a. How do temperature, food, and other factors affect the timing and length of life cycles? How are growth rates affected?

    b. Does feeding ecology of species change as food sources vary? Are there consistent differences in type of food consumed among species? How does food affect the abundances of different species?

    c. Do species require specific habitats and how are habitats partitioned among species? How important is habitat in determining distribution and abundance of taxa?

2. Use these data to compare ecological relationships and strategies among species. Are there distinct differences in resource utilization among species, and how important are different niche axes (habitat, food, time) relative to one another?

3. Describe guild structure and guild relationships among the species examined. Can distinct guilds be distinguished?

Because a detailed analysis of all or most of the species found within even one reach of stream was beyond the scope of this study, it was restricted to a managable group of species. I chose to examine all species within the mayfly family Ephemerellidae occurring within the study area. An alternative approach would have been to study the ten or so most common species in the area. The first alternative was chosen for the following reasons. First, little information is available concerning the interspecific

differences in the ecology of a reasonably large group of related species. Thus the study would contribute significantly to the knowledge of a specific taxon. Second, an ecological analysis of species within a single taxon, coupled with an examination of taxonomic affinities among species, would provide clearer insights into patterns of adaptive radiation in stream insects. This type of analysis could therefore provide an historical or evolutionary perspective from which to view the present ecological relationships of species. Analysis of a group of unrelated species could not be approached in a similar manner.

Background

The family Ephemerellidae is a ubiquitous group found in most stream systems in north temperate regions (Allen 1980). Eighty species in eight genera are recognized in North America (Table 1). Prior to 1980 when Allen (1980) elevated all subgenera to generic status, all species in North America were considered monogeneric. Thirty two species occur in the western United States and Canada, 24 of which occur in Oregon (Table 2).

Although the taxonomy of this group has been well studied (Edmunds 1959, Allen and Edmunds, 1959, 1961a,b, 1962a,b, 1963a,b, 1965, McCafferty 1977, 1978, Johnson 1978, Allen 1980), until recently there has been little attempt to use this knowledge in describing ecological relationships among species. Sweeney and Vannote (1978, 1981) and Vannote and Sweeney (1980) have related growth rates, size of individuals, geographic distributions, and species packing of eastern taxa to temperature regimes. In the west, Gilpin and Brusven (1970) have characterized food habits and described general habitat preferences for species in Idaho. Hartland-Rowe (1964), Radford and Hartland-Rowe (1971), and Barton (1980) described the life cycles of four species in Alberta. Allan

Table 1. Genera of Ephemerellidae in North America. Number of species in both western and eastern regions are given. Data from Edmunds, Jensen, and Berner (1976).

| Genus | Number of Species | | | |
	West	East	Both	Total
Attenella	3	2	1	4
Caudatella	5	0	0	5
Dannella	0	2	0	2
Drunella	6	9	0	15
Ephemerella	10	19	1	28
Eurylophella	1	11	0	12
Serratella	6	7	0	13
Timpanoga	1	0	0	1
Total	32	50	2	80

Table 2. Species of Ephemerellidae in
          Oregon.

Genus	Species
Attenella	soquele
	margarita
	delantala
Caudatella	heterocaudata
	hystrix
	cascadia
	edmundsi
	jacobi
Drunella	coloradensis
	flavilinea
	doddsi
	pelosa
	grandis
	spinifera
Ephemerella	aurivillii
	infrequens
	inermis
	verruca
Eurylophella	lodi
Serratella	velmae
	michneri
	tibialis
	teresa
Timpanoga	hecuba

(1975a) analyzed the distributional ecology of four species in Colorado. Sheldon and Haick (1981) used a multivariate approach to describe habitat relationships of five species in Montana. Ward and Berner (1980) described the distributions of seven species along an altitudinal gradient in Colorado. Other references include those in which some aspect of the natural history of a genus or species is described, often in qualitative terms (Dodds and Hisaw 1925, Muttkowski and Smith 1929, Fox et al. 1934, Ide 1935, Linduska 1942, Day 1956, Warren et al. 1963, Leonard and Leonard 1962, Allen and Edmunds 1959, 1961a,b, 1962a,b, 1963a,b, 1965, Nelson and Scott 1962, Edmunds et al. 1976, Shapas and Hilsenhoff 1976, Minshall and Minshall 1977, Hamilton and Tarter 1977, Gray and Ward 1979, Andrews and Minshall 1979, Corkum 1980, Reice 1981). In short, no comprehensive study integrating feeding ecology, habitat requirements, and life cycles of different species has been attempted for this important family.

Studies explicitly designed to assess niche relationships among stream invertebrates are rare (see Green 1974 for one example), and until recently the term niche was not often used by stream biologists. For example, in his review Hynes (1970) briefly speculated about the mechanisms separating ecologically similar species, but he did not develop a niche perspective in doing so. The few studies of niche problems in stream invertebrates have usually addressed ecological separation of systematically related species (e.g. Grant and Mackay 1969, Allan 1975a), and these studies did not examine all major niche axes (i.e. space, food, and time). Conversely, studies of taxonomic diversity in stream systems and the mechanisms determining it have been much more popular (e.g. Bell 1969, Allan 1975a, Kerst and Anderson 1975, de March 1976, Friberg et al. 1977, Minshall and Minshall 1977, Hart 1978, Wise and Molles 1979, Khalaf and Tachet 1980, Williams 1980). Most of these studies have been correlation analyses (i.e. what factor or combination of

factors is associated with high or low diversity). These studies
have not often used a niche perspective, although the question of
why so many species or so few species exist in nature is intimately
related to resource requirements and adaptations of specific taxa
(see Mackay and Wiggins 1979 for one of the few treatments of
diversity based on a consideration of the natural history and
adaptations exhibited by species of Trichoptera).

The importance for ecosystem functioning of different
strategies and patterns of resource exploitation in stream
invertebrates has been hardly addressed. Preliminary attempts to
bridge natural history and ecosystem functioning have been presented
by Cummins (1974), Wallace et al. (1977), Anderson and Sedell
(1979), Cummins and Klug (1979), and Wallace and Merritt (1980), but
the general relationships between species and community-level
phenomena and ecosystem-level properties are not at all clear.

If we accept that organisms have evolved in response to
environmental pressures (including other species) and conversely can
influence the environment around them, a niche perspective should be
a useful approach in describing the relationships among individuals,
species, communities, and ecosystems (Smith 1975). A niche
perspective is intimately organism-centered (MacMahon et al. 1981)
and can facilitate interpretation of life history strategies (e.g.
Southwood 1976), strategies and patterns of resource utilization
(e.g. Schoener 1974, Pianka 1980), and community structure and
function (MacMahon et al. 1981) in terms of the evolutionary history
and day-to-day activities of different organisms. Furthermore,
ecosystem structure and function might thus be explained in terms of
the structural attributes of both biological and environmental
components and the dynamic interplay between them. Because of the
hundreds of species constituting most communities and the effort
required to thoroughly analyze the niche relationships for even one
species, analyses of all interrelationships as described above are

certainly not feasible. Nevertheless, analysis of data based on only a few species can help distinguish important patterns and help clarify the nature of relationships defining patterns.

Conceptual Framework and Terminology

Hanson (1958) argued that most scientists perceive and interpret basic observations in terms of previously developed and often dogmatically held beliefs (i.e. generalizations, hypotheses, or theories). Such a condition is an inherent attribute of scientific endeavor and is perhaps healthy for it leads to a continual and critical dialectic within the scientific community. Scientific progress or development is, therefore, a function not only of accumulation of facts but also of changes in scientists's views of the world around them (Kuhn 1962, McIntosh 1980). Because concepts differ among scientists, terminology used to express and convey ideas differ in usage and definition. Also, the way ideas are conceptualized changes with time. Although such change is a necessary element of science, it often leads to dissimilar or inconsistent use of terminology and thus blurring of definition. Because this study deals with, in part, a number of abstract ideas, it is useful to provide 1) a general conceptual framework in which ideas are couched, and 2) working definitions for several commonly used but often ambiguous terms.

Conceptual Framework

Interactions among individuals of different species and their environment ultimately produce community structure and determine ecosystem function. In this view the abiotic and biotic environment affects all aspects of an individual's ecology. The combination of evolved traits and phenotypic responses defines the life history

strategy of each individual. The summation of individual strategies over all individuals in a population (see definition of niche below) describes the spatial and temporal distribution of that population and its functional role. These structural and functional characteristics together describe the niche relationships of each population. The summation of niche relationships over all taxa in a community defines that community's structure and organization. It is important to note that, although this view assumes strong deterministic linkages between the ecology of a population and its environment, both population and community patterns are probabilistic in the sense that neither populations nor communities can perfectly and immediately respond to environments that change unpredictably. This broad conceptual view of community structure and organization is compatable with most contemporary views of community structure, development, and maintenance (see Ricklefs 1979, Southwood 1980).

Terminology

Community, ecosystem, niche, guild, and functional group are terms that ecologists frequently use to convey basic ideas about ecological systems. Precise definition of each has been problematic however, because ecosystems, like other biological systems, have various and changing degrees of dimensionality, heirarchy, and interaction and thus resist rigid definition of component elements (Grobstein 1969). Working definitions must necessarily be employed and will in part depend on the system being studied and the goals of the research. I will use the following definition of terms in this thesis.

Ecosystem

The definition of ecosystem offered by MacMahon et al. (1978) is both parsimonious and compatible with the conceptual framework provided here. "An ecosystem is a set of organisms and inanimate entities connected by exchanges of matter and energy." MacMahon et al. leave choice of ecosystem boundaries to the investigator. Because this study is mainly concerned with population- and community-level attributes, ecosystem boundaries need not be specified in great detail. In general, however, I define the wetted perimeter of a stream as the ecosystem boundary in this study.

Community

The term community has been defined in so many ways that Ricklefs (1979) feels the term is almost meaningless. Briefly, community has been used to designate an inclusive, but not necessarily interacting, group of organisms (i.e. a fungal, bird, or fish community). It also has been defined as the entire set of biota found within an ecosystem (e.g. Odum 1971). MacMahon et al. (1978) and Ricklefs (1979) stress that the presence of interactions among species best defines a community. Unfortunately, a natural complex of all interacting organisms likely will never be thoroughly investigated. Thus, limiting the term in this way seems overly restrictive in that practical use of the term would be precluded.

In this study I chose a more flexible definition that in concept follows MacMahon et al. and Ricklefs but in practice specifies a more limited assemblage of organisms. For example, species in the family Ephemerellidae often are conspicuous members of stream communities. They represent, however, only a subset of insect taxa found within the total community. I assume that analysis of their ecological relationships can provide insights on how the entire

insect component of stream communities is structured and organized and also indicate some interactions that are important between insects in streams and the rest of the stream ecosystem. Hence the term community will be used when referring to community-level concepts, even though I worked with only a small portion of the entire community.

Structure and organization are community-level concepts. I will use the term structure to refer to the number of species, their relative abundances, and their patterns of spatial and temporal resource exploitation. The term organization refers to the causal mechanisms (interactions and evolutionary history) that influence structure.

Niche

A voluminous literature exists describing historical changes in use of the term niche (e.g. see Haefner 1980), and recent papers bears witness that such changes are still occurring. It is not my purpose here to review this literature and defend any one definition of the term. Any concept of niche is dependent on concurrently held concepts of community and of what factors are important in structuring and organizing communities. A reasonable definition of niche must satisfy the specific goals of a particular research endeavor while remaining heuristically useful in a more general conceptual sense. Rigor of definition and application must be balanced against utility.

In this study I chose to adopt a flexible definition of niche that is minimally constrained by dependence on any underlying concept of community. Although niche can be approached as an individual- , population- , or species-level attribute (cf. MacMahon et al. 1981), I use the concept as a population-level property to describe both structural and functional relationships of a

population. The term population is used here to specify a local or Mendelian population of interbreeding individuals sensu Mayr (1970) and Dobzhansky et al. (1977). Fundamental and realized niches may be distinguished in the sense of Hutchinson (1957). The fundamental niche is taken to represent all possible patterns of resource exploitation given the genetic makeup of the population. The realized niche of a population is defined by interactions of individuals with the physical and biological environment over ontogenetic and ecological time. These definitions differ from those of Hutchinson (1957, 1978) only in that the importance of competition in influencing the realized niche receives no greater emphasis than other environmental factors.

Guild and Functional Group

A concept allied to that of niche is guild. Root (1967) defined this term as a group of species that exploit the same resource in a similar manner, that is, they have similar niches. MacMahon et al. (1981) also use the term guild to define a group of organisms that use the same resource but state that the resource need not be used in the same manner by different species. In the usage of Root, two species of aquatic insects that both consume leaf litter by shredding would be members of the same guild. Following the definition of MacMahon et al., a species that uses leaf litter for case material but not food is also a member of that guild. Guild as used by Root is closely related to the concept of adaptive syndrome. The term adaptive syndrome was used by Root (1975) to specify the relatively few ways organisms have evolved to exploit resources. The concept is important, because if taxa have evolved in this manner communities ought to have a well defined substructure comprised of generally discrete guilds. Because I am interested in whether such substructure exists in stream communities, I use guild as defined by Root.

It should be noted that Root (1967), MacMahon et al. (1981), and Jaksic (1981) contend that guilds transcend taxonomic affinities. It is still informative, however, to examine guild relationships among related taxa in order to consider whether the process of adaptive radiation leads to evolutionary divergence toward ecologically isolated guilds.

I agree with MacMahon et al. (1981) in distinguishing the terms guild and functional group. Functional group refers to a group of species whose activity results in a defined ecosystem function (e.g. conversion of coarse litter to fine litter, elaboration of organic carbon from CO_2, etc.). It is an ecosystem term and describes a process. Guild as defined above is a community-level term and stresses interspecific similarities among species and differences among groups of species in various ecological traits and has meaning outside of an ecosystem context.

Other Terms

It is difficult to avoid use of some rather cumbersome terms (more properly, phrases) when referring to certain classes and units that describe variables or entities of interest. When possible, I will use acronyms and abbreviations after first defining them. Some of these terms and their definitions are give below. Detritus is defined as dead organic matter and its associated microbial community. Coarse particulate organic matter (CPOM) is defined as detritus greater than 1 mm in diameter, fine particulate organic matter (FPOM) as detritus between 0.05 mm and 1 mm in diameter, and very fine particulate organic matter (VFPOM) as detritus less than 0.05 mm in diameter. Ash-free dry matter (AFDM) is the organic portion of a sample determined by combustion at 550°C in a muffle furnace. I use the German word aufwuchs to refer to organic films on surfaces rather than the word periphyton. Other terms are defined in the text when first encountered.

STUDY SITES AND ENVIRONMENTAL CONTRASTS

Description of Sites

I obtained data by sampling different streams in Oregon and by using relevant published and unpublished data whenever possible. All field sites were located within the McKenzie River Basin of western Oregon (Fig. 1).

Six sites (similar in watershed area, order (3), minimum discharge, and elevation (Table 3)) were studied intensively for over a year. They differed significantly in type and extent of riparian vegetation bordering the streams and in stream gradient. I chose these sites to maximize differences among sites in availability of different food types and some habitat characteristics while minimizing differences in most other parameters. Although I attempted to select streams that differed minimally in temperature regimes, minor to moderate differences in temperature existed among sites (see Results).

Of these six sites (hereafter referred to as the main study sites), one drained an old-growth coniferous watershed (Mack Creek = MAOG), another traversed an experimental clear-cut lying below the old-growth section of Mack Creek (MACC), and a third, North Fork Wycoff Creek (WYCO), was surrounded by a red alder (Alnus rubra) riparian canopy. These three stream reaches were of similar gradient (10%). Three other stream reaches were of lower gradient (1%). Mill Creek (MILL) drained a largely old-growth coniferous watershed, Fawn Creek (FAWN) drained a clear-cut watershed, and Cougar Creek (COUG) was bordered by alder. These six streams are described in detail in Murphy et al. (1981). Published or unpublished data from streams in Alberta, Washington, and Utah were compared with data that I collected. Inclusion of these data allowed me to analyze life-history and growth characteristics of species
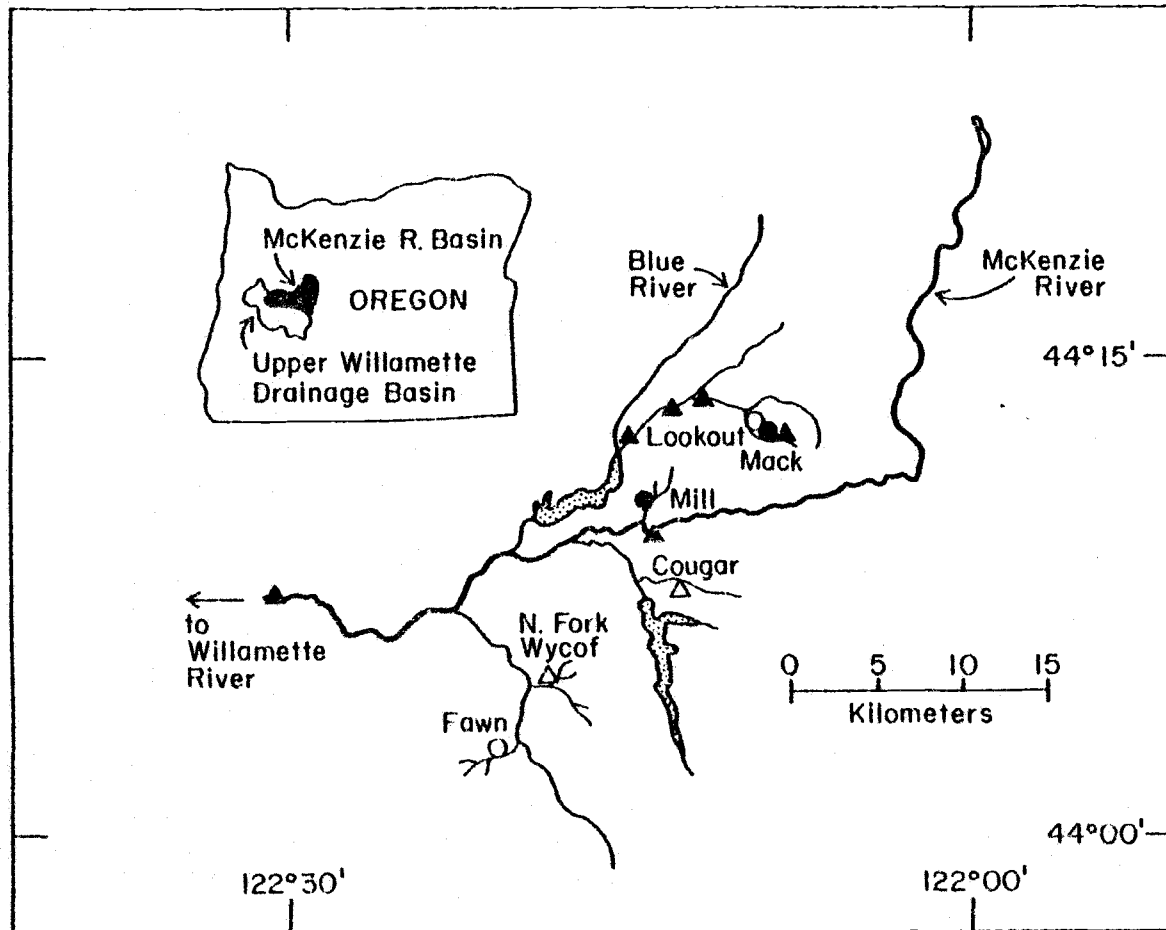
Figure 1. Map of the study area in relation to the upper Willamette
drainage basin and the state of Oregon. Solid triangles
show location of sites along the longitudinal gradient.
Other symbols show location of the six main study sites.

Table 3. Physical characteristics of the six main study sites. All sites are third order.

Name of Stream	Mack	Mack	N.F. Wycoff	Mill	Fawn	Cougar
Abbreviation	MAOG	MACC	WYCO	MILL	FAWN	COUG
Riparian Age (yr)*	>450	14	35	>450	7	35
Canopy type Dominant Riparian Vegetation	coniferous Douglas-fir & Hemlock	open Herbs and Shrubs	deciduous Red Alder	coniferous Douglas-fir & Hemlock	open Herbs and Shrubs	decidious Red Alder
Approximate Summer Shading (%)	75	0	85	75	0	85
Elevation (m)	760	730	500	360	500	500
Watershed Area (Km^2)	5.4	5.5	4.0	6.4	6.8	8.2
Minimum Discharge (m^3/s)	0.07	0.07	0.03	0.02	0.06	0.09
Aspect	N	N	SW	S	E	W
Approximate Gradient (%)	10	10	10	1	1	1

*at the time of study

found in streams that varied in latitude, photoperiod, and temperature. Figure 2 shows the location of sites where data were originally collected.

Animals also were collected at eight sites along a longitudinal gradient extending from the headwaters of Mack Creek to the McKenzie River at Ben and Kay Dorris State Park (Fig. 1). Data on physical characteristics of these sites were measured directly or taken from records of the Oregon State Water Resources Board (1961) and United States Geological Survey (1976), and are given in Table 4.

Methods

I sampled a number of environmental variables at the six main sites at intervals over the study period (Table 5). Stream temperature was monitored continuously on Mack Creek (old-growth section) by personnel of the H.J. Andrews Experimental Ecological Reserve. I recorded temperatures with Ryan[©] thermographs (model H 45) at four other sites: MACC, WYCO, COUG, and FAWN. Additional temperature readings were taken with maximum-minimum thermometers at all six sites. Temperature data for streams other than MAOG were incomplete. For those sites and dates without recorded data, temperatures were estimated with predictive equations that related mean daily temperature of MAOG to mean daily temperature at other sites. By using both recorded temperatures and estimated temperatures, I was able to describe the temperature regimes of all main sites with the exception of Mill Creek. Graphs depicting temperature relationships between MAOG and other streams are given in Appendix A along with the linear regression equations used to predict missing data.

A major physical parameter that varied among sites was substrate particle size. Three core samples in areas of rapid current (riffles) and three in areas of little or no current (pools)
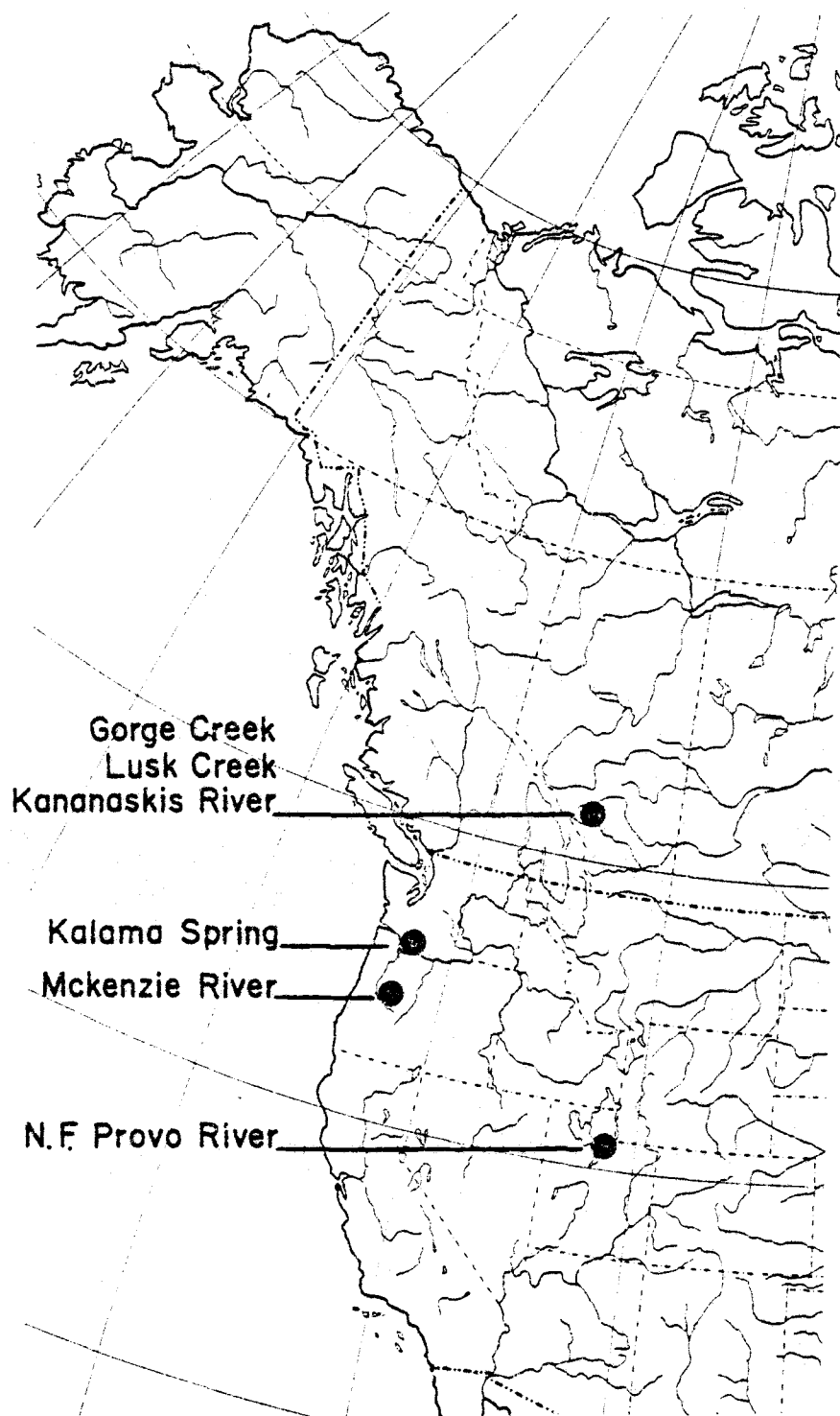
Figure 2. Location of the McKenzie River in relation to other studies.

Table 4. Physical characteristics of sites on the longitudinal gradient from headwaters to the McKenzie River.

Name of Stream	Mack	Mack	Mack	Lookout	Lookout	Lookout	McKenzie	McKenzie
Sampling Station	I	II	III	IV	V	VI	VII	VIII
Order	2	3	4	4	5	5	7	7
Elevation (m)	915	760	549	549	435	420	365	260
Gradient (%)	45	10	5	5	3	3	0.6	0.2
Bank-full width (m)	3	12	20	20	24	18	40	50-60
Dominant Substrates*	BR,M	B,C	B,C	B,C,G	B,C,G,S	G,S	C,G,S,M	G,S
Canopy	coniferous	coniferous	ope	open	open	open	open	open

* BR = bedrock, B = boulder, C = cobble, G = gravel, S = sand, M = moss.

Table 5. Sampling schedule for main environmental variables at the six main sites over the study period.

	Temp	Sediment	Aufwuchs AFDM (per m^2)	Aufwuchs Chlorophyll (per m^2)	Aufwuchs Chlorophyll (per g AFDM)	Detritus AFDM (per m^2)	Detritus Chlorophyll	Respiration
1978								
JUN	X			X	X			X
JUL	X		X	X	X		X	X
AUG	X	X	X	X	X	X	X	X
SEP	X		X	X	X		X	X
OCT	X		X	X	X		X	X
NOV	X			X			X	X
DEC	X		X	X	X		X	
1979								
JAN	X							
FEB	X							
MAR	X			X			X	
APR	X							
MAY	X		X	X	X		X	
JUN	X			X			X	

were taken at each site during August of 1978. A metal cylinder (0.25 m^2) was pushed into the stream bed and approximately 12 liters of sediment removed. Particles were sieved into five size classes: 0.05 - 1 mm, 1 - 16 mm, 16 - 50 mm, 50 - 250 mm and >250 mm. Organic matter associated with each size fraction and sample was decanted from the larger sized particles and removed by burning (550 C for 24 h) from the smallest sized particles. When samples were burned to remove organics, they were first dried and weighed so data on standing crops of organic matter were obtained. Decanted particles larger than 1 mm were assumed to be 100 percent organic matter.

Standing crops of leaves also were estimated during October and November of 1978. These data were collected by removing all large pieces of leaf material (approximately 1 cm^2) from randomly placed 0.05 m^2 quadrants. Three samples from both riffle and pool areas were taken from each stream. Data from the two months were lumped prior to analysis.

At irregular intervals over the study period, aufwuchs and chlorophyll standing crops on cobble substrates (about 10 cm in diameter) were determined, and respiration rate and chlorophyll associated with interstitial organic matter were estimated. Quantity of aufwuchs was estimated by removing attached matter from the upper half of each stone with a stiff wire brush. This method probably underestimated absolute quantities of chlorophyll (Karlstrom 1978) but provided comparable data among sites. By assuming a rectangular shape (A = 2((w x 1) + (1 x d) + (d x w))), I calculated the area of each cobble This area was divided by two to give an approximation of the area of cobble exposed to light. The amount of organic matter removed was measured by drying, weighing, and ashing each sample. Six cobbles, three from riffles and three from pools were sampled each date. On the same day, six other cobbles were randomly selected and aufwuchs removed for analysis of chlorophyll associated with aufwuchs material.

Chlorophyll associated with both aufwuchs and interstitial sediments was estimated by extracting pigments at 4°C in 100% acetone made basic with $MgCO_3$ (Strickland and Parsons 1972). Water in each sample reduced the acetone concentration to approximately 90%. Pigment concentrations were then estimated by spectrophotometric analysis. For reasons discussed below, chlorophyll a and pheophytin a were summed and data presented as "chlorophyll pigment." Chlorophyll analysis on interstitial sediments was performed only on material from quiet water (pools and alcoves), because sufficient material from erosional areas (riffles) could not be collected. Material <0.05 mm was obtained by allowing fine sediment and organic material to settle in a large bucket for 1 hr after particles >0.05 mm had been removed by sieving. Water was then decanted and the concentrated fine material placed in a bottle and refrigerated until analyses were performed.

Microbial respiration associated with organic detritus was measured from June to November 1978. Sediment was randomly scooped from pools and alcoves from each site and sieved into two fractions: <0.05 mm and 0.05 - 1.0 mm. The <0.05 mm fraction was collected as described above for chlorophyll samples. I measured respiration on both fractions in a Gilson Respirometer. Temperatures were adjusted to approximate ambient temperature for each sampling period. Data are reported as $1 \ O_2 \cdot h^{-1} \cdot g^{-1}$ AFDM.

Results and Interpretation

All streams that I sampled showed seasonal variation in temperature typical for Cascade Range streams (Fig. 3). Stream temperatures were at a minimum in January and a maximum in August. Fawn Creek was consistently warmer than the other streams (Fig. 3 and Table 6). The open canopy and lower elevation of Fawn Creek undoubtedly were responsible for its higher temperature. The other
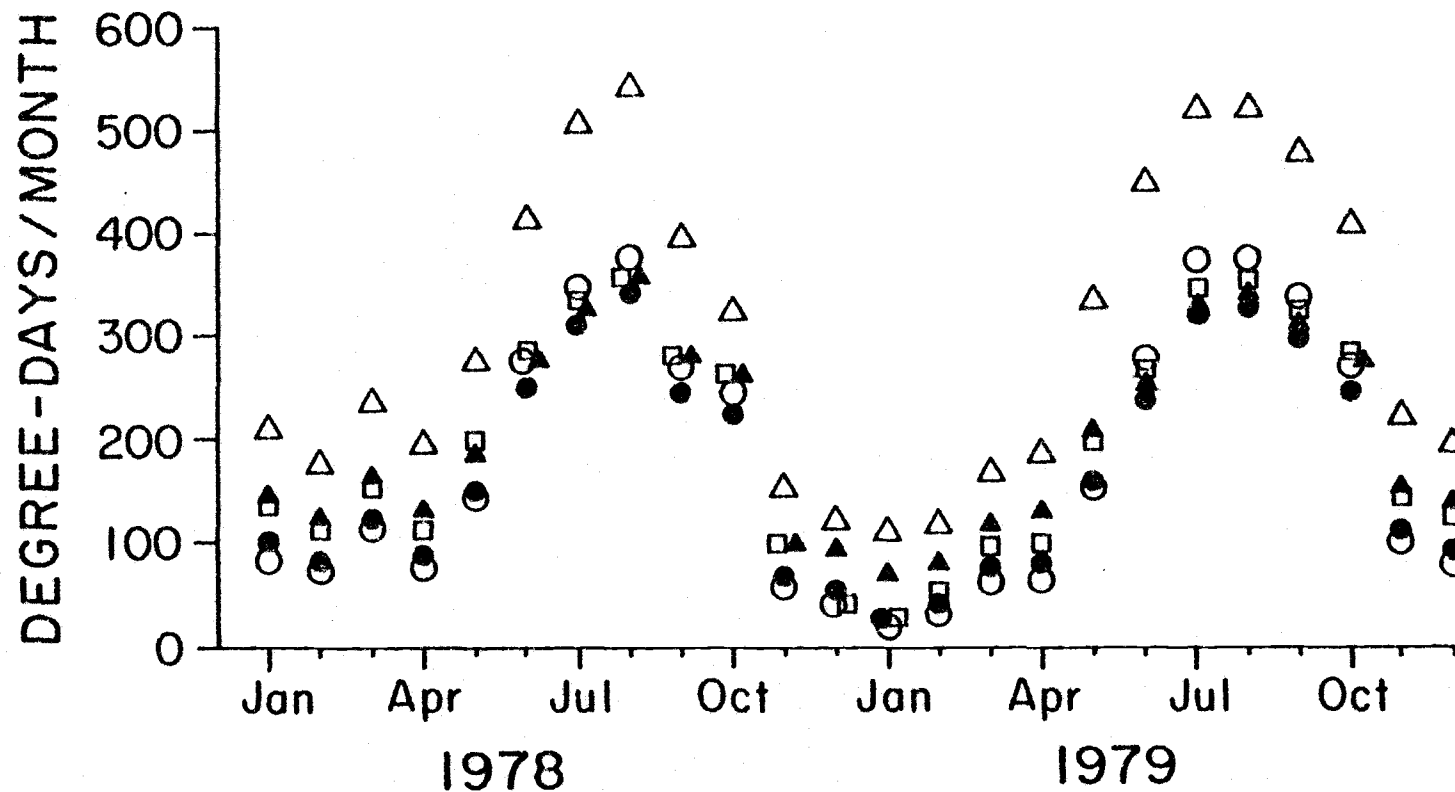
Figure 3. Monthly accumulated degree-days at the main study sites. Symbols represent FAWN (△), MAOG (●), MACC (○), WYCO (□), and COUG (▲).

Table 6. Annual accumulated degree-days for MAOG,
MACC, WYCO, COUG, and FAWN for 1978 and
1979 and degree-days other for sites
compared with Oregon streams.

	Degree-days		
Site	1978	1979	MEAN
MAOG	2036	2007	2022
MACC	2108	2136	2122
WYCO	2362	2290	2326
COUG	2452	2416	2434
FAWN	3552	3718	3635
Gorge CK*			1250
Lusk CK†			999
Kanaskis R.‡			1170
Kalama Spring§			2190
Tributary N.F.# Provo R.			1882

* Data from Hartland-Rowe (1964)
† Data from Radford (1970) and R. Mutch (unpublished data)
‡ Data from Radford (1970)
§ Data from Thut (1967)
# Data from B. Hanson (unpublished data)

streams were similar in temperature regimes and differed in total accumulated degree-days by a maximum of 20 percent. The main seasonal differences among these streams were a tendency for shaded streams to be warmer during the winter months and cooler in summer than MACC.

Stream systems from which other temperature data were available were generally cooler than those from the Oregon Cascades (Table 6). Yearly accumulated temperature varied from approximately 1000 to 2200 degree-days. Seasonal patterns are not shown, but Kalama Spring (Washington) has a constant temperature of 6°C. The Kananaskis River (Alberta) is frozen from about October through April after which it heats up quickly and accrues more heat on an annual basis than Lusk Creek, a tributary that does not freeze. Gorge Creek (Alberta) also is frozen for six months (October - April) and accumulates approximately the same amount of heat as the Kanananskis River. Mean daily temperatures of the tributary of the N. F. Provo River (Utah) are lowest from November to February (ca. 2°C) and highest in July and August (ca. 9°C). Total annual degree-days were slightly less than recorded in the Oregon streams.

Among the main study sites, percent composition of particle sizes of mineral substrates differed between high- and low-gradient sites (Fig. 4). High-gradient streams were dominated by boulders (>250 mm) and cobbles (50 - 250 mm). Low-gradient streams had higher percentages of sand (<1 mm) and gravel (1 - 16 mm). No consistent differences in substrate composition were observed among streams with different canopies.

Data on food sources were analyzed by two-way ANOVA. For this analysis, seasonal samples, when taken, were treated as replicates. If samples from one time period are not independent of samples from other periods, analysis of variance is not valid and the F statistic may not provide an unbiased test of significant differences among sites or lack thereof. The number of samples on which means were
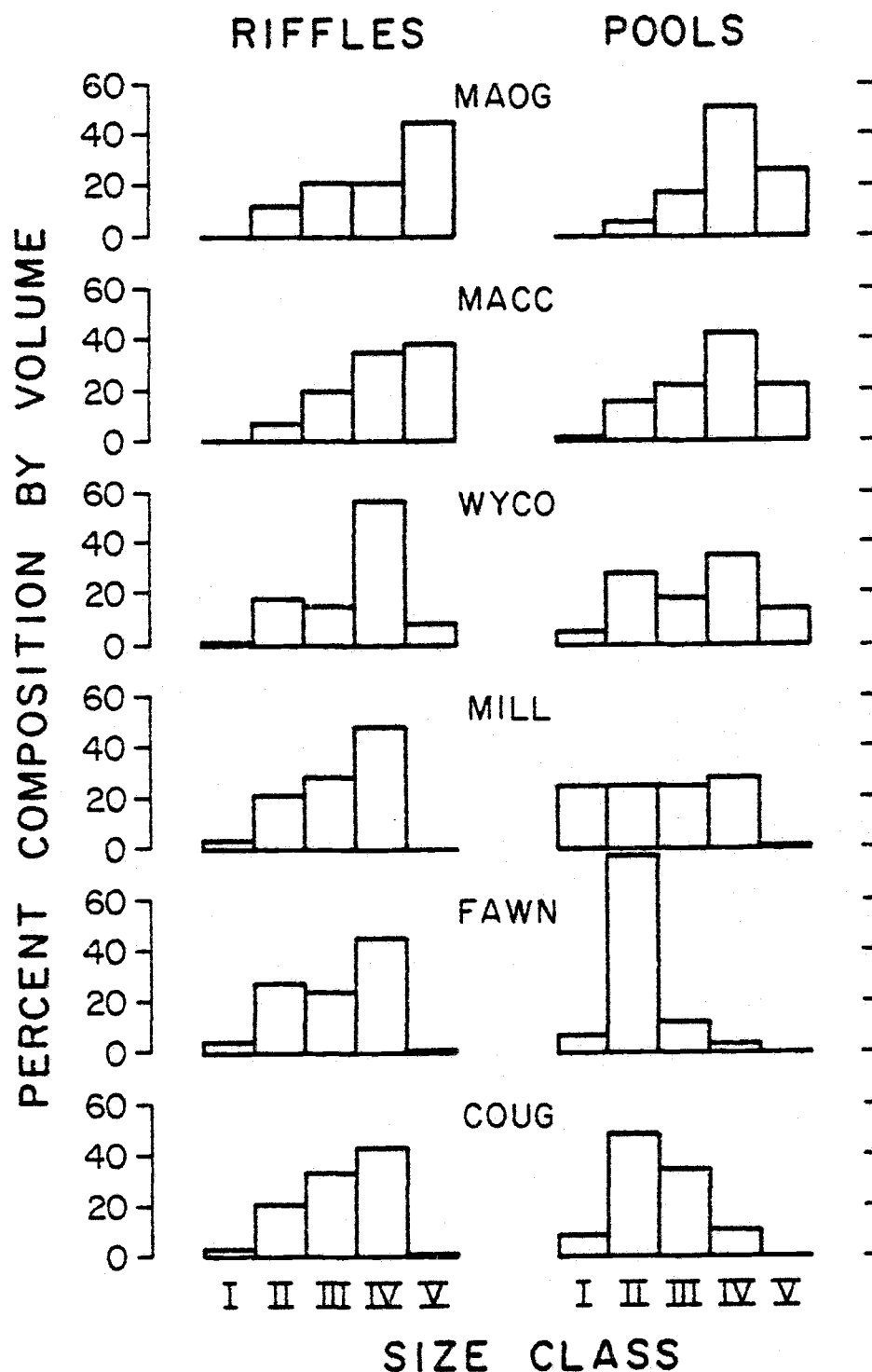
Figure 4. Substrate composition by size at the six main study sites. Size classes are I (< 1 mm), II (1-16 mm), III (16-50 mm), IV (50-250 mm), and V (> 250 mm).

calculated was always rather small (<9), and tests of independence of errors were usually not possible. For this analysis I have assumed that observations over time were independent of one another. Data on which analyses were based are given in Appendix B.

Both gradient and canopy affect food sources (Table 7). Low-gradient streams had larger quantities of detritus than did high-gradient streams. Among streams with different types of canopies, deciduous second-growth sites had more leaf material, whereas open sections (clear-cuts) had higher quantities of aufwuchs and higher quality detritus as measured by respiration rate and chlorophyll. Among streams, mean levels of chlorophyll pigment associated with VFPOM were correlated with respiration rates of both FPOM ($r = 0.95$, $P <0.01$) and VFPOM ($r = 0.81$, $P <0.05$). No differences existed among sites with respect to chlorophyll content of the aufwuchs.

The chlorophyll data should be considered with caution, because high levels of pheophytin a were recorded, occasionally close to 100% of measured pigment. It was not clear why such high levels were observed. From an invertebrate consumer's view, chlorophyll a may be no better a measure of food quality than pheophytin a (i.e. is live algae better than dead and decaying algae?). I have therefore reported chlorophyll pigment as the sum of chlorophyll a and pheophytin a as an index of food quality. These data should not be construed to represent quantitative measures of chlorophyll or algal standing crops, but unless results of the analyses completely misrepresented differences in algal production among sites, they should be sufficient to indicate real qualitative differences in food between sites. Rank differences among sites in chlorophyll levels paralleled those observed between open and shaded streams in other studies (cf. Lyford and Gregory 1975 and Gregory 1980 with data in Appendix B). Also, chlorophyll levels probably were the result of autotrophic production rather than terrestrial inputs,

Table 7. Results of two-way ANOVA for effects of gradient and canopy and quality of food sources. N for leaves and total detritus = six per site. N for quality measures and aufwuchs quantity given in Table 3 (months = replicates). Respiration (Resp.) = ul O_2/h. Symbols for F-tests are: * = P <0.05, ** = P <0.01, *** = P <0.001, NS = not significant. HG = high gradient, LG = low gradient, OG = old growth, CC = clearcut, SG = second growth. No significant interactions were observed.

Habitat		Gradient			Canopy			
		HG	LG	P	OG	CC	SG	P
LEAVES (g AFDM/m^2)								
Riffles		0.8	0.9	NS	0.2	0.1	2.4	**
Pools		6.2	1.9	NS	1.3	0.2	10.6	*
TOTAL DETRITUS (g AFDM/m^2)								
Riffles	Total	36.8	91.4	*	61.2	64.3	66.7	NS
	VFPOM	6.2	14.5	*	10.3	6.9	13.9	NS
	FPOM	15.6	54.4	**	34.8	36.8	33.4	NS
	CPOM	14.9	22.5	NS	16.1	20.6	19.4	NS
Pools	Total	187.3	456.6	*	410.7	211.1	344.1	NS
	VFPOM	20.4	53.6	**	40.3	24.3	46.4	NS
	FPOM	51.2	206.0	**	191.4	80.4	114.0	NS
	CPOM	115.6	197.0	NS	179.0	106.3	183.7	NS
AUFWUCHS								
Riffles	g AFDM/m^2	1.3	1.7	NS	1.3	2.0	1.3	NS
	ug Pigment/m^2	1600	1970	NS	1970	2080	1300	NS
	mg Algae/m^2	99	132	NS	106	156	83	NS
Pools	g AFDM/m^2	1.8	2.3	NS	1.8	3.2	1.3	*
	ug Pigment/m^2	1860	2470	NS	2310	2910	1280	NS
	mg Algae/m^2	125	157	NS	125	218	79	NS
DETRITUS QUALITY								
Pools	ug Pigment/g VFPOM	268	146	NS	93	294	136	**
	mg Algae/g VFPOM	19	10	NS	5	30	9	**
	Resp./g VFPOM	250	194	NS	117	376	172	***
	Resp./g FPOM	185	136	NS	86	269	127	**
AUFWUCHS QUALITY								
Combined	ug Pigment/g AFDM	1401	1141	NS	1504	1246	1054	NS
	mg Algae/g AFDM	83	74	NS	81	93	68	NS

because Gorman and Sanger (1975) noted that terrestrial litter had low chlorophyll levels compared with either living vegetation or lake sediments.

GROWTH AND LIFE CYCLES

Methods

Animals were collected approximately monthly at each of the six main sites. Data from these collections were used to describe life cycles and examine growth rates of species occurring in different streams. Animals were collected with a standard kicknet as they were dislodged from stones, vegetation, and other substrates. Most habitats were sampled in each stream (riffles, pools, alcoves, bedrock, etc.). The mesh size of the net was 0.5 mm. Animals collected during the study period by other researchers also were included in data sets when appropriate. Samples were preserved in 95% ethanol immediately after collection. Dilution by water in the samples brought ethanol concentrations down to about 75 - 85 percent.

Larvae were measured in the laboratory with a dissecting stereo microscope at 15 power magnification. Lengths (tip of head to end of abdomen) were measured to the nearest 0.5 mm. Head-capsule widths (widest point) were measured to the nearest 0.03 mm with an ocular micrometer. Data for head widths or in some cases lengths were transformed to dry mass (mg) with equations describing head width (or length):dry mass relationships. Equations were of the form $mg = aX^b$, where a and b are constants and X is either body length or head-capsule width. For D. coloradensis, doddsi, and spinifera I used the following values of the constants a and b: for length measurements, $a = 1.85 \times 10^{-3}$, $b = 3.57$; for head-capsule measurements, $a = 0.434$, $b = 3.62$. For all other species; $a = 1.02 \times 10^{-3}$, $b = 3.58$ for length; $a = 0.310$, $b = 4.02$ for head-capsule width. These values were taken from Cummins (unpublished data) for robust and slender Ephemerellidae respectively. I converted data on length or head-capsule width from other studies to dry mass to make comparisons with my sites

possible. Estimates of mass in these cases are less accurate than my data because mean lengths or head widths were sometimes estimated from graphed data.

Field data were analyzed by simple inspection of graphed data and by comparison of linear regression lines fitted to data. The relationship between $\log_e$ biomass and time was usually linear over much of the growth curve. Others (Willoughby and Sutcliffe 1976, Brittain 1976, Sutcliffe et al. 1981, Humpesch 1979, 1981) have noted that growth in aquatic invertebrates is often either exponential or logistic. For regression analysis, data were fitted to the equation

$$W_t = W_0 e^{kt}$$

where W_0 is the mean dry mass in mg of an individual at time zero, W_t is the mean mass at time t, and k is the instantaneous rate of growth. Growth was expressed as specific growth rate, G, where $G = 100k$. Means calculated from less than three individuals were graphed but were excluded from regression analyses. Also, data points at either end of the growth curve were excluded if they were obviously not linear with respect to the mid-portion of the growth curve. The last point on the curve was often excluded, because mean individual size declines as individuals emerge as adults (e.g. Sweeney and Vannote 1978). If growth curves showed sections that differed in their slope or if growth was discontinuous, separate regression lines were fitted to the different sections. Generally, an arbitrary date was picked starting at which all lines (different streams) appeared to be linear. Points prior to this date were not included when calculating regression statistics. Some subjective bias is introduced by this treatment but should not compromise comparisons because all data sets were treated similarly.

Biomass data were fitted to three regression models whenever possible. I used days, degree-days, and accumulative hours of daylight as independent variables. Equality of slopes (G) was tested by methods given in Sokal and Rohlf (1981). Values of r^2

for each regression line were also calculated. These values were used to compare the amount of variation in growth explained by the different models. Tabular data from which regression analyses were performed are given in Appendices C (mean individual biomass), D (degree-days), and E (hours of daylight).

Data used in the regression analyses were mean individual size of each species observed on different dates. Growth rates derived from such analyses are valid only if mean size adequately represents the response of a single individual. Davenport (1934) has shown that care must be taken in interpreting such data, especially when significant variation in timing of growth exists among individuals within a population (e.g. adolescent growth in Homo sapiens). Brink (1949) and Thorup (1973) have further cautioned against using population growth curves to calculate rates because of the possible significant influence of differential immigration and emigration by animals of different size. Furthermore, if extended hatching of eggs occurs, rates based on the population mean will be less than true individual rates. For the species of Ephemerellidae examined, these problems appear to be minimal. Duration of hatching is relatively short for this family (usually <1 month, see Sweeney and Vannote 1981), and I observed immigration by drift to be minimal for the species studied. For some taxa (e.g. Heptageniidae and Baetidae), these problems would present significant sources of error, because hatching is often extended (both families) or individuals are active drifters (Baetidae).

The regression statistics provided data from which to evaluate effects of temperature and photoperiod on growth rates and initiation of growth. Coefficients of determination (r^2) and coefficients of variation (CV) assess the amount of variation associated with different independent variables. A high value of r^2 within a site indicates that significant variation in mean size is explained by a certain variable. A high r^2 value for pooled

data (sites combined) indicates that the independent variable used explained a substantial portion of the variation observed among sites. Similarly, a low coefficient of variation (CV) for a statistic compared among sites implies that calculation of that statistic based on a particular independent variable explained more variation among streams than did a variable with a high CV. For example, if growth rate was linearly related to temperature, then growth rates when calculated on a degree-day basis should be more similar than when calculated on another basis (e.g. photoperiod). Similarly, for pooled data values of r^2 should be relatively high wherever CV was low. Effect of food quality also was examined in a laboratory experiment. Individuals of Ephemerella infrequens were separated into two classes: 4.0-4.5 mm and 6-7 mm in length. Seventeen individuals of each size class were placed in 2000 ml of aerated stream water.

Flasks were partially submerged in a water bath to regulate temperatures. Temperature within each flask varied with temperature of the stream source used to supply the water bath.

To each flask was added a layer of gravel and one of five food treatments. Food types were Tetramin® fish food flakes (>46% crude protein, 5% crude fat, <8% crude fiber), algal covered stones (mainly Nitzschia, Melosira and Synedra), conditioned whole alder leaves, ground and conditioned alder leaves (<0.5 mm), and ground and conditioned alder wood (<0.5 mm). Leaf and wood material was conditioned by dripping stream water into separate containers holding these food sources. Food and water in each Erlenmeyer flask were changed weekly. Food was always added in excess quantity so that the weekly portion was never completely consumed. The experiment was terminated after 56 days for small larvae, and 51 days for larger larvae. Each individual was dried at 50°C for 24 h and then weighed on a Cahn® electrobalance to the nearest 0.001 mg.

Data on life cycles and growth in the field are reported on a species by species basis. First, general life cycles for each species are described and then examined for growth relationships. Results of the laboratory growth experiments appear at the end of this section.

Results

Ephemerella infrequens/inermis

Life cycle data for E. infrequens were available from all six streams that I studied. Additional data for a species identified as E. inermis were published by Hartland-Rowe in 1964. Data for a species identified as E. inermis from Kalama Spring in southwest Washington also were available (Thut 1967). E. infrequens and inermis are sister species and are difficult to distinguish with confidence at the larval stage (see Johnson 1978). E. infrequens tends to occur at higher elevations than E. inermis, but populations of the two species can occur in similar streams (elevation, gradient, latitude). Because differences between the two species may reflect clinal variation as much as distinct genotypic difference they are treated as a single taxon.

E. infrequens showed pronounced variation among streams in mean size of individuals for a specific date (Fig. 5). Individuals of E. infrequens began growth in mid- to late summer (July-September) and grew steadily through the rest of the year. The last individuals were observed in early summer (June) of the next year. From these data the period of larval growth is estimated at approximately ten months.

The specific growth rate (G) of E. infrequens varied significantly among streams both in terms of days, degree-days, and hours of daylight (Table 8, see Appendix F for ANOVA tables). The

Figure 5. Mean size of individuals of E. infrequens of different times and sites. Symbols are MAOG (●), MACC (○), FAWN (△), MILL (▲), WYCO (■), COUG (□), Kalama (◖), and Gorge (◑). See Appendix C for data on which growth rates were calculated.

Table 8. Regression statistics for the relationships between mean individual biomass (mg) of E. infrequens and the independent variables days, degree-days, and hours of daylight. Data are W_i = initial size at time zero as estimated from regression equation, and G = specific growth rate. Coefficient of variation among sites for G expressed as a percentage.

Site	n	DAYS			DEGREE-DAYS			HOURS OF DAYLIGHT		
		W_i	G	r^2	W_i	G	r^2	W_i	G	r^2
MAOG	7	0.07	1.62	0.92	0.11	0.57	0.80	0.08	0.13	0.90
MACC	6	0.10	1.18	0.78	0.14	0.48	0.80	0.11	0.10	0.80
WYCO	4	0.41	1.50	0.96	0.52	0.60	0.93	0.44	0.13	0.98
FAWN	3	0.04	2.77	0.98	0.09	0.43	0.98	0.07	0.21	0.97
COUG	3	0.02	2.89	0.98	0.43	0.62	0.99	0.03	0.22	0.99
KALA	6	0.14	2.48	0.99	0.15	0.40	0.99	0.17	0.20	0.97
GORGE	7	0.05	1.37	0.89	0.21	0.23	0.77	0.07	0.09	0.89
Pooled	36	0.17	1.06	0.33	0.21	0.32	0.58	0.20	0.08	0.32
MILL*	5	0.14	1.64	0.81	--	--	--	0.15	0.14	0.77

Ho: G's are equal	$F_{6,22}$ = 7.49 $P < 0.001$	$F_{6,22}$ = 6.76 $P < 0.001$	$F_{6,22}$ = 8.26 $P < 0.001$

Coefficient of variation among sites		36			72	29		101	36	

* Data for Mill not included in comparisons because temperature data were lacking.

population from the clear-cut section of Mack Creek had the lowest
value of G (days), whereas the alder shaded site on Cougar Creek had
the highest growth rate. Inspection of these data suggested few
obvious reasons for the observed variation in growth. Values varied
from low to high among both shaded (MAOG, COUG, MILL) and open
streams (MACC, FAWN, KALA). Correlation between G (days) and mean
amount of chlorophyll in VFPOM was not significant (r = -0.36, n =
6). Correlations between G and either mean respiration rate of FPOM
(r = -0.19) or mean quantity of aufwuchs (r = 0.58) also were not
significant.

Calculations of G based on degree-days reduced variation among
streams by 20 percent, but rates still differed significantly among
streams (Table 8). Growth rate based on daylight showed
relationships among sites and variation similar to that observed for
days.

Growth rates (days) appeared to be a simple linear function of
temperature (Fig. 6). The linear correlation between G (days) and
degree-days for data listed in Table 8 was significant (P < 0.05, n
= 7, r^2 =0.65). In Figure 6, I have also plotted growth rate
estimated from samples taken in January and April from a California
stream (G = 2.24 for days, 0.41 for degree-days; accumulated
degree-days = 527). Including this datum in the analysis also
resulted in a significant correlation (P < 0.05, n = 8, r^2 =
0.66).

The relationship between G (degree-days) and degree-days was
not linear (Fig. 6). The relationship may be curvilinear, although
too few data are available at present to evaluate this possibility
with confidence.

Variation among growth rates based on days and daylength was
much higher than variation among rates based on degree-days (Table
8, cf. CV and pooled r^2), although significant differences existed
among values of G based on degree-days. The variation in growth
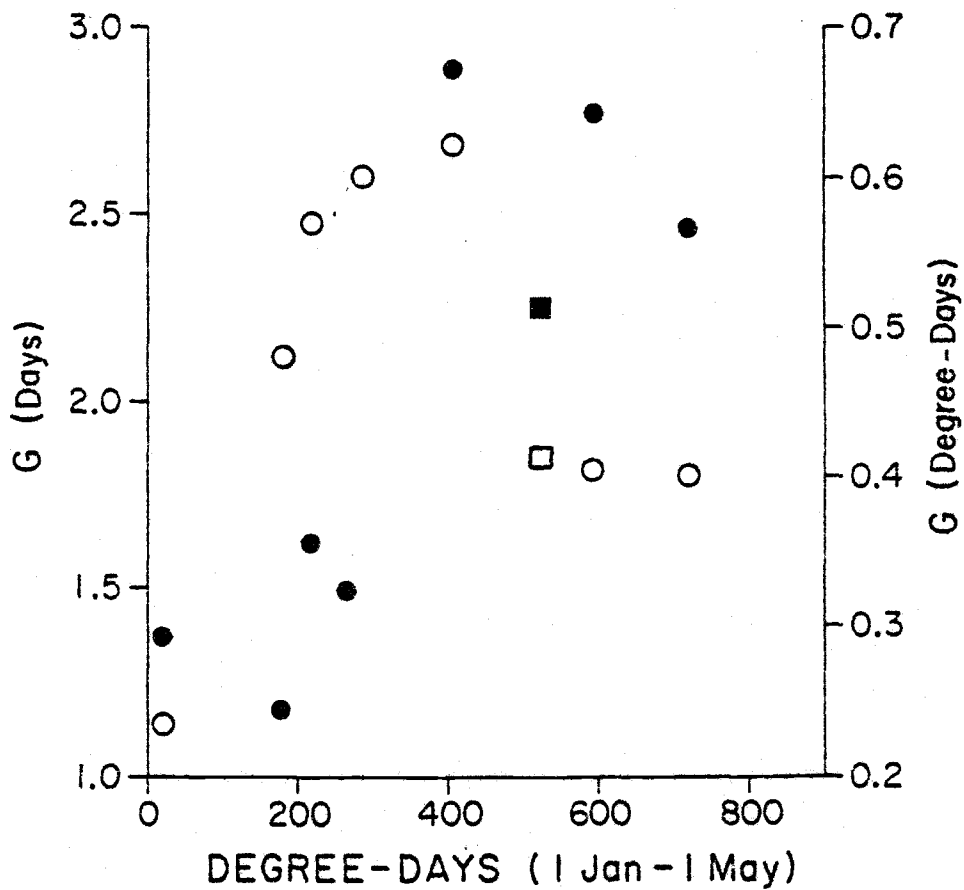
Figure 6. Relationship between growth rate of E. infrequens and
accumulated temperature between 1 January and 1 May.
Dark symbols represent G (days); open symbols represent
G (degree/days). Circles are data from Table 8.
Squares represents unpublished data of the author from
Weber Creek, California. These data were calculated
from mean individual size at two time periods only.

rates based on degree-days could not be accounted for based on estimated differences in food availability among streams. Correlations between G and measures of food availability were all not significant. Rather, observed variation may also be associated with differences in temperature (Fig. 6) as were other measures of G.

The relationships shown in Figure 6 probably reflect causal linkages between growth and temperature, but these relationships are qualitative. Use of degree-days is at best a coarse measure of the temperature regime as it affects an animal. For example, over the same period of time, a similar number of degree-days may accrue either very rapidly at first and then more slowly, or vice-versa. Such differences among sites would, of course, result in added and unexplained variation in an analysis of growth based simply on accumulated degree-days. A much greater degree of control of temperatures during specific periods of growth is necessary to develop quantitative and less variable relationships.

For two sites it was possible to make a preliminary comparison of G in relation to size and temperature (Table 9). These data indicated that G decreased with increasing size, but the data were equivocal with respect to temperature. Of interest, however, is the high G observed at 0°C for the Gorge Creek population (Table 9), a result in contrast to the generally low overall G observed for this site and statements regarding the depressant effect of low temperature on growth rate for this species (see Hartland-Rowe 1964).

I included both initial size (W_i from Table 8) and accumulated degree-days as independent variables in an analysis of variation in growth rate among sites. Multiple regression resulted in a coefficient of multiple determination (R^2) of 0.74 (n = 8, Weber Creek datum included). Including initial size in the regression analysis increased the amount of variation explained among sites, albeit only slightly so. The multiple regression

Table 9. Specific growth rates (G) of $\underline{E}$. $\underline{infrequens}$ at different temperatures and sizes.

Site	Size Range (mg)	G_R	G_m	Temperature
Gorge Creek	0.085 - 0.189	8.20	7.61	0°C
	0.189 - 1.161	1.46	1.30	5-6°C
Kalama Spring	0.005 - 0.145	2.65	3.89	6°C
	0.040 - 0.145	--	4.15	6°C
	0.145 - 1.39	2.50	2.51	6°C

G_R= Specific growth rate (days) based on regression.

G_m= Specific growth rate (days) based on initial and final mass.

$$G_m = \frac{\log_e (W_t/W_0)}{t}$$

equation was G (days) = 1.30 + 0.0024 (degree-days) - 1.124 (initial size). I discuss the probable consequences of size-temperature interactions on growth rate in a following section.

Drunella coloradensis/flavilinea

Data were sufficient to examine growth from seven stream systems for D. coloradensis. I collected data from four of these streams (MAOG, MACC, FAWN, WYCO). Published data of Hartland-Rowe (1964) from Gorge Creek (Alberta), unpublished data of Sakaguchi and Barnes from a tributary of the North Fork of the Provo River (Utah), and data from Kalama Spring, Washington (Thut 1967) also were used. Data from both 1978 and 1979 were available for MAOG, so eight data sets were analyzed. Hartland-Rowe (1964) identified the species he studied as D. lapidula, which has since been identified as a synonom of D. flavilinea. Drunella flavilinea is a sister species of D. coloradensis. The substantial variation in taxonomic characters among these two species create reasonable doubt as to how distinct these species are. I treat D. flavilinea and coloradensis as the same taxonomic entity in the same manner that I treated E. infrequens and inermis.

D. coloradensis begins larval qrowth in autumn (October-December) and adults emerge in mid- to late summer (July-September) (Fig. 7). The period of larval development is approximately eleven months. Substantial variation in mean individual biomass existed among streams at any date. Differences in the size of individuals among streams was as high as four to ten fold.

Growth rate also varied significantly among streams (Table 10). Highest G (days) was observed in Gorge Creek, Alberta; the lowest rate occurred in the tributary stream of N.F. Provo. When growth was calculated on a degree-day basis, the Gorge Creek population still exhibited the highest growth rate, but Fawn Creek showed the
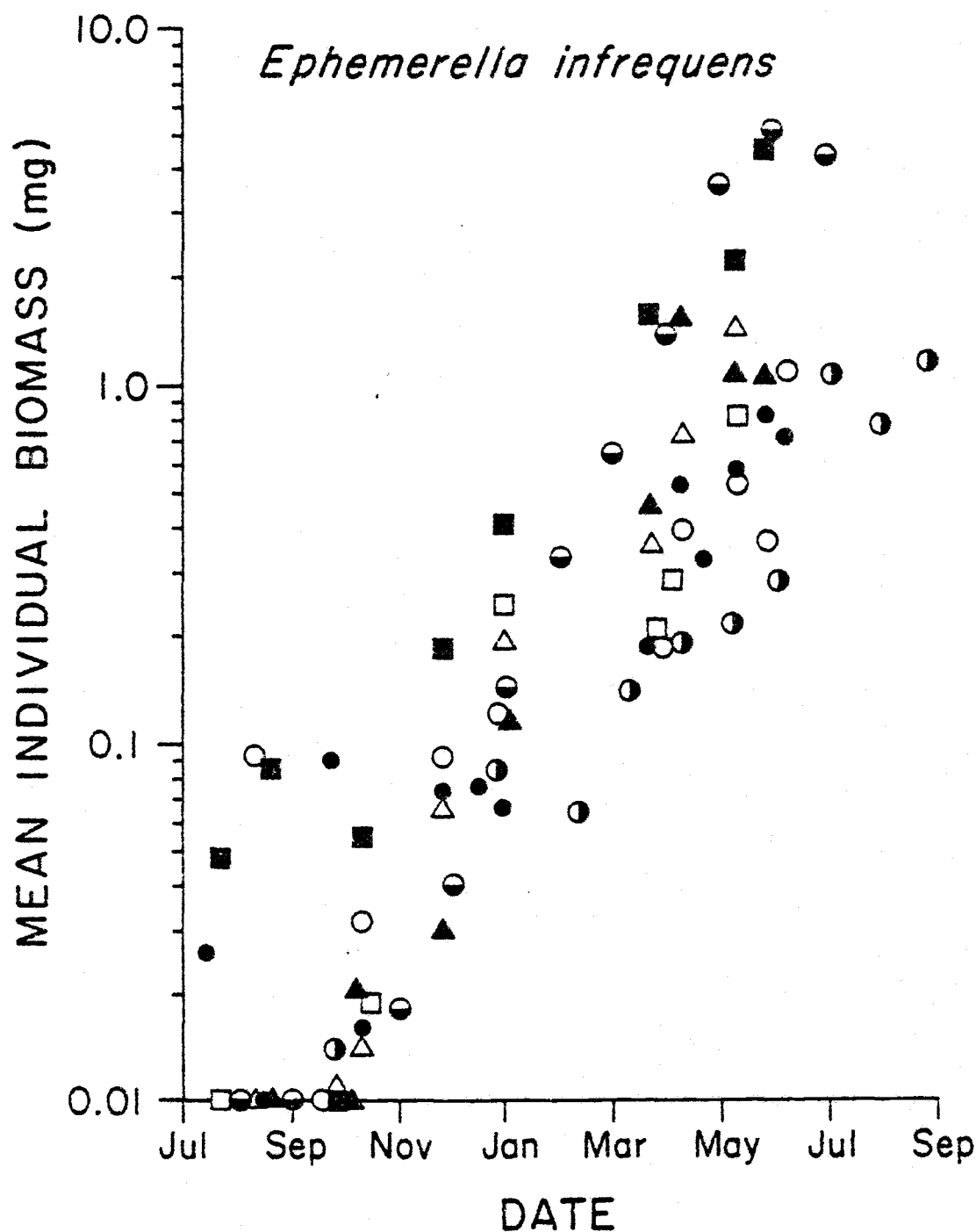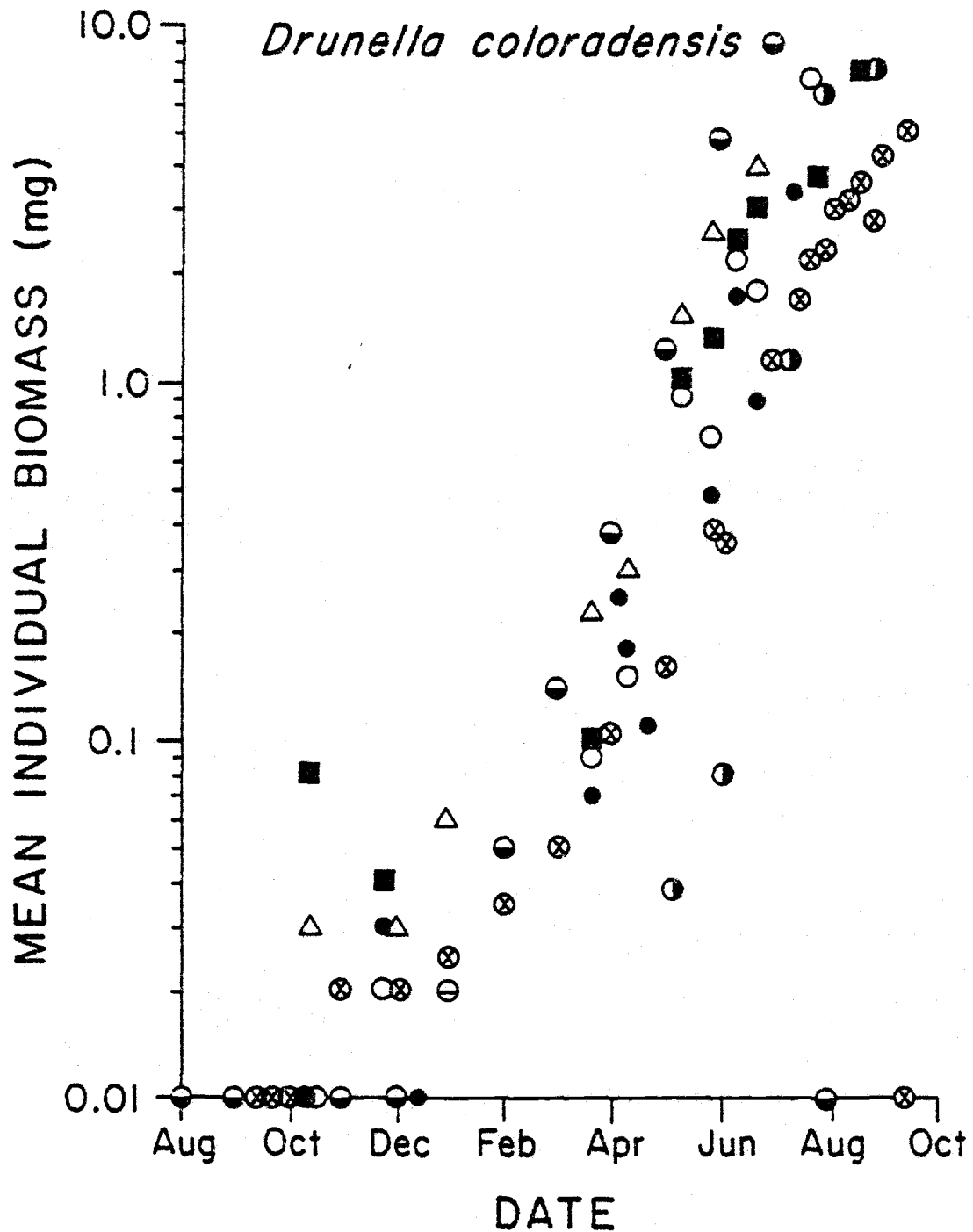
Figure 7. Mean size of D. coloradensis at different times and sites. Symbols are MAOG (●), MACC (○), FAWN (△), MILL (▲), WYCO (■), COUG (□), KALAMA (◒), Gorge (◗), and N. F. Provo (⊗). See Appendix C for tabular data.

Table 10. Regression statistics for the relationship between mean individual biomass (mg) of D. coloradensis and the independent variables days, degree-days, and hours of daylight. Variables as in Table 7.

Site	n	DAYS W_i	G	r^2	DEGREE-DAYS W_i	G	r^2	HOURS OF DAYLIGHT W_i	G	r^2
MAOG 78	4	0.10	2.63	0.99	0.18	0.41	0.94	0.13	0.18	0.99
MAOG 79	4	0.05	2.57	0.97	0.08	0.56	0.91	0.06	0.18	0.95
MACC 79	5	0.05	3.28	0.93	0.12	0.67	0.76	0.06	0.23	0.91
FAWN	5	0.11	3.39	0.96	0.20	0.34	0.86	0.14	0.24	0.94
WYCO	4	0.06	3.67	0.98	0.13	0.67	0.82	0.07	0.26	0.95
PROVO	10	0.04	2.52	0.99	0.06	0.41	0.98	0.05	0.18	0.99
KALA	5	0.14	3.55	0.99	0.14	0.60	0.98	0.16	0.25	0.98
GORGE	5	0.03	5.31	0.94	0.05	0.68	0.88	0.00	0.34	0.94
Pooled	42	0.10	2.55	0.71	0.13	0.42	0.71	0.10	0.17	0.67

Ho: G's are equal	$F_{7,26} = 11.06$ $P < 0.001$	$F_{7,26} = 6.06$ $P < 0.001$	$F_{7,26} = 9.01$ $P < 0.001$
Coefficient of variation among sites	27	25	24

lowest rate. Growth rates calculated by the daylength model showed differences among sites similar to the day model.

The variation in growth rates among streams could not be unequivocally attributed to differences in temperature, food, or latitude. Calculation of growth rates by degree-days reduced the coefficient of variation (CV) among growth rates approximately 16 percent compared to that of the day model, but a systematic relationship between G and temperature was not observed as it was for E. infrequens. Growth rate (days) may have been influenced by food. Streams that were not shaded during most of the growing season (MACC, FAWN, WYCO, KALA, Gorge) generally had high rates, whereas the one stream that was heavily shaded (MAOG) had low rates for both years data were collected. Substantial variation existed in G among the open streams though, and no definite conclusions can be drawn regarding effects of food or other variables. Growth rate varied with size as observed in E. infrequens (Table 11). Small larvae grew more rapidly than larger animals.

Drunella doddsi

Larvae of Drunella doddsi were collected from all six Oregon sites, and data on field growth were available for three other streams. Larvae were found in each stream the entire year (Fig. 8). Earliest instars occur between June and September, and larvae reach maximum size approximately twelve months later.

In all streams examined, two growth phases occurred (Fig. 8). Young larvae grew rapidly until reaching a size of 1-2 mg, after which growth was slower. The only exception was the Kananaskis River when growth was negligible during winter when ice covered the river (see Radford and Hartland-Rowe 1971).

Variation in timing of initiation of growth and magnitude of growth rate was evident among sites by inspection. Individuals in

Table 11. Specific growth rates (day model) of $\underline{D}$. $\underline{coloradensis}$ in relation to size.

Site	Size Range (mg)	G_r	G_m
Provo	0.05-1.15	2.48	2.55
Gorge	0.04-1.16	5.76	5.71
MAOG 79	0.07-0.89	2.57	2.73
MACC	0.09-1.80	3.28	3.22
Provo	1.15-4.36	1.95	2.15
Gorge	1.16-7.56	3.43	3.47
MAOG 78	1.75-3.88	2.04	2.04
FAWN	1.55-3.96	2.13	2.18
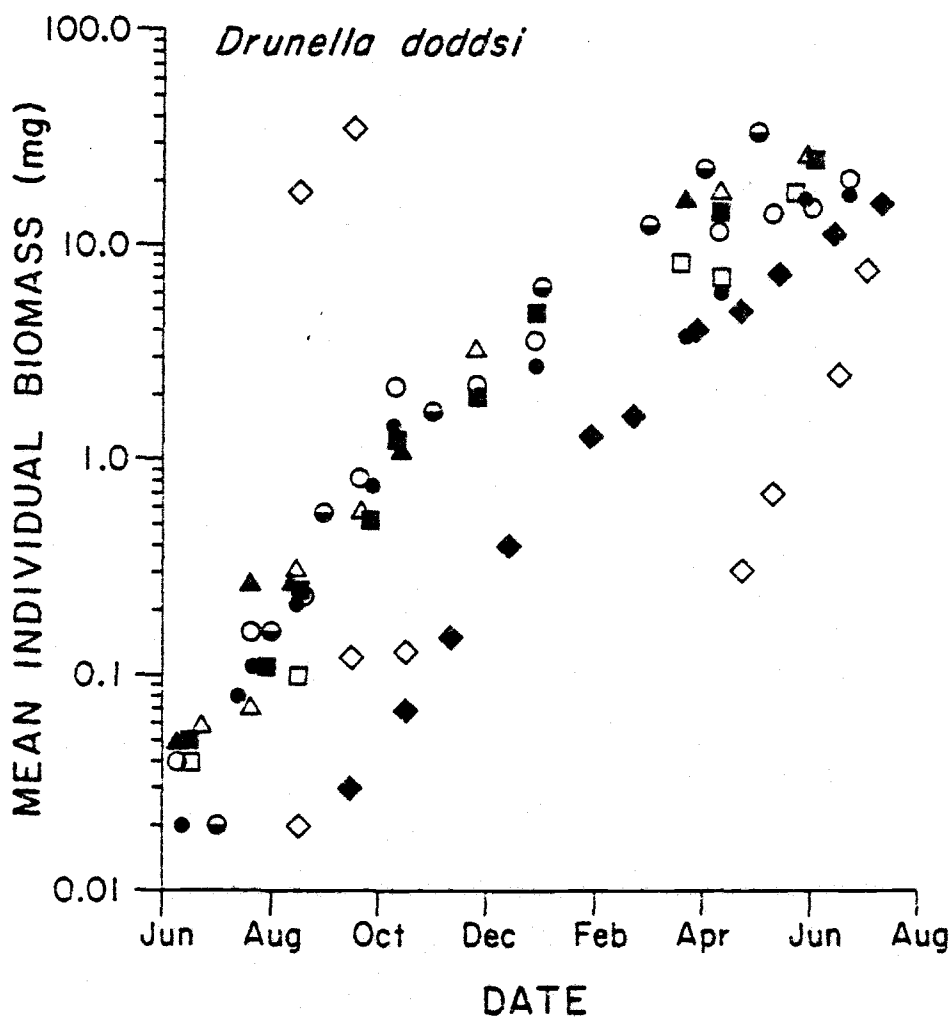
Figure 8. Mean size of individuals of D. doddsi at different dates and sites. Symbols are MAOG (●), MACC (○), FAWN (△), MILL (▲), WYCO (■), COUG (□), Kalama (◓), LUSK (◆), and Kananaskis (◇). See Appendix C for tabular data. The two largest values for the Kananaskis River are from the same cohort as other data for this stream.

streams at higher latitudes began growth later (August-September) and adults emerged later (August-September) than in streams at lower latitudes. Comparison of regression lines (G) calculated for data on larger larvae showed significant differences in growth rate among streams (Table 12). For pooled data, the degree-day model explained approximately three times as much total variation as did the other models. The coefficients of variation associated with estimates of growth for different streams was lowest for the photoperiod model and highest for the day model.

Smaller larvae did not show the same differences in growth among streams that were observed for larger larvae (Table 13, cf. Table 12). Regression analysis always explained a high percent of variation, but the degree-day model for pooled data did not explain substantially more variation than the day model. The photoperiod model was not examined. Variation (CV) among growth rates was almost five times smaller in the day model than in the degree-day model.

Most of the variation among streams in growth rate of both small and large larvae of D. doddsi was explained when both temperature and inital size were considered. For small larvae, multiple regression of G (days) on degree-days and W_i produced an R^2 of 0.95 (n = 6). The equation for this regression was:

$$G \text{ (days)} = 2.62 + 0.00043 (X) - 23.1 (W_i)$$

where X equals degree-days and W_i equals inital size. For large laarvae, $R^2 = 0.66$ (n = 7) and

$$G \text{ (days)} = 3.54 - 0.0020 (X) + 0.12 (W_i)$$

Drunella spinifera

Small larvae of D. spinifera were first observed in July (Fig. 9). After a brief period of rather rapid growth, growth appeared to be relatively constant for much of the life cycle (September

Table 12. Regression statistics for D. doddsi (large larvae). Variables as in Table 8. Growth rates calculated over the period 28 December to 15 September.

Site	n	DAYS			DEGREE-DAYS			HOURS OF DAYLIGHT		
		W_i	G	r^2	W_i	G	r^2	W_i	G	r^2
MAOG	5	2.17	1.17	0.89	2.98	0.38	0.90	2.32	0.096	0.92
MACC	5	3.50	1.00	1.00	5.09	0.32	0.82	3.72	0.081	0.99
WYCO	3	4.71	1.11	1.00	5.21	0.44	0.97	4.89	0.095	1.00
COUG	3	2.63	1.20	0.78	3.96	0.24	0.85	3.21	0.092	0.83
LUSK	6	0.79	1.65	0.98	1.33	0.74	0.88	1.04	0.127	0.96
KANA*	6	1.59	3.03	0.94	1.11	0.50	0.87	0.05	0.197	0.94
KALA	4	5.77	1.40	0.99	6.09	0.24	0.99	6.12	0.126	0.99
Pooled	32	2.99	0.78	0.21	3.06	0.36	0.67	3.24	0.062	0.23

	DAYS	DEGREE-DAYS	HOURS OF DAYLIGHT
Ho: G's are equal	$F_{6,18} = 12.18$ $P < 0.001$	$F_{6,17} = 5.24$ $P < 0.005$	$F_{6,18} = 9.14$ $P < 0.001$
Coefficient of variation among sites	48	43	34

* Degree-days summed beginning 31 April for Kananaskis River and 28 December for all other sites. Also n = 5 in degree-day regression model for Kananaskis River because temperature data were not available for 21 April.

Table 13. Regression statistics for D. doddsi (small larvae).
Growth rates calculated over the period 1 Jun - 1 Jan.

Site	n	DAYS			DEGREE-DAYS		
		W_i	G	r^2	W_i	G	r^2
MAOG	9	0.030	2.48	0.93	0.020	0.33	0.99
MACC	7	0.049	2.26	0.92	0.032	0.29	0.98
MILL	5	0.052	2.36	0.97	--	--	--
FAWN	3	0.018	3.27	0.90	0.019	0.21	0.94
WYCO	7	0.042	2.28	0.99	0.031	0.28	0.97
LUSK	4	0.001	2.87	1.00	0.000	1.09	0.89
KANA	3	0.002	3.48	0.90	--	--	--
KALA	5	0.019	2.87	0.92	0.019	0.49	0.92
Pooled	43	0.038	2.14	0.70	0.027	0.29	0.79

Ho: G's are equal		$F_{7,26} = 4.39$ $P < 0.005$			$F_{5,23} = 12.08$ $P < 0.001$		
Coefficient of variation among sites			15			73	
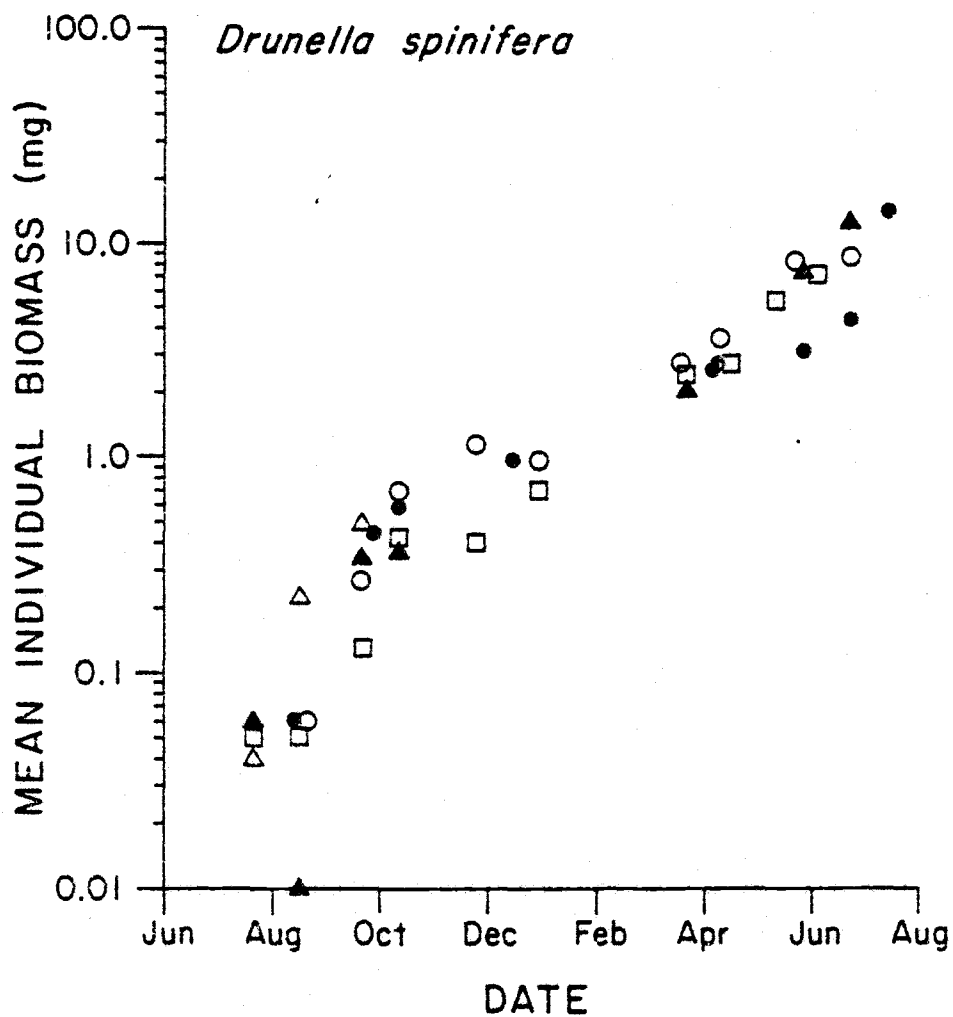
Figure 9.   Mean individual size of D. spinifera at different dates and sites.   Symbols are MAOG (●), MACC (○), MILL (▲), FAWN (△), and COUG (□).

onward). Larvae probably complete growth the next June or July.

Sufficient data for regression analysis were available for only four streams, all of which I sampled in the Oregon Cascades. Growth rates varied significantly among streams when calculated on both a day and degree-day basis (Table 14). Coefficients of determination (r^2) were generally higher for the day model than the degree-day model for both individual streams and pooled data. The coefficient of variation (CV) associated with growth rates, however, was 25 percent lower for data analyzed by degree-days than days.

Because only four data sets were examined (three for degree-days), it is difficult to evaluate relationships between growth rate and environmental factors. When rates were based on days, growth was highest in the lower elevation and generally warmer streams (COUG, MILL) than in the higher elevation and cooler streams (MAOG, MACC) (Table 14). Growth rates also may have been affected by food sources for this species (see results for comparison of growth rates between MAOG and MACC at the end of this section).

Drunella pelosa

Small larvae of Drunella pelosa were difficult to distinguish from small larvae of D. coloradensis. Both appear to begin growth during autumn (October-November) (Fig. 10, cf. Fig. 7). Whereas D. coloradensis grows for approximately eleven months, D. pelosa probably emerges during early summer (June) in Oregon. The period of growth for this species is therefore about eight months. This species was found in four of the Oregon streams. No published data on its life cycle were found.

Growth rates based on both days and degree-days were significantly different among streams (Table 15). Because of the small sample size, it was difficult to examine relationships between growth rate and environmental variables, although growth rate based

Table 14. Regression statistics for <u>Drunella</u> <u>spinifera</u>. Variables as in Table *.

Site	n	DAYS				DEGREE-DAYS		
		W_i	G	r^2		W_i	G	r^2
MAOG	6	0.40	0.81	0.99		0.26	0.26	0.96
MACC	8	0.31	1.14	0.95		0.14	0.40	0.93
COUG	8	0.14	1.43	0.96		0.07	0.35	0.96
MILL*	5	0.23	1.29	0.98		--	--	--
Pooled†	27	0.25	1.17	0.92 (0.90)†		0.16	0.31	0.81

Ho: G's are equal	$F_{3,19} = 13.41$ $P < 0.001$	$F_{2,16} = 11.43$ $P < 0.001$
Coefficient of variation among sites	28	21

* MILL excluded from calcuations of CV.
† For pooled data n = 22 for degree-day model; r^2 for pooled data (days) excluding MILL given for comparison with degree-day values.
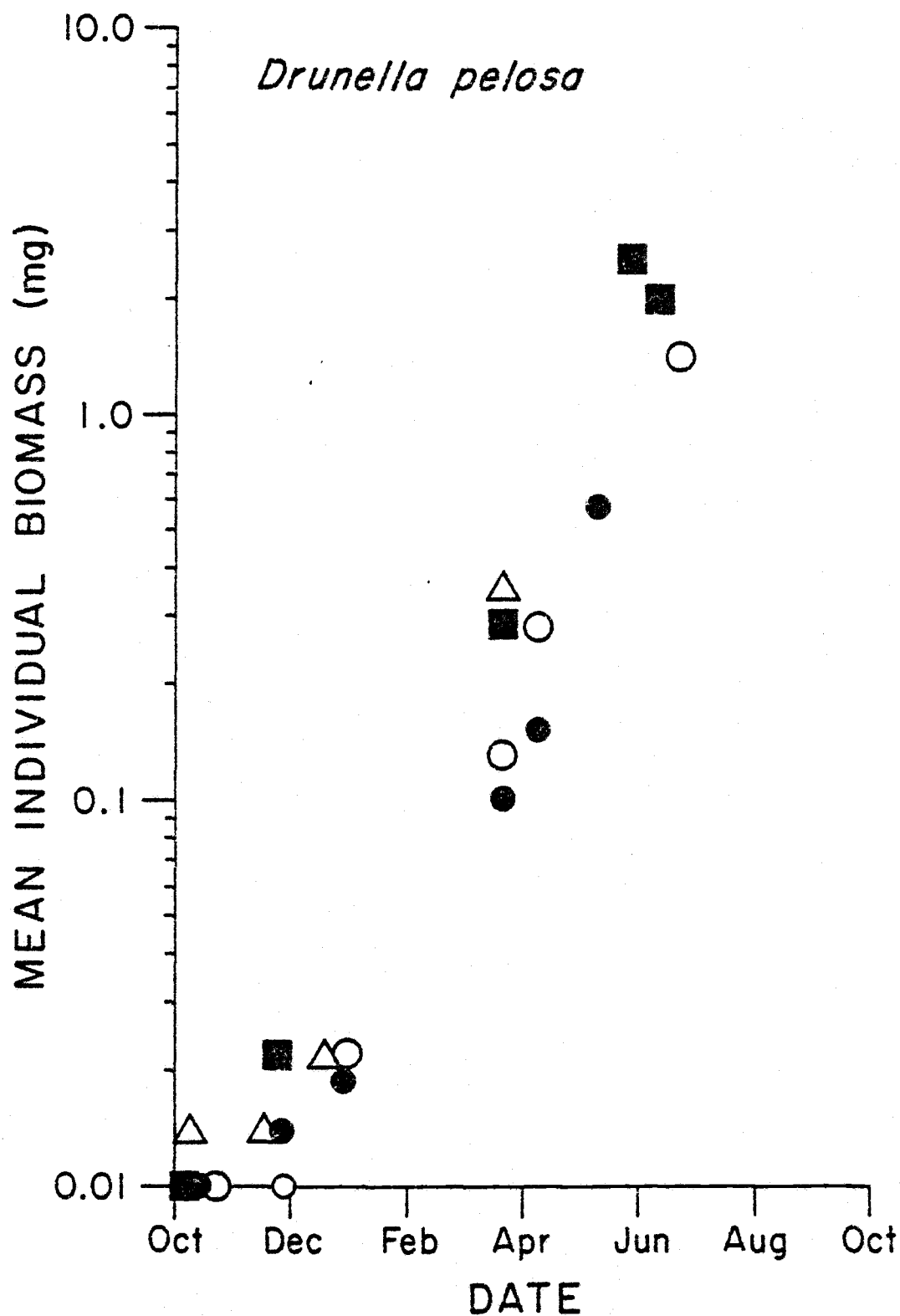
Figure 10. Mean individual size of D. pelosa at different dates and sites. Symbols are MAOG (●), MACC (○), FAWN (△), and WYCO (■).

Table 15. Regression statistics for $\underline{D.\ pelosa}$. Variables as in Table 8.

Site	n	DAYS			DEGREE-DAYS		
		W_i	G	r^2	W_i	G	r^2
MAOG	5	0.0088	2.28	0.97	0.0089	1.24	0.99
MACC	5	0.0092	2.41	1.00	0.0210	0.84	0.84
WYCO	3	0.0177	2.61	0.99	0.0260	1.09	0.97
FAWN	3	0.0083	3.14	0.99	0.0086	0.75	0.99
Pooled	16	0.0101	2.49	0.94	0.0160	0.92	0.81

Ho: G's
   are equal

$F_{3,8} = 4.84$
$P < 0.05$

$F_{3,8} = 3.31$
$P = NS$

Coefficient of
variation among
sites

15

23

on days apparently varied directly with temperature ($r^2 = 0.90$, n = 4).

Serratella tibialis

Larvae of Serratella tibialis were found in all six Oregon streams and Kalama Spring from early April to late September (Fig. 11). In any one stream larvae appeared to complete growth in approximately five months.

Data were sufficient to examine growth in only three streams (Table 16). Growth rates varied significantly among streams when based on either days or degree-days. Growth rate in S. tibialis appears to be negatively correlated with temperature. A difference in 400 degree-days (36%) between streams (mean temperature difference of 2.2°) was associated with a 45 percent decrease in growth rate. There was no evidence that differences in food availability affected growth rates.

Caudatella cascadia

Young larvae of Caudatella spp. are difficult to distinguish from one another or other ephemerellid genera. Data for larvae that were suspected to be C. cascadia are graphed with data for larvae distinguished with certainty (Fig. 12).

I fitted a regression line to data where mean biomass was >0.1 mg. Parameters of that line are $W_i = 0.03$, $\underline{G} = 1.35$, and $r^2 = 0.92$ (n = 12). By extrapolation, the growth period of this species is about eleven months.

Caudatella hystrix

As with C. cascadia limited data were obtained from which to determine growth rates. Distinguishing smaller larvae also was a
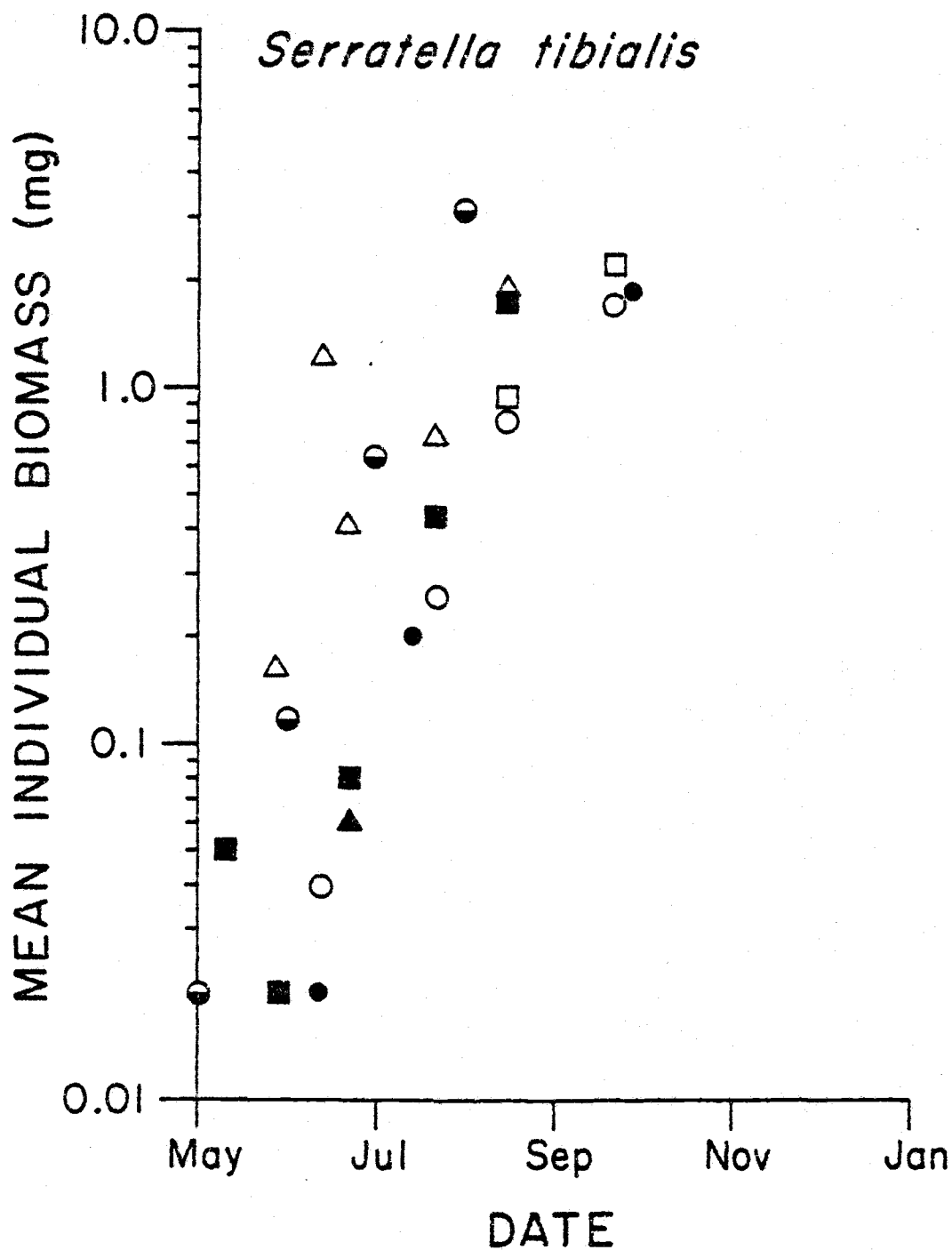
Figure 11. Mean individual size of S. tibialis at different dates
and sites. Symbols are MAOG (●), MACC (○), MILL (▲),
FAWN (△), WYCO (■), COUG (□), and Kalama (◓).

Table 16. Regression statistics for <u>Serratella tibialis</u>. Variables as in Table 8.

Site	n	DAYS			DEGREE-DAYS		
		W_i	G	r^2	W_i	G	r^2
MAOG	3	0.0018	3.97	0.94	0.0087	0.41	0.93
MACC	4	0.0036	3.74	0.96	0.0176	0.35	0.96
KALA	5	0.0037	5.44	1.00	0.0040	0.91	1.00
Pooled	12	0.0058	3.60	0.82	0.0139	0.41	0.75

Ho: G's are equal

$F_{2,6} = 6.97$
$P < 0.05$

$F_{2,6} = 24.24$
$P < 0.005$

Coefficient of variation among sites

21

55
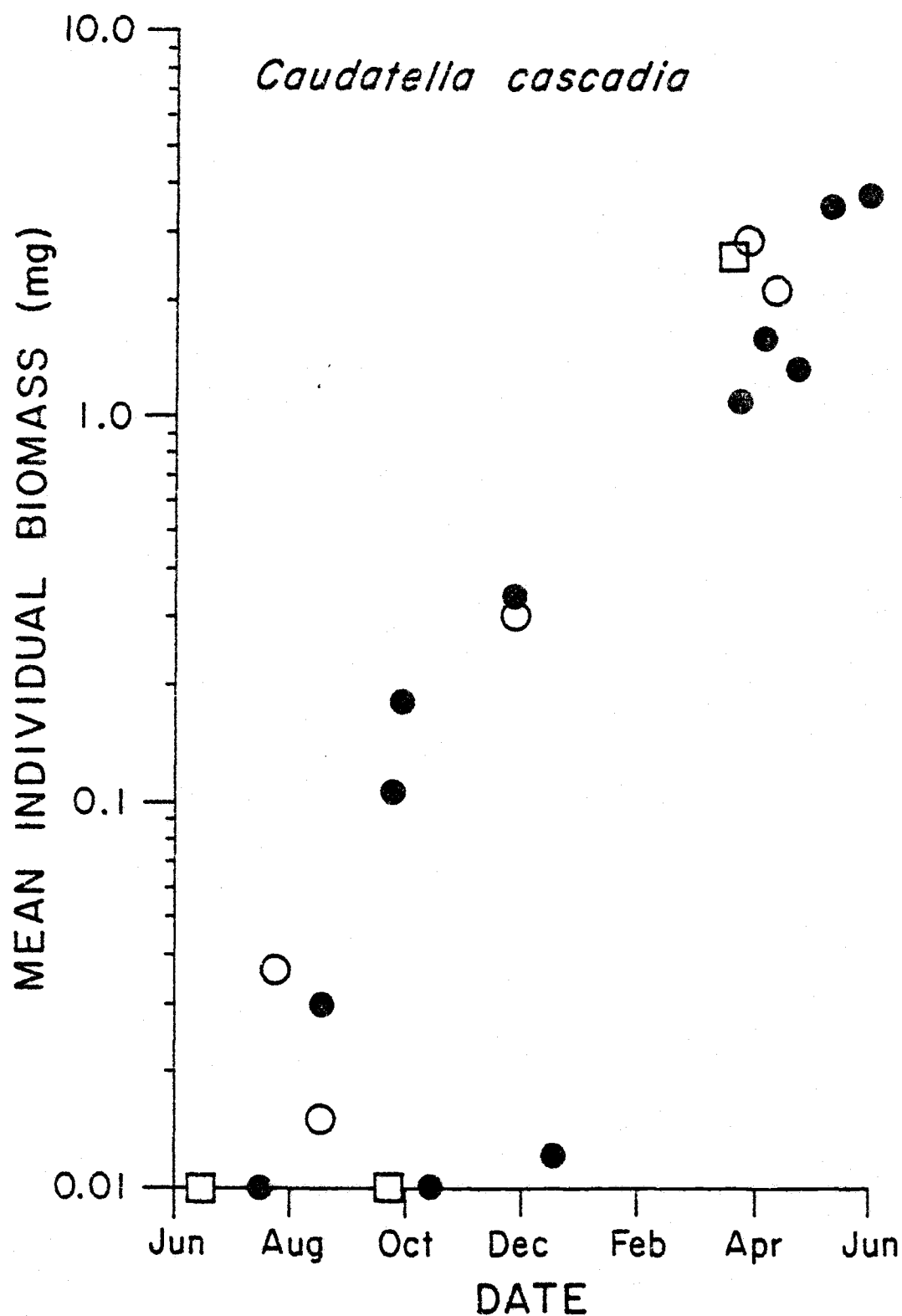
Figure 12. Mean size of individuals of C. cascadia at different sites and dates. Symbols are MAOG (●), MACC (○), and COUG (□).

problem. The growth period of <u>C</u>. <u>hystrix</u> is apparently about ten months long (September-June) (Fig. 13). A regression line fit to the data (excluding means based on fewer than three individuals) gave the following parameter values: W_i = 0.02, <u>G</u> = 1.65, r^2 = 0.90, n = 15.

Other species

Data for other species were insufficient to estimate growth rates with confidence. Two species encountered, <u>Serratella</u> <u>teresa</u> and <u>S</u>. <u>velmae</u>, were often difficult to distinguish but appear to be separable when data are graphed (Fig. 14). Distinctions based on this method are tenuous at best, but it is worthwhile to consider these data and obtain a rough estimate of growth rate for these taxa. Regression lines were fitted by eye to each set of points. Specific growth was calculated by estimating biomass at two points in time for each regression line.

Growth rate was calculated by the formula:

$$\underline{G} = \frac{\log_e (W_t/W_o)}{t} \cdot 100,$$

where W_t = mg at time t, W_o = mg at time 0, and t = the time interval between W_t and W_o in days. Growth rates calculated by this method were approximately 2.7 for both <u>S</u>. <u>velmae</u> and <u>teresa</u>. It is uncertain what the growth period of each species is. Allen and Edmunds (1963a) reported mature larvae in Oregon streams about 1 July for <u>S</u>. <u>teresa</u> and 1 August - 1 September for <u>S</u>. <u>velmae</u>. Projected individual size from Figure 14 do not correspond well with these observations. Data in Figure 14 would predict <u>S</u>. <u>velmae</u> to reach maturity first rather than the converse.
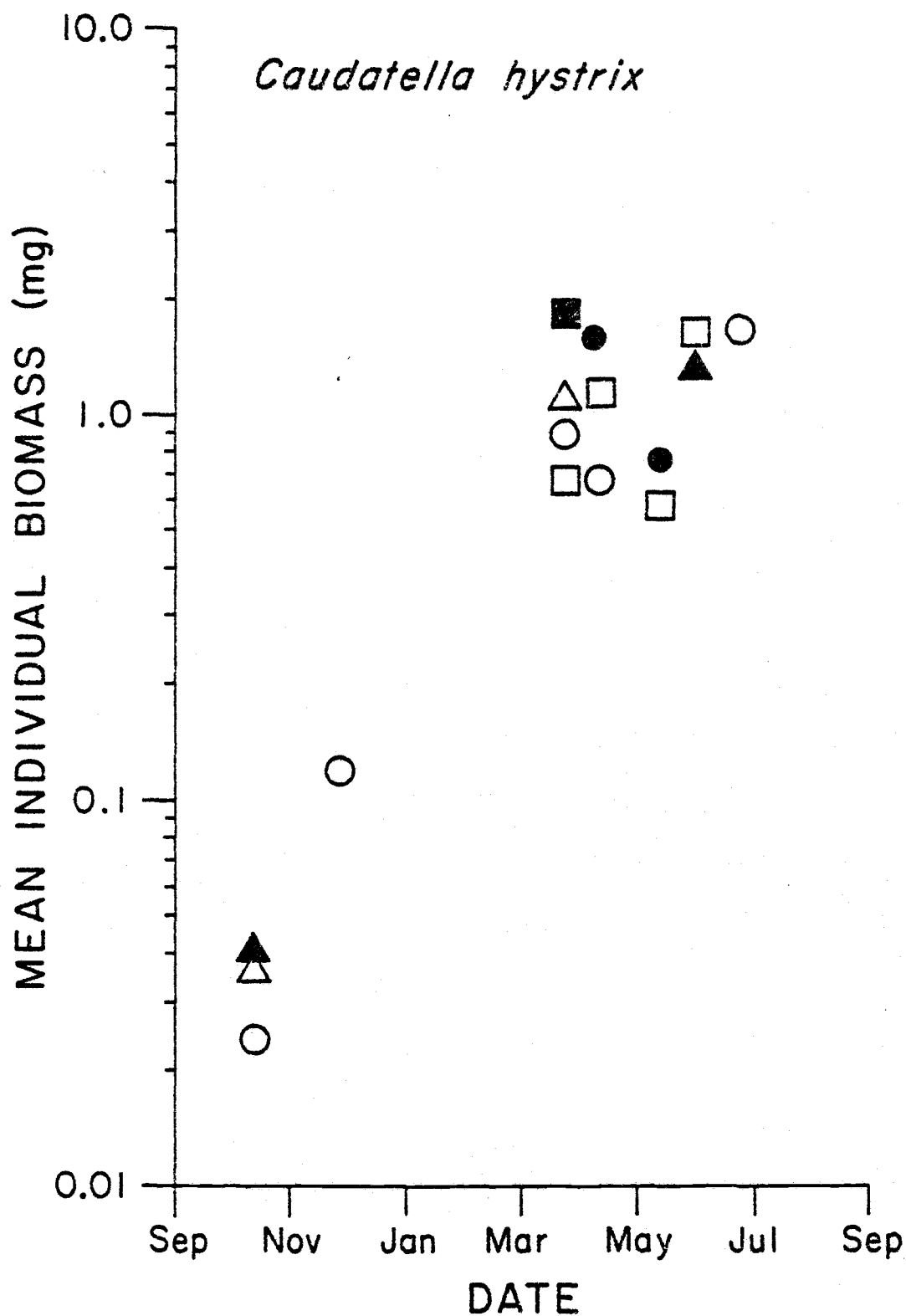
Figure 13. Mean size of individuals of C. hystrix at different sites and dates. Symbols are MAOG (●), MACC (○), MILL (▲), FAWN (△), WYCO (■), and COUG (□).
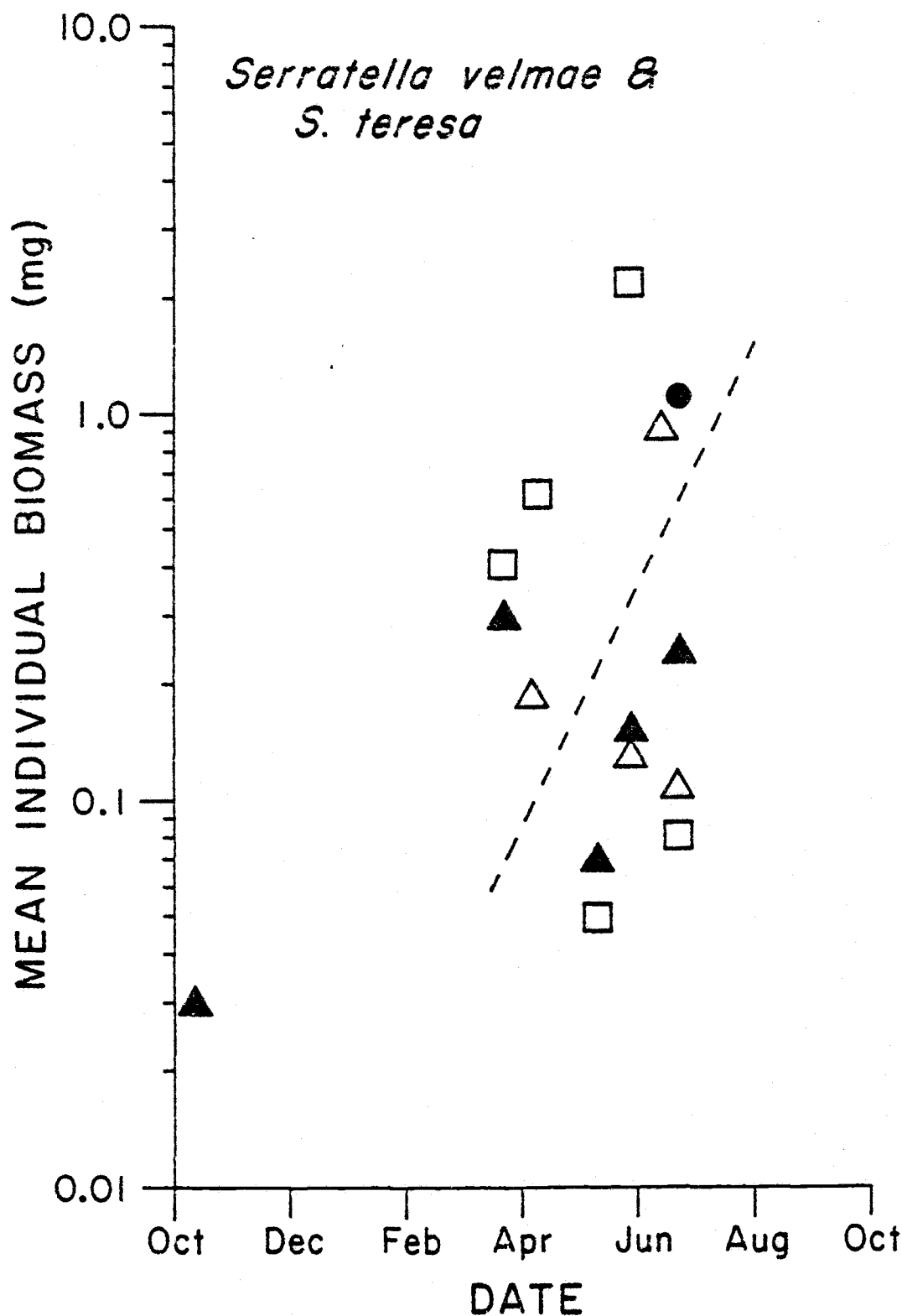
Figure 14. Mean size of individuals of S. velmae and S. teresa at different dates and sites. Symbols are MAUG (●), MILL (▲), FAWN (△), and COUG (□). Points above dashed line are S. velmae; points below line are S. teresa.

Data for three other species (<u>Attenella margarita</u>, <u>A</u>.
<u>delantala</u>, and <u>Caudatella heterocaudata</u>) were so sparse that
analyses of growth relations was not attempted.

Effect of Food on Growth Rate

One of the Oregon sites traversed an experimental clear-cut
(MACC) located below a site surrounded by old-growth forest (MAOG).
These sites were used to compare the effect of food on growth rates
as they differed significantly in type and quantity of food
available to consumers (see Table 7 and Gregory 1980), but were
similar in most physical characteristics. The two sites differed by
only 5% in annual degree-days (Table 6, Fig. 3).

Six species were sufficiently abundant in both sites to compare
growth rates. Three species consume predominantly algae (<u>D</u>. <u>doddsi</u>,
<u>D</u>. <u>pelosa</u> and <u>D</u>. <u>coloradensis</u>), two are predominantly detritivores
(<u>E</u>. <u>infrequens</u>, and <u>S</u>. <u>tibialis</u>), and one is a carnivore (<u>D</u>.
<u>spinifera</u>) (see following section on Food Habits). Only <u>D</u>.
<u>spinifera</u> exhibited different growth rates between sites (Table 17).
It grew faster in the clear-cut section.

In the laboratory, differences in food resulted in different
growth rates for <u>E</u>. <u>infrequens</u> (Table 18). For small larvae,
animals grew rapidly on an artificial diet (Tetramin®), algae, and
alder fines. Growth was slower on whole alder leaves, and slowest
on wood fines. Larger larvae grew equally well on all foods except
wood fines. Growth on wood fines was at least three times slower
than rates observed for other food sources. Interestingly,
laboratory growth rates were generally much higher than those
observed in the field (cf. Tables 18 and 8).

Table 17. Growth rates at MAOG and MACC for six different species. F^1 = test of Ho: lines are congruent, F^2 = test of Ho: growth rates are equal.

| Species | DAYS | | | | | | DEGREE-DAYS | | | | | |
| | G | | | | | | G | | | | | |
	MAOG	MACC	F^1	P	F^2	P	MAOG	MACC	F^1	P	F^2	P
E. infrequens	1.62	1.18	0.69	NS	--	--	0.57	0.48	0.23	NS	--	--
D. coloradensis	2.57	3.28	2.46	NS	--	--	0.56	0.67	1.32	NS	--	--
D. doddsi (L)	1.17	1.00	2.39	NS	--	--	0.38	0.32	2.09	NS	--	--
D. doddsi (S)	2.48	2.26	0.71	NS	--	--	0.33	0.29	2.24	NS	--	--
D. spinifera	0.81	1.14	6.19	<0.01	17.59	<0.005	0.26	0.40	4.78	<0.05	16.76	<0.005
D. pelosa	2.28	2.41	0.45	NS	--	--	1.24	0.84	1.00	NS	--	--
S. tibialis	3.97	3.74	0.47	NS	--	--	0.41	0.35	0.14	NS	--	--

Table 18. Effect of food on growth rates (G) of E. infrequens. Initial biomass estimated from length-mass equations. Data are mg dry mass with 95% confidence intervals and sample size. Experiments were run for 56 days (small larvae) and 51 days (large larvae). Initial number of larvae in each treatment was 17. Number of larvae removed at end of experiment shown in parentheses.

Treatment	Initial Biomass	Percent Survival	G*	All Larvae†	♂ Larvae	♀ Larvae	♂ Subimagos	♀ Subimagos
Tetramin®	0.18	88	4.51	2.35	2.06 ± 0.29 (10)	2.64 ± 0.82 (5)		
Algae	0.18	76	5.25	3.38	3.09 ± 0.46 (6)	3.66 ± 0.70 (7)		
Alder leaves	0.18	41	2.52	0.74	0.75 ± 0.33 (4)	0.72 ± 0.40 (3)		
Alder fines	0.18	88	4.44	2.16	2.21 ± 0.94 (6)	2.12 ± 0.46 (9)		
Wood fines	0.18	35	0.79	0.28	0.27 ± 0.44 (2)	0.29 ± 0.21 (4)		
Tetramin®	0.83	65	2.52	3.46	2.98	3.93 ± 0.26 (4)	2.28 ± 1.25 (4)	2.54 ± 4.16 (2)
Algae	0.83	88	2.26	3.33	3.07 ± 0.57 (4)	3.59 ± 0.16 (3)	1.92 ± 0.35 (7)	2.93
Alder leaves	0.83	71	2.15	2.60	2.30	2.90 ± 0.55 (7)	1.65 ± 0.45 (3)	2.26
Alder fines	0.83	94	2.43	3.44‡		3.89 ± 0.36 (7)	1.79 ± 0.27 (6)	2.60 ± 1.55 (3)
Wood fines	0.83	76	0.67	1.16	1.23 ± 0.36 (7)	1.10 ± 0.37 (6)		

* Based on difference between initial biomass and mean final biomass of all larvae.
† Unweighted mean of ♂ and ♀ mean values.
‡ Calculated as mean of ♂ and ♀ after assuming ♀ mass as 1.30 that of ♂.

Seasonal Differences in Life Cycles

For nine species I estimated the monthly contribution to growth as percent of individual mass attained at maturity (Table 19). To obtain estimates of individual mass at the start of each month, I fitted a line to combined data from the Oregon sites. Final mass was estimated by extrapolating to the beginning of the month nearest to when adults emerged. The formula of Levins (1968) was used to describe how individual growth was partitioned among months (seasonal niche breadth).

$$\text{Niche breadth } (B_i) = 1/\textstyle\sum p_{ij}^2,$$

where p_{ij} = the proportion of growth observed each month (j) for a species (i), and p_{ij}'s are summed over j months.

Niche breadth was generally correlated with length of the growing period (Table 19). Species that took close to 12 months to complete growth had highest values of niche breadth, those species with shorter growing periods had lower values. An exception was $\underline{D.}$ $\underline{coloradensis}$, which took eleven months to grow but had the lowest niche breadth. If the number of months needed to complete 90 percent of growth is compared with niche breadth, the relationship between length of growth period and niche breadth is stronger.

Timing of growth also varied considerably among species, but all species completed their growth during spring or summer. I used the statistical test developed by Poole and Rathcke (1978) to determine if timing of growth among species was random, aggregated, or uniform in distribution. The formula and method of application for this test are given in Appendix G. Dates at which each species had accrued 50 percent of its final mass were compared. When the entire year was considered, separation of growth among species was not significantly different from random ($X^2_{(9)}$ = 4.54, see

Table 19. Percent of total growth in each month for different species of Ephemerellidae. Those months encompassing 90% of growth are underlined.

Species	JAN	FEB	MAR	APR	MAY	JUN	MONTH JUL	AUG	SEP	OCT	NOV	DEC	B$_i$
E. infrequens	2.2	4.0	7.5	13.5	25.0	45.0	--	--	0.2	0.4	0.7	1.2	3.43
D. coloradensis	0.2	0.3	0.4	1.8	4.1	10.4	25.0	58.0	--	0.06	0.08	0.1	2.43
D. doddsi	6.0	10.0	15.3	21.7	31.7	0.1	0.3	0.7	1.7	3.8	3.0	5.7	5.25
D. spinifera	3.7	5.0	7.0	10.0	14.7	22.0	30.0	0.6	1.7	1.1	1.7	2.2	5.56
D. pelosa	0.7	2.2	4.8	11.2	24.4	55.6	--	--	--	--	0.3	0.4	2.60
S. tibialis	--	--	--	--	1.5	8.1	11.3	25.3	53.3	--	--	--	2.72
S. teresa	--	--	1.1	2.4	5.6	10.9	24.5	54.5	--	--	--	--	2.68
C. cascadia	5.8	9.5	15.0	22.8	33.2	--	0.4	1.0	2.1	2.4	2.4	5.2	4.96
C. hystrix	4.8	6.8	10.5	14.5	21.0	32.5	--	--	0.6	1.2	2.6	5.2	5.20

Appendix G for interpretation of X^2). When only the six month period defined as the interval between dates for the earliest and latest growing species was considered, timing of growth among species also was random ($X^2_{(9)} = 11.69$). I will defer discussion of these patterns until I discuss general niche relationships.

Discussion

The entire life cycle of mayflies consists of egg, larvae, and adult stages. In this study, I have considered only the larval stage. The following discussion treats factors that may affect variation in the larval part of the life cycle. Because the larval stage is the dominant part of the entire cycle (Edmunds et al. 1976) and because no simple term exists that distinguishes only the larval cycle from the rest, I use the more inclusive term of life cycle when referring to only the larval stage.

Life cycles of larvae may be characterized by three major traits: timing (when), duration (length), and rate of growth (how fast). All three may be influenced by natural selection and in part define the life history "strategy" of an organism. Strategies are often assumed to reflect an optimal solution to the problem of maximizing individual fitness. A consideration of different patterns that species show with respect to combinations of these traits should lead to a more clear understanding of the factors that have been important in the evolution of life cycles in aquatic insects and that continue to influence community structure.

In Figure 15, I show selected and idealized examples of how life cycles of univoltine insects can vary. Initiation of growth is an important aspect of timing, and different species may vary in when eggs hatch and larvae begin to grow (cf. A's in Fig. 15). Duration of the growth period describes when and for how long an
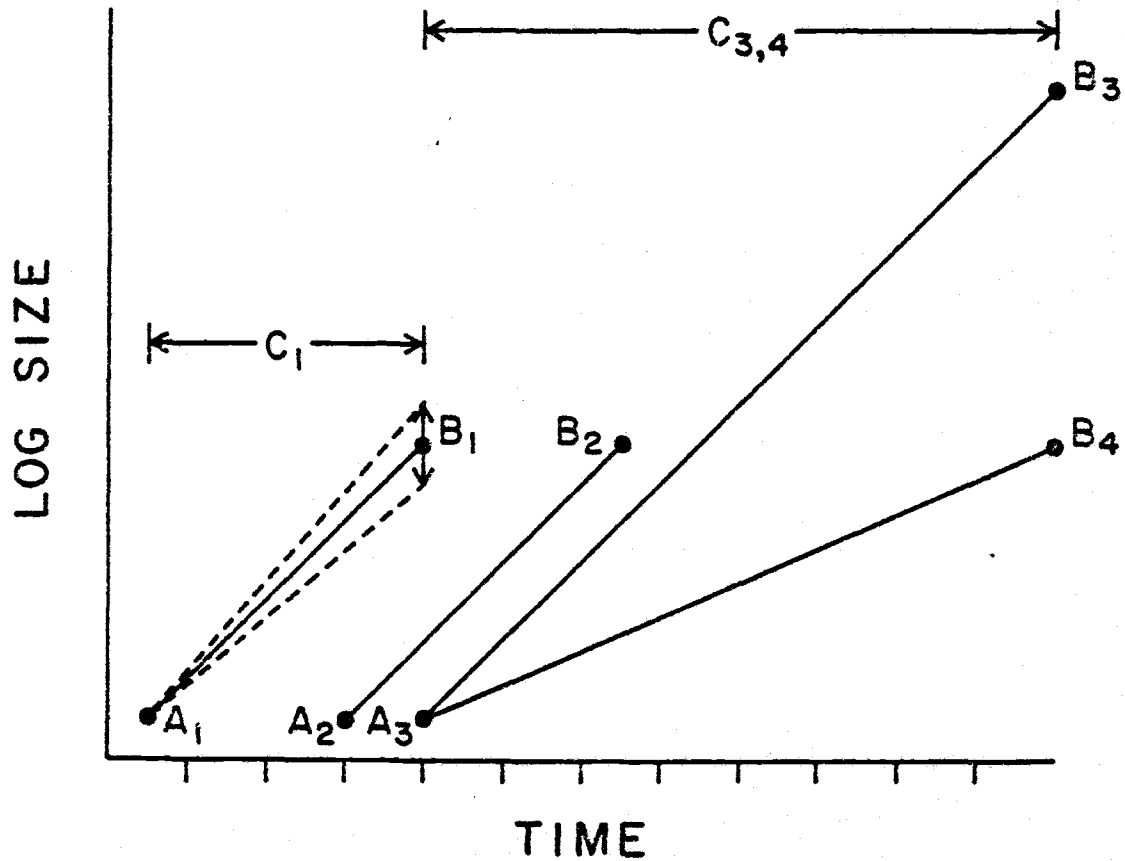
Figure 15. Idealized diagram showing differences in length and timing of life cycles and differences in growth rates. A's represent time that growth is initiated; B's represent time growth is completed and final size; C's represent different lengths of growth periods. Subscripts indicate association of A, B, and C's of different taxa.

organism is affecting its environment by exploitation of resources.
Duration can be defined as the period encompassing initiation of
growth to emergence of adults (cf. C's in Fig. 15). Rate of growth
and duration of the life cycle together determine final size of an
individual (cf. B's in Fig. 15). I will argue later that duration
of growth may be constrained by adaptations to cope with
environmental variability. If duration is relatively fixed for a
species, differences in growth rate may be extremely important in
determining final size and fitness (see Fig. 15, line A_1B_1),
because fecundity has been shown to be directly related to size in
mayflies (Clifford and Boerger 1974).

In this study I have attempted to determine how variable
certain traits are and how some aspects of environment (temperature,
photoperiod, food) may influence these traits. I have not attempted
to directly assess the degree of genetic variability exhibited
within a species but infer genetic differences among species by
comparing the range of responses within a species.

Effects of Temperature and Photoperiod

Growth-temperature relationships for the species I studied
cannot be completely specified, because data were not examined over
all temperatures that each species might encounter. Of those
species for which some data were available, only three (infrequens,
pelosa, and spinifera) showed increased growth rates with increasing
temperature. Two showed apparently decreasing rates with increasing
temperature (doddsi, tibialis), and one showed no apparent
relationship with temperature (coloradensis). Others have also
shown that specific growth rate of aquatic insects does not always
increase with mean temperature (Markarian 1980, Humpesch 1979).
Data of Heiman and Knight (1975) show that growth rate of Acroneuria
(=Calineuria) californica declined over much of the temperature

range examined, although they did not examine growth at low
temperatures. Their data do suggest, however, that an optimal,
intermediate temperature produced most rapid growth, a pattern
similar to the developmental curves shown by Taylor (1981) for
terrestrial insects. It is important to note that my data allow
examination of growth over rather coarse differences in temperature
(total accumulated degree-days). Relationships should not be
construed as precise descriptions of the response of growth to
specific temperatures.

Although it is difficult to generalize among species with
respect to specific growth-temperature relationships, recent
empirical studies in aquatic environments strongly suggest that
temperature may be the most important single factor influencing
growth rates (Brittain 1976, Mackey 1977, Humpesch 1979, 1981). For
my data, calculation of growth based on degree-days generally
explained more pooled variation than when calculations were based on
days or photoperiod. This was true, however, only when sites were
compared over a substantial latitudinal, and thus temperature,
range. Within a site, little difference existed in the amount of
variation explained by the three different variables (Table 20).
Lack of difference is almost certainly due to the three variables
being highly autocorrelated within a site.

There was, however, no clear trend among species for growth
rates to be more similar when calcualted on a degree-day basis than
with other variables (cf. values of CV, Table 20). The reason that
calculation of growth rates based on degree-days did not result in
more similar rates among sites may be because either: 1) a unit of
temperature may not produce an equivalent amount of growth at all
temperatures encountered (e.g. Fig. 6), or 2) an interaction with
photoperiod, initial size, or food confounds effects. I used median
daily temperature to calculate degree-days and summed all
temperatures greater than zero. All temperatures encountered during

Table 20. Coefficients of determination (r^2) within (mean of sites) and among sites (pooled data) and coefficients of variation (CV) for G. Values given for the day (D), degree-day (DD) and hours of daylight (DL) regression models. Values expressed as percentages.

Species	r^2 within			r^2 among			CV (G)		
	D	DD	DL	D	DD	DL	D	DD	DL
E. infrequens	91	89	91	33	58	32	36	29	36
D. coloradensis	97	89	96	71	71	67	27	25	24
D. doddsi (L)	94	90	95	21	67	23	48	43	34
D. doddsi (S)	94	95	-	70	79	--	15	73	--
D. spinifera*	97	95	-	90	81	--	28	21	--
D. pelosa*	99	95	-	94	81	--	15	23	--
S. tibialis*	97	96	-	82	75	--	21	55	--

*Values for these three species for Cascade Range sites only.

a single day may not be used as efficiently as others. Temperatures may be suitable for growth for only a few hours on some days (see Vannote et al. 1980). If this is true it may be unsuitable to use mean daily temperatures to standardize growth rates for temperature among sites. Far more precise records of temperature changes within a day and over the growth period as well as rather precise knowledge of the metabolic response to temperature by a species would be needed to accurately account for the effect of temperature in the field.

Temperature and size may interact to influence the shape of growth curves. Specific growth rate is always affected by size, and $\underline{G}$ invariably decreases as mass increases (Minot's Law; Minot 1908, Brody 1927, 1945, Medawar 1945, Richards and Kavanagh 1945), This relationship has been clearly demonstrated for an aquatic amphipod by Sutcliffe et al. (1981) and has important implications for patterns of growth and emergence in aquatic insects.

Unless growth is exactly exponential (i.e. $\underline{G}$ does not change with mass) comparison of growth rates can be difficult unless initial sizes of animals compared are equal. Many of the species that I examined showed declining growth rates as mass increased. This trend was especially evident over the entire growth curve of the species. I attempted to minimize confounding effects of size by calculating growth rates over sections of the curves where growth was exponential. In doing this I was not able to control exactly for the size range over which growth was calculated. Including initial size as a parameter in the growth models often increased the percent of the total variation in size explained over time. The interaction of temperature and size is probably manifested through an effect on values of Q_{10} for growth. For a unit increase intemperature, specific growth will increase more for a small individual than for a larger one (Brody 1927, also see Fig 16).
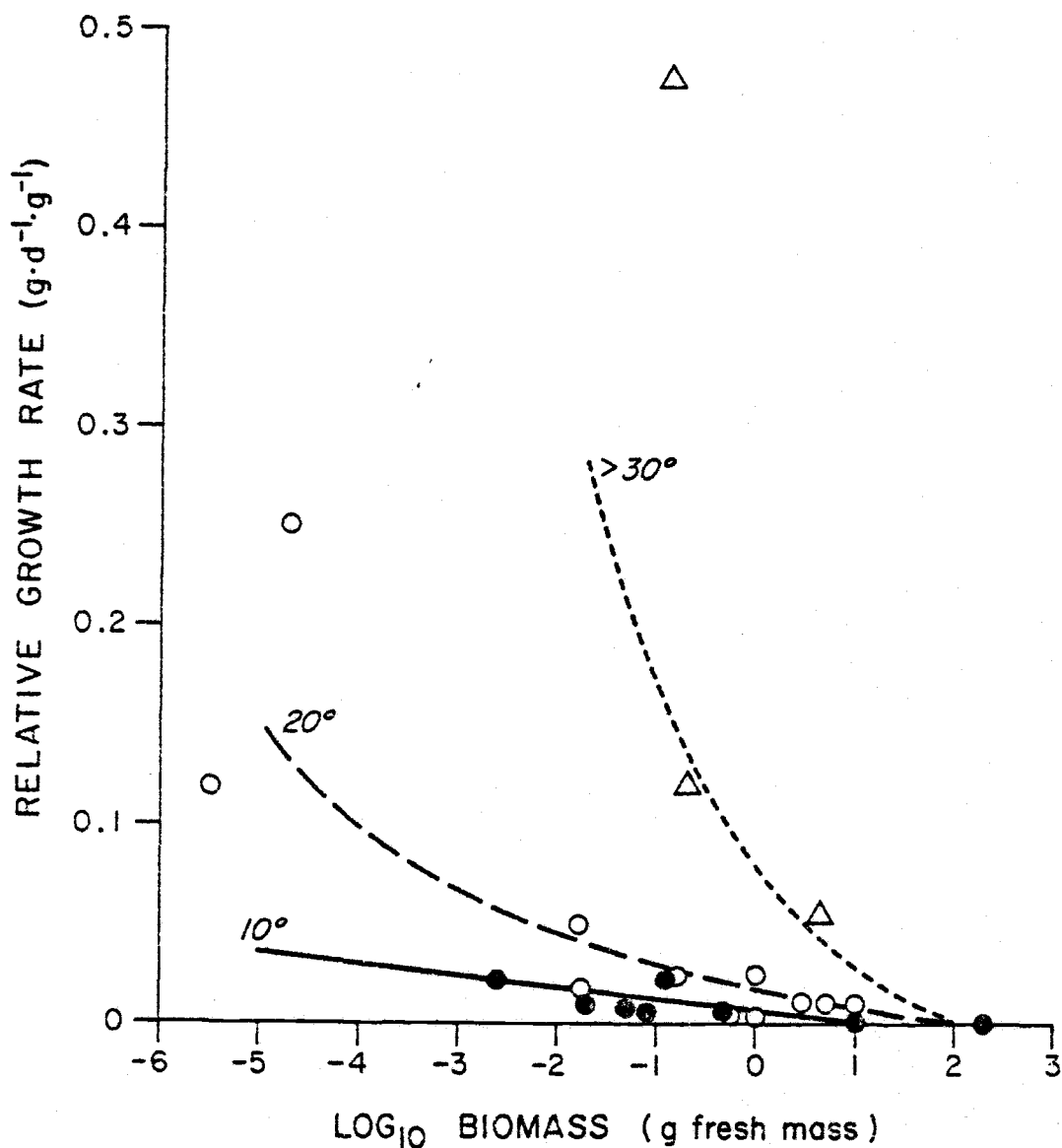
Figure 16.   Relationship between relative growth rate, size, and
             temperature. Symbols represent growth rates at 10° (●),
             20° (○), and > 30° (△). Size is fresh mass at maturity.
             Relative growth rate calculated as maximum observed growth
             rate (g/d) divided by adult mass (g). Data are for a
             variety of invertebrates. Figure from unpublished
             manuscript of the author.

A common pattern for northern streams was delayed hatching of eggs with subsequent rapid growth. Inhibition of hatching or slow growth apparently occurs during winter followed by rapid growth as streams warm up quickly. The difference between winter and summer temperatures for Alberta streams is greater than for more southern streams. Thus, Alberta streams warm up more rapidly and may reach higher temperatures than Oregon streams. The consequence of such differences in temperature regime appears to be a short pulse of rapid growth for species that begin growth in late winter (e.g. coloradensis, Fig. 7, Gorge Creek) or whose growth is interrupted by ice cover during the winter (doddsi, Fig. 8, Kananaskis River). This trend is not evident for infrequens which begins growth in late summer or early autumn (Fig. 5) and that grows continually over the winter.

The relationship between size and growth rate has implications beyond explanation of differences in growth rate among streams. Timing and duration of the life cycle are important life-history traits: both of which are probably tightly linked to habitat characteristics. In a subsequent section (Habitat Relationships), I consider the relationship between growth rate, habitat specificity, and habitat stability.

Although temperature and photoperiod may interact to influence shape of developmental curves (Beck 1980), no obvious effect of photoperiod on growth rate was observed. Multiple regression models with degree-days and photoperiod as independent variables did not explain more variation for pooled data than did temperature alone (infrequens, $R^2 = 0.58$, r^2 for temperature $= 0.58$; coloradensis, $R^2 = 0.72$, $r^2 = 0.71$; doddsi, $R^2 = 0.68$, $r^2 = 0.67$). Because temperature and daylength are often correlated, the relative influence of either variable cannot be convincingly determined from these data. Direct manipulation of temperatures and photoperiod by experimentation is necessary to do so.

Effect of Food on Growth Rate

Many studies now exist that implicate food (either quantity or quality) as an important factor influencing growth in aquatic invertebrates (see reviews by Monakov 1972, Cummins 1973, Anderson and Cummins 1979, Cummins and Klug 1979, and recent papers by Willoughby and Sutcliffe 1976, Mackey 1977, Ward and Cummins 1979, Sutcliffe et al. 1981, Fuller and Mackay 1981). Many more studies exist for terrestrial insects (see Waldbauer 1968, Mattson 1980, Scriber and Slansky 1981 for extensive reviews). Most of the literature describes response of animals to laboratory experiments, whereas no study of which I am aware has unequivocally related growth in the field to differences in food sources. McMahon et al. (1974) report significant correlations between growth of snails and limpets with aufwuchs quality but did not report possible effects of temperature. Anderson and Cummins (1979) also report a significant correlation between food, as measured by P/R ratio, and individual mass attained as prepupae for Glossosoma nigrior (r^2 = 0.95, n = 4 as determined from data in Table 3 of Anderson and Cummins 1979). It is impossible, however, to determine whether growth was influenced by food or temperature, because biomass of prepupae was also correlated with degree-days (r^2 = 0.95, n = 4).

Consideration of my results leads to the conclusion that differences in food availability among streams will seldom affect individual growth rates, but rather response to food will more often be an adjustment of population densities. In this view, population responses act to limit food availability so that field growth rates are lower than those under ideal conditions (e.g. laboratory rearing), but differences in per capita food availability among streams will vary little. Thus, individual growth rates will vary little among streams as a result of differences in food. This type of response was observed by Cummins et al. (1980) for a shredder of

coarse detritus. Indeed, high overall food availability may actually lead to depressed individual growth rates relative to food supply rather than higher rates because of interference interactions among individuals as demonstrated for frog larvae by Wilbur (1977) and Hota and Madhab (1981).

There is reason to suspect that food limitation exists in the stream systems that I examined. Densities of most species were more abundant in streams with highest amount of high quality algal food (e.g. cf. MAOG and MACC, MILL and FAWN in Table 7, see Gregory 1980 for primary production in MAOG and MACC, see section on Food Habits for abundances). Specific growth rates of E. infrequens were much higher in the laboratory (up to 5.2) when provided unlimited food than observed under any field situation (1.2-2.9). Humpesch (1979) has noted similar differences between laboratory and field growth rates for other mayfly taxa. Food has been experimentally determined to be limiting for a stream caddisfly consuming aufwuchs (Hart 1981) and implied to be so for a snail, Juga plicifera, common in many of the streams that I studied. Growth rates of this snail when given unlimited food in the laboratory, were much greater than in nature (McCullough, unpublished data). Indirect evidence for food limitation is given by Bohle (1978) and Thorup (1966) who demonstrated that density and aggregation of Baetis mayflies were correlated with amount and distribution of algal food. In a comparison of the invertebrate and vertebrate communities of the same six Cascade streams considered here, Murphy et al. (1981) and Hawkins et al. (1982a, see also 1982b) showed sites open to sunlight to have significantly greater abundances of invertebrates than similar but shaded sites. Other studies cited in Murphy et al. (1981) have shown similar differences between open and shaded streams.

In Figure 17, I show how growth rate may vary as a function of both temperature and food. I use the concept of "scope for growth"
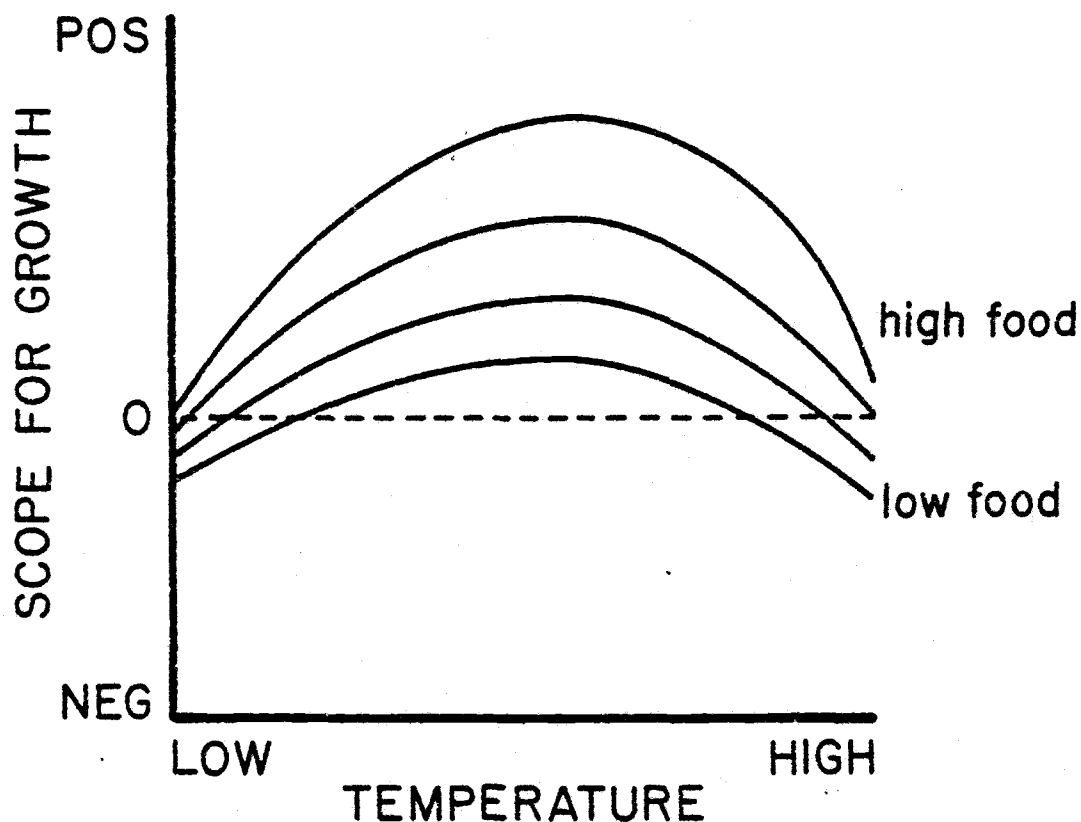
Figure 17. Theoretical relationship between growth rate, temperature, and food. The model is based on bioenergetic relations discussed by Warren and Davis (1967). Scope for growth is defined in the text. Note that the range of growth rates possible both within a level of food availability and among sites that differ in food availability is greatest at an optimal intermediate temperature and low for both low and high temperatures.

developed by Warren and Davis (1967) as modified from Fry's (1947) original use of the term scope. Scope for growth is defined as the difference between the energy value of all food an animal could consume and the energy losses and uses of food other than growth.

I have portrayed these relationships (Fig. 17) to show how scope changes with temperature and food. Each line represents maximum growth possible at a given temperature and level of food. Actual growth rates depend on the particular set of environmental conditions present other than food and temperature and will usually be somewhat less than maximum.

From this model, it can be hypothesized that a range of growth rates is possible at temperatures optimal to growth both within a single food treatment and among food levels. At suboptimal temperatures, range of growth is limited by metabolic constraints, and few differences ought to be expected either within systems of similar food availability or among streams.

This model does not consider how density and individual growth are related. It is useful, therefore to consider how the two parameters may interact. My data show no relationship between growth and density. Streams with high densities showed similar growth rates as streams with low densities. Other studies have shown that density and growth are often inversely related (see Warren 1971). Either high densities reduce per capita food availability and cause low individual growth and stunted animals as has been observed with many fish populations (e.g. Beckman 1941, Yoshihara 1952, examples in Calhoun 1966), or conversely high individual growth may cause low density as argued by Botsford (1981) for some fisheries. I think it is significant, however, that this inverse relationship has been most often observed for populations in closed systems such as lakes (also see Bowen 1979) rather than in open systems like streams.

I suggest that in stream systems increased food production results in increased carrying capacity and an accompanying increase in density. However, with higher densities, per capita food availability may change very little. Hence, although densities in open systems like streams may attain levels sufficient to limit individual growth (cf. laboratory results), they do not reach high enough levels to cause severe depression of growth rates. The reason severe depression of growth rates does not occur may be due to the open nature of stream systems. "Excess" individuals are lost by drifting out of the system (see Waters 1969) in contrast to closed systems like lakes in which excess individuals cannot leave.

FOOD HABITS AND ABUNDANCE

Methods

Food Habits

I examined the contents of 362 individual guts from 20 different species. These data were used to examine the following relationships.

1. What food sources did different species ingest?
2. How did site (stream reach) affect percent composition of food consumed?
3. How did habitat (cobble, gravel, etc.) affect percent composition of food consumed?
4. How did diet vary with size of animal?
5. To what extent were species food specialists or generalists?

I determined gut contents by the methods described in Coffman et al. (1971). After noting the length of each animal, the anterior portion of the gut (foregut) was removed. Contents were teased out into numbered wells of a spotting plate, each of which was filled with distilled water. The gut wall was carefully separated and removed from gut contents. The remaining bolus was then dispersed by agitating with a dissection needle. Once gut contents were thoroughly mixed, the suspension was filtered through a 13 mm gridded Millipore filter (0.45 m). Filters were then placed on a drop of light immersion oil. After the filter had cleared (24 h), excess oil was blotted from the underside of the filter and a permanent slide prepared with Permount and a #1 cover slip.

I examined each slide to determine the proportions of diatoms, detritus, animal matter, moss, wood, fungal mycelia, and other algae (unicellular and colonial green, and bluegreen forms). The number of diatom frustules observed within an entire ocular grid (196 squares) at 450 power magnification was counted in ten randomly chosen fields. At 100 power magnification, the total number of squares within the grid that were covered by the other food sources was noted for five randomly chosen fields. At 450 power the ocular grid covered 2.46×10^{-2} mm^2 of filter. At 100 power the ocular grid covered 0.49 mm^2 of filter and each square represented 2.5×10^{-3} mm^2.

The area of filter covered by each food class was calculated based on either direct measures of area (all food classes but diatoms) or conversion of diatom counts to area of diatoms. The most commonly observed diatoms in guts were large <u>Achnanthes</u> and <u>Melosira</u> spp. I assumed that each diatom covered 2×10^{-4} mm^2 of filter. This value was based on occasional measurements of individual diatoms and literature values for these taxa. If significant numbers of smaller diatoms were observed, they almost always were present as dense aggregations. In this case I estimated area directly in the same manner described for detritus.

Abundances

During spring, summer, and autumn of 1978, quantitative samples of the benthos were taken at the six main study sections. These samples were collected as part of a larger study of differences in macroinvertebrate communities among these sites (see Murphy et al. 1981, Hawkins et al. 1982a for details). Three riffle samples and three pool samples were collected from each site on five different dates. Samples were collected with a modified Surber sampler (see Newbold et al. 1980 for design). Animals as small as 100 m were

captured, but only individuals retained by a 1 mm mesh sieve are considered here. On three of the sampling dates (June, August, and October) replicate samples were processed separately. On the other two dates (July and September) replicates were pooled before processing. Data are presented as mean density or standing crop observed each month.

Data for different species from these samples were used to compare abundances between streams that differed markedly in availability of food sources. I used data from only four of the six streams, because these reaches provided two sets of paired (shaded:open) sites. The old-growth section of Mack Creek (MAOG) was paired with the downstream clearcut section (MACC), and Fawn Creek (open) was paired with Mill Creek (shaded). These data were limited in that they did not include all habitats or all species found in each stream. Data are compared by inspection and paired t-tests.

Additional data on abundance were collected during April and June of 1979 and February of 1980 in conjunction with transect sampling for habitat preferences (see Habitat Section). From these data I calculated mean abundances of all species at each sampling station. These data are more extensive than the other benthos data in that more samples over specific habitats were taken.

Results

Food Habits

Among the 20 species examined, diatoms and detritus were the most commonly consumed food items and together composed from 48-100 percent of material ingested (Table 21). Animal matter was an important component in five species. Of these species, four belong to the genus _Drunella_, and animal matter represented 15-48 percent

Table 21. Mean percent composition by area of different food classes and dietary niche breadth (B_i) for 20 species of western Ephemerellidae. Data are combined over all sites and habitats.

Species	n	Diatoms	Detritus	Animal	Moss	Wood	Fungus	Algae	B_i
C. cascadia	21	37	41	0	20	1	1	0	2.90
C. hystrix	23	44	35	4	15	2	0	0	2.94
C. edmundsi	17	55	26	0	19	0	0	0	2.46
C. heterocaudata	6	39	30	15	15	0	0	1	3.48
S. teresa	21	33	48	1	17	0	1	0	2.71
S. tibialis	13	32	58	10	0	0	0	0	2.23
S. velmae	9	56	43	1	0	0	0	0	2.01
E. infrequens	60	18	55	5	8	12	1	1	2.79
E. inermis	3	20	73	0	0	0	0	7	1.73
E. verruca	3	25	75	0	0	0	0	0	1.60
E. aurivillii	2	0	96	0	0	0	2	2	1.08
D. spinifera	34	21	27	48	3	1	0	0	2.87
D. doddsi	36	57	9	31	0	0	1	1	2.34
D. pelosa	29	72	26	0	2	0	0	0	1.71
D. coloradensis	65	53	19	25	1	2	1	0	2.63
D. grandis	5	17	50	23	4	0	1	5	2.98
A. delantala	6	1	99	0	0	0	0	0	1.02
A. margarita	3	20	80	0	0	0	0	0	1.47
E. lodi	2	0	99	0	0	0	0	1	1.02
T. hecuba	4	46	54	0	0	0	0	0	1.99

Column header span: Food Class (Diatoms, Detritus, Animal, Moss, Wood, Fungus, Algae)

Handwritten margin annotations: Caudatella; Serratella; intestinal forager; Drunella; mobile grazer; Eurylophella; Timpanoga. "most general" (next to C. heterocaudata); "most specal" (next to E. aurivillii); "sit and wait predator" (next to D. spinifera).

of ingested material among these species. Moss composed up to 20 percent of the gut contents. Five species had 15 percent or greater of total gut contents represented by moss. Of these species, four belong to the genus Caudatella, the other to Serratella. Wood, fungal mycelia, and other algae were poorly represented (<12% but usually <5%) in all species.

Dietary niche breadths varied from 1.02 to 3.48. The most highly specialized species (B_i <1.80) were all detritivores (1.02 - 1.73) with the exception of D. pelosa (1.71) that mainly consumed diatoms. The most general species (B_i >2.80) were species of Caudatella and Drunella. In the former, diatoms, detritus, and moss were found in significant quantities; in the latter, diatoms, detritus, and animal matter were important items.

Consumption sometimes varied with type of food associated with a site or habitat. For example, Mack Creek (clear-cut section), Lookout Creek, and Fawn Creek were all open to full sunlight, whereas the old-growth section of Mack Creek and Wycof Creek were shaded. In the open streams 57 percent of food consumed by D. coloradensis was diatoms, whereas in the shaded streams diatoms constituted only 38 percent of ingested material (Table 22). Also note that both coloradensis and E. infrequens ingested more wood when collected from wood than from other habitats (Table 23). When all species are considered, these trends were not always so clear, and differences in food consumption among sites or habitats could not easily be attributed solely to differences in food availability.

I examined 11 species to determine whether size influenced composition of the diet. Six species showed significant correlations between size and percent of at least one food class (Table 24). All species did not respond in the same manner, but when all individuals were examined over all species, consumption of animal matter was positively correlated with size. Conversely, percent diatoms in the gut was negatively correlated with size.

Table 22. Proportions of different food classes observed in the guts of different species collected at different sites.

Species	Site*	n	Food Class							G^+	d.f.‡	P
			Diatoms	Detritus	Animal	Moss	Wood	Fungus	Algae			
C. hystrix	MACC	9	39	46	8	7	0	0	0			
	LOKC	8	59	25	4	12	0	0	0	66.06		<0.001
	COUG	3	40	17	0	43	0	0	0	(6)		
C. cascadia	UMACK	6	27	33	0	37	1	2	0			
	MAOG	6	48	40	0	10	1	1	0			
	MACC	4	31	69	0	0	0	0	0	95.04		<0.001
	COUG	2	26	12	0	62	0	0	0	(8)		
	PARK	3	53	45	0	2	0	0	0			
S. teresa	UMACK	6	13	62	0	21	0	4	0	8.87		<0.012
	MILL	10	33	43	2	22	0	0	0	(2)		
E. infrequens	UMACK	6	5	54	0	27	13	2	0			
	MAOG	3	16	77	0	6	0	0	0			
	MACC	12	12	73	7	2	1	1	3			
	FAWN	3	34	50	16	0	0	0	0	2140.85		<0.001
	MILL	3	33	16	0	50	0	0	0	(30)		
	COUG	2	0	86	0	14	0	0	0			
	LOKC	18	26	65	3	5	0	0	0			
D. coloradensis	MAOG	7	39	39	13	2	0	7	0			
	MACC	15	58	22	19	0	0	0	0			
	LOKC	11	52	19	27	0	0	0	1	99.68		<0.001
	FAWN	11	62	7	31	0	0	0	0	(15)		
	COUG	2	86	13	0	2	0	0	0			
	WYCO	11	32	10	53	4	0	0	0			
D. spinifera	MAOG	11	22	26	45	2	3	1	1			
	MACC	7	14	18	64	3	0	1	0			
	LOKC	1	0	8	90	0	0	0	2	65.60		<0.001
	MKZR	9	35	34	24	5	0	0	0	(15)		
	MILL	3	8	30	62	1	0	0	0			
	COUG	3	6	29	62	2	2	1	0			
D. doddsi	MAOG	6	50	29	19	2	0	0	0			
	MACC	11	56	5	37	0	0	2	0	117.91		<0.001
	LOCK	7	59	3	31	0	0	0	7	(6)		
	FAWN	3	96	3	0	0	0	0	0			
	COUG	1	0	5	95	0	0	0	0			
	WYCO	1	75	25	0	0	0	0	0			

* Abbreviation of sites given in text except for: LOKC = Lookout Creek (Sites IV and V), UMACK = Upper Mack Creek (Site I), PARK = Parker Creek (Marys River Drainage), and MKZR = McKenzie River (Sites VII and VIII).

† A G-test (Sokal and Rohlf 1981) was used to test for differences in diet among sites. Sites with n < 3 are not included in the test. If all cells in a column < 5, then those cells were combined with the next largest cell in each row.

‡ Degrees of freedom given in parentheses.

Table 23. Proportions of different food classes observed in the guts of different species collected from different habitats.

Species	Habitat*	n	Diatoms	Detritus	Animal	Moss	Wood	Fungus	Algae	G†&d.f.	P
C. hystrix	TB	3	51	15	5	29	0	0	0	--	--
	CR	1	16	17	0	67	0	0	0		
	W	1	9	43	0	0	47	0	0		
C. cascadia	W	3	65	32	0	0	3	0	0	2.96	<0.084
	M	3	53	45	0	2	0	0	0	(1)	
S. teresa	M	3	72	28	0	0	0	0	0	43.31	<0.001
	CR	6	38	40	1	21	0	0	0	(2)	
E. infrequens	W	12	12	24	9	0	52	2	0		
	CR	9	29	57	3	10	0	0	0	183.21	<0.001
	G	10	22	75	3	0	0	0	0	(8)	
D. coloradensis	CR	18	40	16	40	3	0	0	1		
	G	11	57	16	27	0	0	0	0	686.97	<0.001
	TB	3	17	14	68	1	0	0	0	(9)	
	W	6	65	19	0	0	16	0	0		
D. spinifera	W	9	23	27	45	1	4	0	1	17.48	<0.001
	CR	4	6	24	70	1	0	0	0	(3)	

* Abbreviations for habitats are: top of boulder (TB), cobble or rubble (CR), gravel (G), wood (W), and moss (M).

† G-test and degrees of freedom as in Table 22.

Table 24. Correlations between size (mm) and percent composition of different food items in the gut. Percentages transformed (arcsin) prior to analysis. Values given are correlation coefficients (r). $P < 0.05 = *$, $P < 0.01 = **$.

Species	n	Diatoms	Detritus	Animal	Moss	Wood	Fungus
C. cascadia	18	0.191	0.149	--	-0.369	0.027	-0.518*
C. hystrix	23	-0.550**	0.166	0.203	0.398	-0.213	-0.117
C. edmundsi	17	-0.115	-0.609**	0.313	0.573*	--	--
S. teresa	21	0.660**	-0.550**	-0.183	0.001	--	-0.412
S. tibialis	13	-0.095	-0.199	0.160	0.424	--	--
E. infrequens	60	-0.129	-0.177	0.109	0.295*	0	0.080
D. spinifera	33	0.037	0.050	-0.016	-0.057	-0.035	-0.128
D. doddsi	36	-0.067	-0.324	0.211	-0.255	--	-0.165
D. coloradensis	65	-0.313**	-0.138	0.433**	0.144	-0.168	-0.142
D. pelosa	29	-0.463*	0.256	0.179	0.330	--	--
D. grandis	5	-0.863	-0.371	0.394	0.245	--	0.158
ALL SPECIES	359	-0.115*	-0.099	0.257**	0.008	-0.034	-0.067

Three species (hystrix, coloradensis, and pelosa) showed
negative associations between size and percent consumption of
diatoms. In S. teresa the relative amount of diatoms consumed
increased as size increased. Of all 11 species, eight showed
negative (although not necessarily significant) correlations
between size and percent ingestion of diatoms, a result not expected
by chance alone (P = 0.03, two-tailed test, Binomial distribution).

The proportion of detritus consumed also tended to decline with
size. Two species, teresa and edmundsi, showed significant negative
correlations; and among all 11 species, seven correlations were
negative (P = 0.11).

Both animal matter and moss increased in relative abundance
with size. Percent animal matter in D. coloradensis was strongly
correlated with size, and percent moss was significantly correlated
with size for both infrequens and edmundsi. The number of species
exhibiting positive correlations between either animal matter or
moss and size was eight in both cases. Both results were probably
not due to chance (P = 0.01 for animal matter, P = 0.03 for moss).

Abundances

I compared the abundance of four species (infrequens,
coloradensis, doddsi, and tibialis) at the two sets of paired sites
(shaded vs. open). Open sites always had higher mean densities of
these four species than the shaded sites, although differences
between sites were not always statistically significant when
compared by paired t-tests (dates = paired samples, Table 25). The
maximum differences observed between densities in riffles were a
32-fold difference for infrequens, a 3.8-fold difference for
coloradensis, and 3.1-fold difference for doddsi, and over a
200-fold difference for tibialis. Ephemerella infrequens was the
only species common in pools and showed a maximum abundance in the

Table 25. Mean densities and standing crops (mg) per 0.1 m^2 for different dates. Sites were paired MAOG:MACC and MILL:FAWN to provide contrast between shaded and open sites.

Riffles

Species & Date	Density				Biomass			
	MAOG	MACC	MILL	FAWN	MAOG	MACC	MILL	FAWN
E. infrequens								
19 Jul	0	.0	0.3	0	0	0	0.01	0
14 Aug	0.3	0.7	0	16.0	0	0.04	0	0.02
20 Sep	2.0	64.3	5.7	51.3	0.24	0.64	0.03	0.93
10 Oct	15.0	62.0	9.0	95.3	0.32	1.88	0.23	2.16
	$t(6) = 2.97, P < 0.05$				$t(6) = 2.43, P < 0.10$			
D. coloradensis								
10 Jun	2.3	8.7	0	2.0	0.87	4.09	0	4.90
19 Jul	1.5	5.0	0	0	6.14	30.28	0	0
14 Aug	0	0.3	0	0.3	0	0.62	0	0.05
	$t(5) = 2.04, P < 0.10$				$t(5) = 1.44, P < 0.40$			
D. doddsi								
10 Jun	6.7	8.0	0.3	0	0.42	0.04	0.05	0
19 Jul	15.0	42.0	0.3	2.7	3.08	6.06	0.09	0.40
14 Aug	27.0	84.7	0.7	1.0	1.03	2.93	0	0.05
20 Sep	16.0	26.0	0	0.3	10.95	24.06	0	0.60
10 Oct	10.3	18.7	0.3	0	16.25	43.10	0.38	0
	$t(9) = 1.82, P < 0.20$				$t(9) = 1.61, P < 0.20$			
S. tibialis								
10 Jun	4.3	14.7	0	3.7	0.19	0.92	0	3.35
19 Jul	0.5	11.7	0	4.0	0.04	6.10	0	3.60
14 Aug	0	6.7	0	5.3	0	2.21	0	5.04
20 Sep	0	1.0	0	0	0	1.72	0	0
	$t(6) = 4.33, P < 0.01$				$t(6) = 4.59, P < 0.01$			

Pools

Species & Date	Density				Biomass			
	MAOG	MACC	MILL	FAWN	MAOG	MACC	MILL	FAWN
E. infrequens								
10 Jun	0	0.7	0	0	0	0.60	0	0
19 Jul	0	0	0	0	0	0	0	0
14 Aug	3.0	1.0	0	0	0.03	0.07	0	0
20 Sep	3.7	29.0	0	3.0	0.05	0.44	0	0.05
10 Oct	10.0	187.0	24.7	6.0	0.14	4.65	0.26	0.25
	$t(6) = 1.04, P < 0.40$				$t(6) = 1.28, P < 0.40$			
D. coloradensis								
10 Jun	9.3	6.7	0	0	5.21	3.86	0	0
19 Jul	0.7	0.7	0	0	2.55	3.99	0	0
D. doddsi								
14 Aug	0	12.3	0.3	0	0	0.22	0.04	0
20 Sep	0	1.0	0	0	0	1.17	0	0
10 Oct	1.7	3.3	0.3	0	0.20	1.57	0.09	0
	$t(5) = 1.18, P < 0.40$				$t(5) = 1.64, P < 0.20$			

sunlit streams of about 19 times that observed in the shaded sites. Differences in biomass generally paralleled differences in density.

Seven species were collected during transect sampling of the old-growth site (II) and clear-cut site (III) sections of Mack Creek. Six of these species were more abundant in the clear-cut section (Table 26.). I also compared mean densities among samples from all shaded reaches of Mack Creek (sites I, II) to mean densities among samples collected from three downstream reaches that were open to sunlight (sites III, IV, V). Of the 12 species collected, 10 were more abundant in open reaches than shaded sections (Table 26). Both of these comparisons indicate that most species were more abundant under those environmental conditions associated with full sunlight.

Discussion

Food Habits

Because they have been reported to be extremely facultative in the type of food they consume, many aquatic insects are considered to be trophic generalists (Muttkowski and Smith 1929). The difficulties that opportunistic feeding habits impose on development of trophic models have led some researchers to adopt alternative classifications of trophic relationships (e.g. Cummins 1973, 1974). Few studies, however, have been thorough enough to examine variation both within and among species. I believe such an approach is necessary if concepts of specialization and opportunism are to be meaningful. I therefore was interested in determining how much variation existed among species, and whether variation within species could mask differences observed among taxa.

Examination of gut contents can lead to insights regarding food requirements only if such static measures are truly representative

Table 26. Mean densities of species of Ephemerellidae in open and shaded reaches. Comparisons are between sites II (shaded) and III (open) and between two shaded sites (I, II) and three open sites (III, IV, V). Data are number per 0.1 m^2 and are means of densities observed on three dates (April, June, February.

Species	Two Sites		Five Sites	
	Shaded	Open	Shaded	Open
C. cascadia	0.4	0.1	0.7	<0.1
C. hystrix	0.2	1.8	0.2	1.6
C. edmundsi	---	---	0	<0.1
C. heterocaudata	---	---	0	0.3
S. teresa	---	---	1.2	0
S. tibialis	---	---	0	0.7
E. infrequens	0.4	1.7	0.7	6.8
D. spinifera	0.1	0.2	0.1	0.1
D. doddsi	0.5	0.6	0.4	0.7
D. pelosa	0.1	2.4	0.1	4.4
D. coloradensis	0.1	0.5	0.1	3.7
A. delantala	---	---	0	0.1

of the dynamic relationship between ingestion, assimilation, and growth. Because so few studies exist describing such relationships, I have assumed that gut contents do reflect ingestion of preferred and thus "nutritious" food items. I recognize that the validity of this assumption is open to criticism. Some correspondence, however, between ingested food and assimilatable food is expected if animals maximize their fitness through their feeding behavior.

When I considered all individuals and taxa, species differed in their gut contents (Table 21). It is possible that chance differences can be erroneously interpreted as significant and thus of ecological importance. Nevertheless, these data seem to indicate that among species in this family, preferences for certain food items exist that transcend variability within taxa due to differences in site or habitat (cf. Tables 22, 23).

Gilpin and Brusven (1970) presented the only other comprehensive data on gut contents of western Ephemerellidae. Comparison of their data (Table 27) with mine (Table 21) show certain similarities in food items ingested by different species, but there are also some major differences. For example, E. infrequens/inermis (they lumped these species) show similar food habits in both data sets, as do S. tibialis, D. grandis, A. margarita, and T. hecuba. In constrast, D. doddsi and D. coloradensis/flavilinea show distinct differences.

Differences in these two sets of data may be due to a variety of factors. Dissimilarity of food sources associated with each stream system may be important, but some of the apparent differences may be an artifact associated with small sample size. When comparing dietary niche breadths among species, small values of B_i were associated with small sample size. The reason sample size can influence B_i is because niche breadth was calculated based on mean proportions of different food items ingested over all individuals in a species and not by averaging B_i's for each individual within a

Table 27. Data on diet of 12 species of Ephemerellidae from Gilpin
and Brusven (1970). Data are percent composition by area.

Species	n	Food Class					B_i
		Diatoms	Detritus	Animal	Moss	Algae	
C. hystrix	4	31	47	0	5	17	2.87
C. edmundsi	3	21	70	0	3	7	1.85
S. teresa	2	22	70	0	0	8	1.84
S. tibialis	88	29	55	1	2	14	2.46
E. infrequens*	104	24	60	1	3	12	2.31
D. spinifera	1	5	15	80	0	0	1.50
D. doddsi	30	29	45	3	1	22	2.98
D. coloradensis	7	28	51	7	0	13	2.78
D. flaxilinea	74	24	56	2	0	17	2.50
D. grandis	81	27	50	5	2	16	2.85
A. margarita	10	25	54	0	0	21	2.51
T. hecuba	33	38	44	1	1	16	2.75

* includes inermis.

species. Sample size and niche breadth were correlated ($r = 0.45$, P <0.05, $n = 20$) for my data although not significantly so for the data of Gilpin and Brusven (1970) ($r = 0.27$, P = NS, $n = 12$). When both data sets are combined, the correlation coefficient also is significant ($r = 0.35$, P <0.05, $n = 32$).

When I compared niche breadths between sites for each species, no correlation existed between values of B_i ($r = -0.14$, $n = 11$). If species with less than four individuals are excluded the correlation coefficient becomes positive, although not significantly so ($r = 0.60$, $n = 6$). These data further indicate that sample size may bias estimates of niche breadth, and also suggest that the dietary breadth of a species is not entirely determined by locality (see below).

The observation that both site and habitat affected proportions of ingested material lends credence to the conclusion of Muttkowski and Smith (1929) and later echoed by Cummins (1973) that "local conditions beget local results" (see Fox and Morrow 1981 for a cogent discussion of such phenomena among terrestrial insects). It must be noted, however, that even though the percent of a food class consumed varied with locality for some species, such variation did not appear to be sufficient to completely mask differences that exist among species (cf. Tables 21, 22, 23). For example, plotting dietary niche breadths for species studied by others against niche breadth that I observed for the same species showed a positive relationship (Fig. 18). Species that had small niche breadths in my study had small niche breadths in other studies, and species with large niche breadths in my study had large niche breadths elsewhere. Points that were not close to the theoretical line predicting exact agreement were derived from data based on small sample size (white circles on graph).

Other examples exist that suggest ephemerellid species often consume a restricted range of food types. Shapas and Hilsenhoff
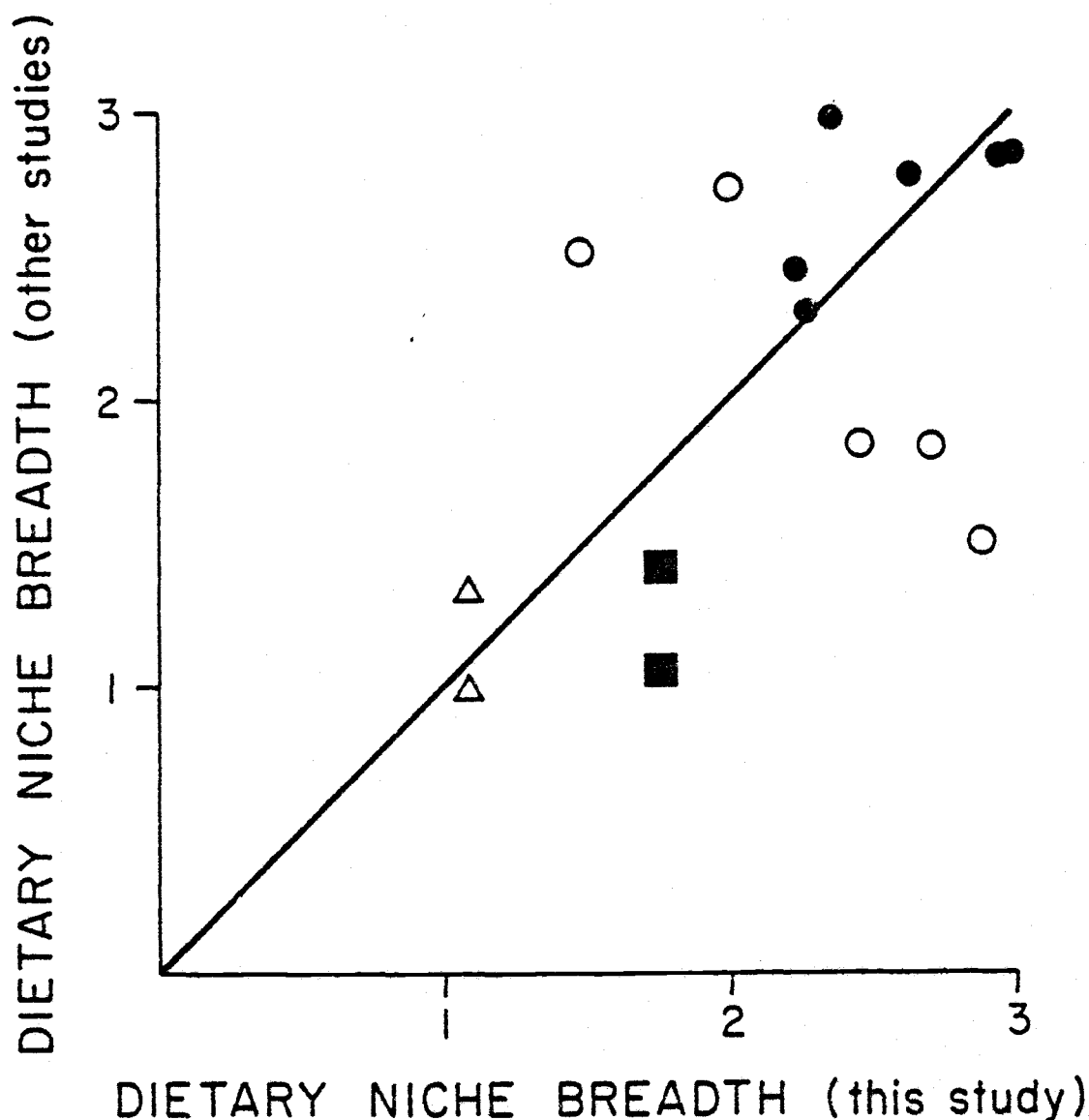
Figure 18. Relationship between dietary niche breadth of species observed in this study compared with other studies. Circles represent comparison of my data with that of Gilpin and Brusven (1970). Triangles are comparison of data with Shapas and Hilsenhoff (1976). Squares are comparison of data with Gray and Ward (1979). Open symbols represent values derived from data based on small sample size.

(1976) report that E. aurivillii in Wisconsin consumes between 85-100 percent detritus depending on the season; the rest of the diet was composed of diatoms (4-15%) or filamentous algae (4%). In Oregon, I found that it consumed 96% detritus, 2% filamentous algae, and 2% fungal mycelia (Table 21). Gray and Ward (1979) found the E. inermis consumed between 68 and 98 percent detritus and 2-31 percent diatoms depending on the season. The overall value they gave for the one site was 82 percent detritus and 18 percent diatoms; for another site the percentages were 98 and 2 respectively. Both sites produced results similar to those that I observed.

The data of Gray and Ward (1979) and of this study suggest that diet may not always vary within species as strongly as previously observed. Gray and Ward showed that diet of major herbivore-detritivore species did not differ significantly between sites that differed markedly in food availability. I compared diet of 11 species studied by Gilpin and Brusven (1970) to diet of the same species in my study. For each species I calculated overlap values by the formula of Pianka (1973) where:

$$O_{ij} \text{ (overlap)} = \sum_{a}^{n} p_{ia}p_{ja} / [(\sum_{a}^{n} p_{ia}^2)(\sum_{a}^{n} p_{ja}^2)]^{1/2},$$

and

p = proportional use of some resource a by two species i and j, and

n = number of resource classes.

The mean overlap between populations of these species was 0.858. Mean overlap among all species that I studied was 0.764 (see Niche Section). These results indicate that populations of the same species are more alike in their diets than are populations of

different species (P <0.05, n = 11, t-test after arcsin transformation). In an earlier study, Coffman et al. (1971) suggested "that availability of food is the dominant factor influencing composition of the diet." Coffman et al. qualified their statement by implying differences in diet may occur mainly within food categories (i.e. detritus, algae, etc.). It seems apparent, however, that far more detailed and comprehensive data are necessary in order to determine the relative influence of locality (i.e. food availability) and the dietary constraints specific to a species.

Consumption of certain food items also varied with size of the animal, often in a systematic manner. Age- or size-specific variation in feeding habits is well documented (Coffman et al. 1971). and has been cited as evidence of the opportunism of feeding (Cummins 1973). Coffman et al. (1971) noted that the percent of diatoms and algae in guts increased as size increased. This trend was not evident for most of the species that I studied (Table 24). Although it is difficult and often dangerous to offer a posteriori explanations, the causes responsible for the relationship that I observed likely involve changes in feeding efficiency or ability with size. As size increased, animal material (live prey) and moss increased in relative abundance in guts, whereas detritus and diatoms decreased. Both fine detritus and loose diatoms can be ingested by small larvae. On the other hand, to engulf animals or to shred large pieces of plant material, organisms require larger gapes, more powerful mouthparts, or both.

Data presented in the section on Life Histories and Growth (Table 18) show that large larvae of E. infrequens grew well on alder leaves but that smaller larvae did not. This result could be due to the inability of small larvae to shred particles from the leaf surface when feeding. In Figure 19, I show leaf discs that were offered to large and small infrequens and the relatively large
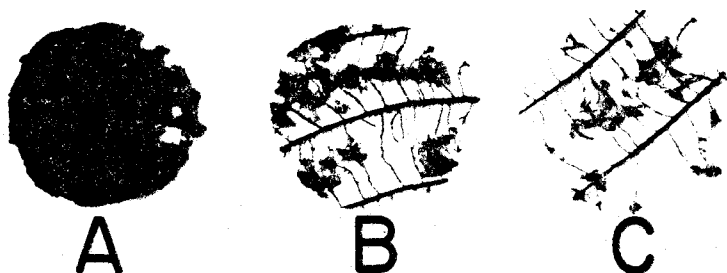
Figure 19. Leaf discs fed upon by small and large larvae of
Ephemerella infrequens and large larvae of E. verruca.
Discs were placed in flasks for seven days. Each flask
had five mayflies. Disc A = small E. infrequens; disc
B = large E. infrequens; disc C = large E. verruca.

E. verruca. Large larvae fed easily on leaf tissue, whereas small larvae did not.

In summary, I have shown that site, habitat, and size all influence composition of the diet. Given such trends, it is understandable that stream insects have often been considered trophic generalists or opportunists. The relationship between locality and consumption may indeed reflect a certain degree of flexibility in what is consumed. The relationship with size is apparently more systematic and often describes shifts toward larger food. In part, this trend may reflect a tendency to take in more nutritious food (animal prey, see e.g. Anderson 1976), but it probably involves some incidental ingestion of large pieces of vegetation and animal material as other food items are fed upon.

It is unclear whether moss is preferentially consumed because of its food value or if pieces are bitten off when attached diatoms are fed upon. Of the aquatic macrophytes in streams (not including macroalgae), mosses are more often eaten than others (Hynes 1941, Chapman and Demory 1963, Gaevskaya 1969), and two species of European Ephemerellidae have been shown to consume copious amounts of moss (Percival and Whitehead 1929). It would therefore be surprising if these species were not deriving some direct benefit from the consumption of such quantities of moss.

Even considering the influence of locality and size, differences in ingestion among species persisted. To use Hutchinson's (1981) terminology, many species of aquatic insects may be selective omnivores. This is an important point, I think, for it draws attention to the necessity of determining how selective and how opportunistic species are. Part of the problem, and hence perhaps the solution, lies in a matter of perspective and context. The relative amount of variation in diet among populations of a species must be compared with variation in diet among different species. Such partitioning of variation must be recognized to develop a broad perspective of trophic relations of aquatic insects.

My data are not thorough enough to precisely specify the relative importance of locality and size compared with differences in consumption due to species specific preferences. Considering the rather marked differences in data and inferences concerning food habits, it would seem worthwhile to examine these relationships in far more detail. Finally, it also is likely that inferences are partly dependent on the theoretical orientation of each researcher. An investigator interested in niche relationships among species and another interested in modeling of general ecosystem trophic structure may interpret the same data differently. In fact, interpretations must always be considered in context of the objectives and scope of each study.

Feeding Guilds

During this study I examined mouthpart morphology of all species encountered and noted feeding behavior whenever possible. It was my intention to relate mouthpart structure to method of feeding. I had wished to know whether systematic correlations existed between either degree of dentation or fusion of teeth on the galea-lacinia and type of feeding (e.g. scraping, shredding). For example, I thought leaf shredders might have robust, separate teeth at the tip of the galea-lacinia, whereas an aufwuchs scraper may have these teeth fused to form a flat scraping blade. Similarly, it would not be surprising for predators to have long, relatively sharp teeth to capture and hold prey. After examining 20 different species, I concluded that structure of the mouthparts was extremely similar and of a generalized nature among species.

On the other hand, feeding behavior was often distinctly different among species. For example, D. spinifera is a sit-and-wait predator that seldom roams in search of food. D. pelosa is a mobile grazer on the tops of stones, and E. infrequens forages actively in interstitial crevices.

I have attempted to identify different feeding groups (guilds) within this family based on what species eat and how they forage. In Table 28, I show six guilds. In all but one case, a combination of traits was necessary to define a guild (cf. Cummins 1973, 1974, Cummins and Klug 1979, Hawkins and Sedell 1981, Hawkins et al. 1982a). Species were placed into a group based on the following criteria: degree to which they 1) scraped (SC) diatoms, 2) shredded (chewed) moss (SH_m), 3) shredded coarse detrital material (SH_d), 4) consumed loose fine detritus (CG), and 5) engulfed living prey (P). These groupings are tenuous, because I lack detailed data describing feeding method or behavior for most species. I offer them as a tentative description of the major avenues along which Ephemerellidae have evolved to exploit food resources. I discuss guild structure further and in more detail in the section on Niche Relationships.

An alternative approach would be to define guilds based strictly on traditional groupings of herbivore, detritivore, and predator. I felt that this approach was of a coarser resolution and therefore less appealing. Because such a classification does not incorporate both food eaten and method of aquisition, it conveys little information regarding important ecological similarities and differences among species.

Abundances

For those species that I examined, a strong tendency existed for abundances to be greater in open streams than shaded ones (Table 25, 26). This occurred regardless of feeding guild, with the exception of species that consume moss or are strongly associated with that habitat.

The differences in abundance among sites for species of Ephemerellidae was similar to that observed for the rest of the

Table 28. Feeding guilds among western Ephemerellidae.

SC	SC/SH$_M$	SC/SH$_D$/CG	SC/P	P/SH$_D$	SH$_D$/CG
D. pelosa	C. cascadia	S. tibialis	D. doddsi	D. spinifera	E. verruca
	C. hystrix	S. velmae	D. coloradensis	D. grandis	E. aurivillii
	C. edmundsi	A. margarita			A. delantala
	C. heterocaudata	T. hecuba			E. lodi
	S. teresa	E. infrequens			
		E. inermis			

SC = diatom scraper, SH$_M$ = moss shredder, SH$_D$ = detritus shredder, CG = fine particle collector-gatherer, P = predator.

invertebrate community (Hawkins et al. 1982a, also see Murphy et al. 1981). Almost all taxa seem to respond positively to an increase in high-quality food as measured by either amount of chlorophyll pigment or microbial respiration (see Table 7). Other researchers have noted similar differences between shaded and open streams (Albrecht 1968, Woodall and Wallace 1972, Lyford and Gregory 1975, Aho 1976, Newbold et al. 1980, Murphy and Hall 1981). Enhanced autochthonous primary production due to high light levels in open sites is apparently the causal link determining high food availability. Primary production in Pacific Northwest streams is often limited by light (Gregory 1980). High levels of primary production apparently can increase food availability to scrapers (diatoms), detritus-shredders (possibly by sloughed and decaying algae), collector-gatherers (high quality FPOM), filterers (high quality seston), and predators (enhanced prey availability).

HABITAT RELATIONSHIPS AND DISTRIBUTIONS

Methods

In April and June of 1979 and February of 1980, I sampled extensively at eight different sites on a longitudinal transect along the McKenzie River system (Fig. 1). At each site I collected from all distinguishable habitats using a standard kicknet (mesh = 0.5 mm). Each sample consisted of 0.1 m^2 of stream bed. Habitats were sampled approximately in proportion to the extent that different habitats occurred at each site. Between five and 22 samples were taken at each site on each date depending on size of stream and diversity of habitats. Habitats were defined on the basis of substrate: 1) tops of boulders and bedrock (TB), 2) areas of cobble and rubble of approximately fist sized stones (CR), 3) areas of gravel and sand with stones <20 mm diameter (G), 4) growths of filamentous and sheetlike algae attached to boulders and cobbles (usually _Prasiola_ or _Vaucheria_), and 5) patches of moss (M). Mosses consisted of _Fontinalis_ sp. in the McKenzie River and a mixture of species at other sites. Each sample was sorted in the field. During sorting I found very few Ephemerellidae associated with algae, so I have deleted that habitat from comparisons.

I used these data to examine distributions of species along the longitudinal gradient of small stream to large river and to describe specific habitat associations of the different species. Densities of different species at each site are reported as unweighted mean densities over all samples. I did not weight densities by habitat because areal proportion of each habitat of each site was not estimated. Similarly, densities for a specific habitat are calculated as mean number observed in a habitat over all sites. Abundances at Site VI (Lookout Creek) were always low (see Appendix H). Because data from this station are so anomalous compared with the rest, I have excluded these data from comparisons.

Results

I collected 14 species during this phase of sampling. Most species showed well-defined distributions with maximum numbers occurring at one or two sites (Fig. 20). Among sites, a longitudinal progression of species occurred. Species that were abundant in the headwaters were usually not found at the river sites and vice-versa. Approximately one third of the species were most abundant at reaches on intermediate sized streams. Data in Figure 20 represent abundances of each species averaged over all sampling periods. Presentation of data in this manner partially adjusted for seasonal shifts in abundance among sites. Tabular data on the abundance of each species for each of the three dates are given in Appendix H.

To compare distributions of different species, I expressed the abundance of each species at a site as the percent of the total number of that species collected over all sites (Table 29). I used these data to calculate the tendency for species to be distributed among few or many sites (i.e. site niche breadth, B_i). Values of B_i given seven sites can vary from 1.00 to 7.00.

Of the 14 species, ten had values of B_i less than 3.00. These species were generally found at three or fewer sites. Five species were found only at one site (B_i = 1.00). Very low values of B_i (<2.00) were occasionally due to a species being rare in general (margarita, hecuba), but more often a species showed moderate to high abundances only at one site (teresa, edmundsi, tibialis; see Fig. 20). An apparently low B_i can also be an artifact of sampling only a portion of a species' true range. Such is probably the case for both hecuba and margarita. Two species were broadly distributed over most sites (doddsi, infrequens; B_i = 4.29 and 3.99 respectively), although infrequens showed a progressive increase in density at downstream sites. Other species
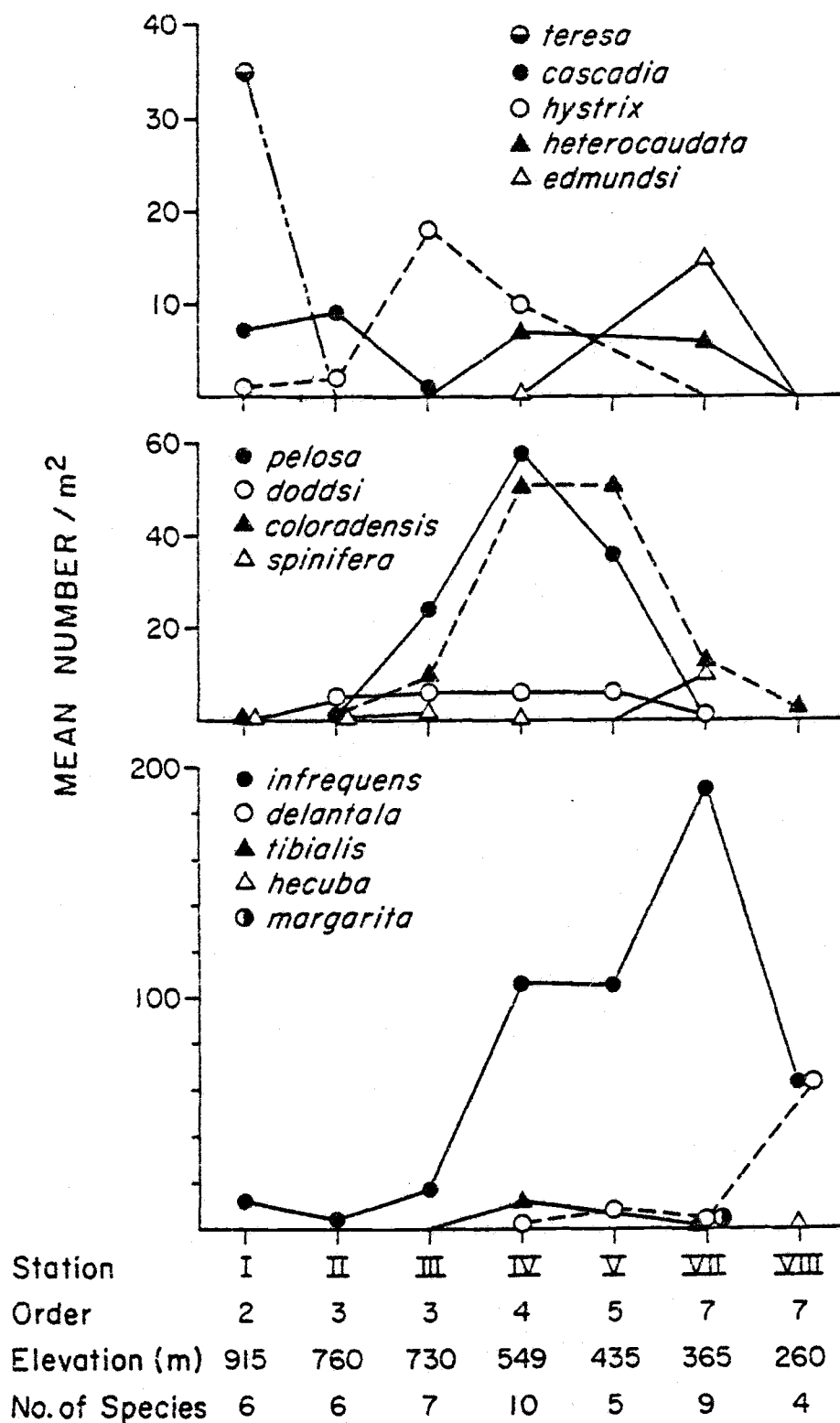
Figure 20. Mean density of species observed at different
            longitudinal stations.

Table 29. Distribution of species of Ephemerellidae among transect stations. Data are percent of total number observed over all stations. Values rounded to nearest percent.

Species	Total Individuals	Station							B_i
		I	II	III	IV	V	VI	VIII	
C. cascadia	29	41	53	6	0	0	0	0	2.21
C. hystrix	84	3	6	58	32	0	0	0	2.26
C. heterocaudata	52	0	0	0	34	33	33	0	3.00
C. edmundsi	611	0	0	0	0	0	100	0	1.00
S. teresa	75	100	0	0	0	0	0	0	1.00
S. tibialis	52	0	0	0	100	0	0	0	1.00
D. pelosa	351	0	1	20	49	30	0	0	2.70
D. doddsi	88	0	21	25	25	25	4	0	4.29
D. coloradensis	149	0	1	11	38	38	10	2	3.21
D. spinifera	41	0	6	12	6	0	75	0	1.71
E. infrequens	968	2	1	3	21	21	38	13	3.99
A. margarita	1	0	0	0	0	0	100	0	1.00
A. delantala	86	0	0	0	1	11	4	84	1.39
T. hecuba	6	0	0	0	0	0	0	100	1.00

(heterocaudata, pelosa, coloradensis) were intermediate in their
distribution among sites (B_i = 2.70 - 3.21).

Each species also showed rather restricted distributions among
different habitats (Table 30). Five species were commonly found in
gravel/sand, nine in cobble, three on tops of boulders, and five in
moss. I arbitrarily considered a species to be common in a habitat
if 10 percent or more of its total density was observed in that
habitat. Data in Table 30 also are averages over all three sampling
dates (see Appendix I for data for each date). The values for
tibialis, delantala, and margarita are approximate because
abundances for these species were generally low. I also considered
data from Gilpin and Brusven (1970) and qualitative observations of
my own to derive approximate values for these three species.

Niche breadths among habitats could vary between 1.00 and 4.00.
Only two species had niche breadths greater than 2.00 (spinifera,
infrequens). Six species had niche breadths less than 1.50
(heterocaudata, edmundsi, teresa, tibialis, doddsi, coloradensis).
These data indicate that species prefer only one or two of the
habitat classes examined. No species showed abundances greater than
10 percent of total density in three or four habitats.

I also was interested in determining if habitat specificity was
associated with either length or timing of life cycles.
Specifically I wished to relate life cycles to the temporal dynamics
(persistence) of different habitats. Quantitiative measures of the
stability or persistence of different habitats in streams are
practically nonexistent. I did not directly measure stability at my
sites, but instead I attempted to rank them relative to one another
and describe in qualitative terms their seasonal dynamics.

Many mosses are perennial plants and form relatively persistent
habitats in streams. Moss was most common in small, shaded
headwater streams and in the McKenzie River. Moss occurred on
boulders and bedrock in the main stream channel of small streams and

Table 30. Percent habitat use by 14 species of Ephemerellidae. Data are mean of three sampling dates.

Species	Habitat				
	Gravel	Cobble	Top of Boulder	Moss	$\underline{B}_i$
$\underline{C}$. cascadia	0	0	54	46	1.99
$\underline{C}$. hystrix	0	6	72	22	1.75
$\underline{C}$. heterocaudata	0	91	9	0	1.20
$\underline{C}$. edmundsi	0	0	0	100	1.00
$\underline{S}$. teresa	1	14	0	85	1.35
$\underline{S}$. tibialis	10	90	0	0	1.22
$\underline{D}$. pelosa	0	32	66	2	1.86
$\underline{D}$. doddsi	9	89	2	0	1.25
$\underline{D}$. coloradensis	8	81	9	2	1.49
$\underline{D}$. spinifera	7	40	0	54	2.19
$\underline{E}$. infrequens	51	46	1	2	2.12
$\underline{A}$. delantala	30	70	0	0	1.72
$\underline{A}$. margarita	70	30	0	0	1.72
$\underline{T}$. hecuba	100	0	0	0	1.00
Number of species with >10% of density in a habitat	5	10	3	5	

was almost always in direct current or wetted by constant splashing. In the McKenzie River, Fontinalis and other mosses occurred in large dense masses on boulders near the stream bank.

Boulders are a physically stable substrate in streams, but offer habitats that differ in their seasonal suitability. The tops of boulders are often the site of torrential currents during late autumn and winter and also are exposed to air as water levels drop during summer. The "window" of relatively benign conditions for this habitat is early spring through mid-summer, a period of approximately five months.

The interstitial spaces beneath boulders and cobbles are relatively stable and present all year. These habitats experience severe physical perturbance only if discharge is sufficient to move large substrates along the stream bed. Periods of high discharge occur during late autumn and winter. The rest of the year (>8 months), cobbles form a stable and dominant substrate in many stream systems.

Gravel and sand are associated with areas of slack current (pools, backwaters, and margins of streams). This habitat is probably the least stable of the four considered here. Moderate to high discharge can scour sand and gravel. The only stable period for this habitat in most Cascade streams is during periods of low flow from late spring to early autumn (<4 months).

Considering only length of time each habitat is stable, their ranking from most to least stable is: moss, cobble, tops of boulders, gravel/sand. The season during which each habitat is suitable, however, varies considerably.

No simple linear correlation emerged between duration of habitat stability and length of life cycle (Table 31). Lack of a significant correlation occurred because species in persistent habitats had both long and short life cycles. There was a tendency, however, in species selecting relatively unstable habitats (top of

Table 31. Length and timing of growing period compared with habitat specificity for 11 species of Ephemerellidae. Habitats are ranked from least to most stable.

Species	Months to Complete Growth		Period of Growth*	Habitat†	Period of Suitability
	100%	90%			
A. margarita	<5	<2	Jul-Aug	G,C	late. spring-summer
A. delantala	<6	<3	Jun-Aug	G,C	spring-summer
E. infrequens	10	4	Mar-Jun	G,C	late spring-summer
D. pelosa	8	3	Apr-Jun	TB	early spring-early summer
S. tibialis	5	3	Jul-Sep	C	spring - autumn
U. coloradensis	11	3	Jun-Aug	C	spring - autumn
D. doddsi	12	6	Dec-May	C,BB	all year
C. cascadia	11	6	Dec-May	M,TB	all year
C. hystrix	11	6	Jan-Jun	M,TB	all year
D. spinifera	12	7	Jan-Jul	M,BB	all year
S. teresa	6	3	Jun-Aug	M	all year

* Months over which 90% of growth is completed (See Table 18).

† Abbreviations are: G = gravel, C = cobble, TB = top of boulder, M = moss, BB = bottom of boulder.

‡ Association with both stable and unstable habitats may make these estimates somewhat inaccurate.

boulders, gravel/sand) for either the entire larval growth period to
be short or for 90 percent of their growth to be completed in a
relatively short period (e.g. pelosa, infrequens, delantala,
margarita).

Timing of growth showed similar relationships with habitat
specificity. Species inhabiting unstable habitats completed their
development (90% of growth) during periods when these habitats were
most stable. For example, D. pelosa grew rapidly in spring and
emerged before tops of boulders were exposed by declining water
levels. Ephemerella infrequens, A. delantala, and A. margarita grow
during spring and summer when gravel and sand is less likely to be
scoured by high discharge. Timing of growth varied considerably for
species associated with more stable habitats.

Discussion

Zonation of stream faunas along longitudinal gradients is well
documented (see reviews by Illies and Botosaneanu 1963, Hawkes 1975,
Williams 1981). Species of most taxa invariably show restricted
ranges along gradients, a phenomena also true for Ephemerellidae
(e.g. Allan 1975a,b, Ward and Berner 1980). The mechanisms
determining these patterns are not always clear, although among the
speculations and hypotheses advanced include the effects of
temperature (Dodds and Hisaw 1925, Ide 1935), food (Wiggins and
Mackay 1978), substrate (discussed in Maitland 1966 and Hynes 1970),
and competition (Beauchamp and Ullyot 1932, Allan 1975b).

Similarly, the spatial distributions of species over smaller
scales (i.e. within a reach) has been shown to vary among species.
These patterns have often been linked to substrate type (Linduska
1942, Cummins and Lauff 1969, de March 1976, Rabeni and Minshall
1977, Williams and Mundie 1978, Wise and Molles 1979, Williams 1980,
and reviews by Hynes 1970, Williams 1981). Other factors, however,

are often correlated with substrate characteristics (e.g. current, depth, food), so it is usually difficult if not impossible to isolate the role of substrate alone.

If habitat is a key factor determining the distributions of stream benthos, pattern at small scales should provide insights into pattern at larger scales. For many of the species that I examined, distributions of species seemed to be correlated with the distribution of suitable habitats among sites.

Among the species I studied, none appeared to be extreme generalists with respect to habitat requirements and thus distributed independently of type of habitat. Although the level of resolution used in distinguishing habitats was rather coarse and emphasized broad differences, it was still somewhat surprising that no species appeared to be a habitat generalist. In fact, habitat specialization may be the rule among stream invertebrates. In a far more extensive analysis of organism-substrate relationships of stream invertebrates, Tolkamp (1980) demonstrated that each of 84 taxa he encountered was overrepresented on one or more of seven habitat classes. The term overrepresented means that the individuals of a taxon were non-randomly distributied among habitats examined. Exactly half of these taxa were strongly associated with only one of the habitats. Only 12 were overrepresented on three or more classes. These results are in apparent contrast to those of Williams (1980) who noted only six of 23 taxa showing strong substrate associations, but differences in habitat classes in Williams's study were not as distinct.

Strong associations with specific habitats have consequences for species beyond the partitioning of spatial resources. To persist, animals also must survive adverse periods, time their life cycles to avoid them, or both. Because habitats differ in their duration of stability and temporal variability, strategies of species exploiting different habitats will likely vary (Southwood 1976, 1977).

Ecologists in general have begun to direct significant attention to the relationship between environmental stability or predictability and life-history phenomena (see reviews by Stearns 1976, 1977, Southwood 1977). Ecologists studying freshwater benthic communities also have explored some of these relationships. Previous studies have emphasized temporary and intermittent streams and ponds (Abell 1956, Clifford 1966, Williams and Hynes 1976, 1977, Wiggins et al. 1980). These authors have mainly attempted to develop empirical lists and classifications of the different groups of taxa that exploit these systems, although both Clifford (1966) and especially Wiggins et al. (1980) developed evolutionary arguments concerning strategies of exploitaiton. Differences in strategies among benthic taxa inhabiting permanent aquatic systems have received far less attention. In fact, very few studies have examined the relationships between life cycles and habitat use among closely related species of any aquatic insects (see e.g. Spence and Scudder 1980).

My data indicate that within and among permanent streams, habitat use places constraints on the type of life cycle that a species may have (Table 30). Both timing and length are restricted for those species on habitats of short duration, whereas a variety of options (presumably influenced by other factors) are available on stable habitats. Because I did not attempt to rank the stability of entire stream reaches, I cannot meaningfully compare the length and timing of life cycles of taxa among different sites. Other data, however, that I have examined indicate that a strong relationship between environmental stability and length of life cycle may exist among stream reaches and systems. In Figure 21, I show typical stream hydrographs of mean weekly discharge for Aravaipa Creek, Arizona, and the Metolius River in Oregon. Aravaipa Creek experiences unpredictable flash floods over more than half of the year that can scour most stream substrates. Conversely, the

ARAVAIPA CREEK

METOLIUS RIVER

MONTH

LENGTH OF LIFE CYCLE
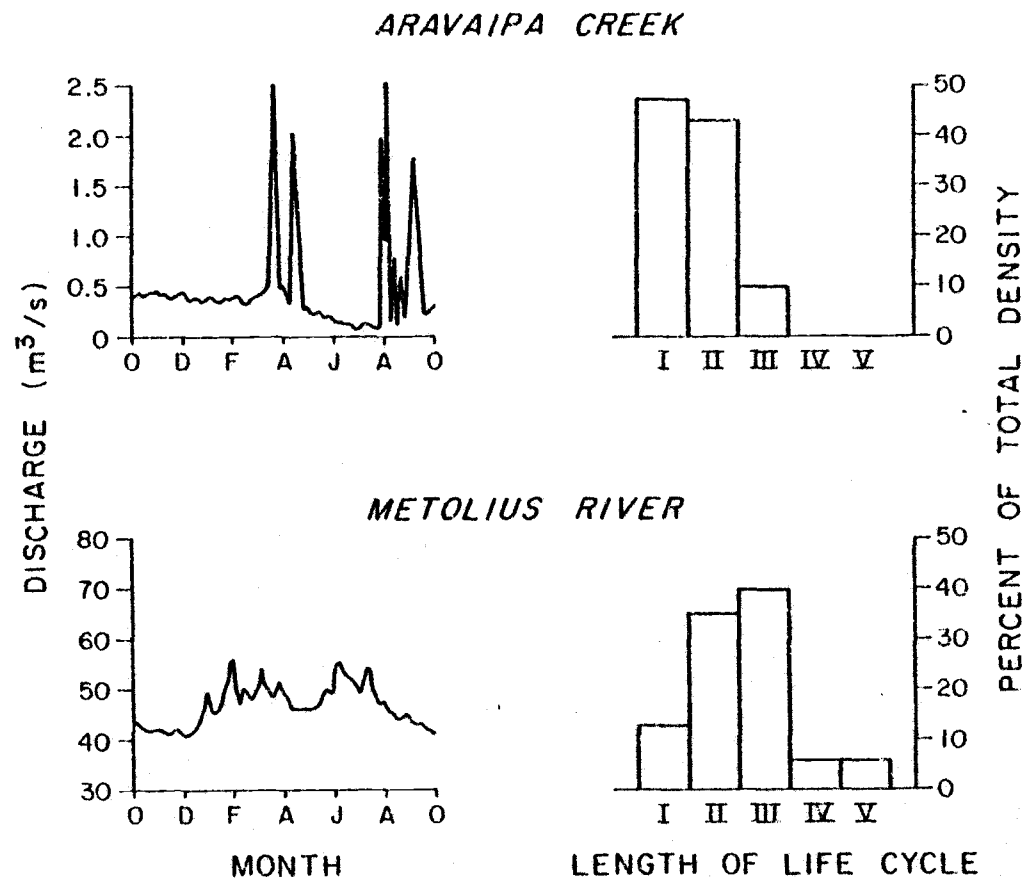
Figure 21. Length of life cycles in two streams of different habitat stability. Life cycles in months are: < 2 (I), 2-6 (II), 6-12 (III), 12-24 (IV), and > 24 (V). Data for Aravaipa Creek from Bruns (1977); data for Metolius River from Anderson (unpublished).

Metolius River has a stable and predictable hydrograph, and as a result substrates are very stable. The ratio of maximum discharge over minimum discharge is 25.0 for Aravaipa Creek and 1.6 for the Metolius River.

Beside each hydrograph I show the percent of total macro-invertebrates (individuals) with life cycles of different lengths. Mean length of life cycle and range of length of life cycles are larger in the stable stream than in the unstable system. These community-level data, together with my data for ephemerellid species, support the contention that life cycles of stream invertebrates are constrained within reasonably defined limits that are imposed by habitat stability. Although many species may inhabit unstable environments merely because they are preadapted by having short life cycles (e.g. constraints associated with phylogeny), some are probably far more intimately tuned to the specific periodicity of a habitat. I discuss adaptations to specific habitats in the next section.

I believe that these data indicate that habitat dynamics are an important factor structuring stream communities. Surprisingly, understanding of the patterns and nature of habitat stability in streams is poorly developed except at rather gross scales (see Lane and Borland 1954, Wolman and Miller 1960, Leopold et al. 1964, Leopold 1973, West 1978, Wolman and Gerson 1978). In the past, relationships between biota and habitat dynamics have most often been viewed in terms of catastrophic events such as severe floods (e.g. Moffett 1936, Hoopes 1974) or more recently volcanos (Anderson and Hawkins, unpublished data). In these cases, the entire stream fauna was either eliminated or greatly reduced in number. Some researchers have noted that habitats within a stream reach vary in their stability (Allen 1951, 1959, Maitland 1964). Unfortunately, these observations have evidently not stimulated steam ecologists to consider how important differences in the dynamics of specific

habitats are for the development and maintenance of community structure and composition in streams. Certainly the recent recognition in other ecosystems that disturbance can differentially affect habitats and their biota and thus influence overall community dynamics (e.g. Horn 1976, Connell 1978, Paine 1979) ought to prompt a critical examination of habitat stability in streams.

NICHE RELATIONSHIPS AND PATTERNS OF ADAPTIVE RADIATION

The primary purpose of this section is to examine how species partition four resource axes (timing of growth, food, and two scales of space) and to describe the interaction of these axes in defining the ecological status of each species. In the context of the niche relationships described, I discuss adaptive radiation within the Ephemerellidae and consider the mechanisms by which present patterns may have arisen. When I use the terms partition, separation, or segregation, I do not imply causation through biological interaction but merely patterns of resource use among species.

Methods

I used data from the previous three sections to analyze niche relationships. For each niche axis, I calculated overlap values (O_{ij}) among species. The equation of Pianka (1973, see Food Habits) was used to calculate overlap values for each niche axis. Values of O_{ij} can vary from zero (no overlap) to one (complete overlap). I also computed values of overall overlap (multiplicative and summation; see May 1975, Pianka et al. 1979). Both estimates of overall overlap give biased values, but represent a measure of maximum (summation method) and minimum (multiplicative) true overlap.

There is some controversy over calculation and use of niche metrics (Colwell and Futuyma 1971, Hulbert 1978, 1982, Abrams 1980, 1982, Linton et al. 1981). Part of the problem stems from use of these indices to "measure" competition. Other problems involve adequacy of different indices to realistically measure true overlap. In this study, I have used overlap only as a descriptive tool to assess pattern among species. Because at this time the relative merits of one index versus another are not clear, I chose a commonly used index (Pianka, 1973) that was relatively easy to calculate.

I examined multidimensional patterns of resource use among species by plotting, for each species pair, values of O_{ij} on one dimension (e.g. food) against values of O_{ij} on another axis (e.g. habitat). The number of points varied from 36 to 82 and depended on the number of species pairs for which I had calculated overlap values for both resource axes.

To determine whether species were clustered into groups (guilds), I used the nearest neighbor technique of Inger and Colwell 1977 (see also Joern and Lawlor 1981). This method consists of first ranking pairwise overlaps for each species along rows. After rankings for each species are computed, a n x n matrix is formed. Means and standard deviations of each column are then calculated. These values are sequentially plotted (n-1 points) on graph paper. If guilds exist and are of approximately the same size, distinct breaks will occur in the line connecting values of mean overlap. If guilds differ in size, distinct breaks in this graph may not be observed, but standard deviations should increase and then decrease (see Inger and Colwell 1977 for a detailed discussion of this technique).

Most methods used to detect pattern within assemblages of organisms are open to methodological criticism. For example, Thompson and Rusterholz (1982) point out problems associated with use of mean pairwise overlap to assess degree of separation among species. The method of Inger and Colwell (1977) to detect groupings of species does not show actual groupings and is not always easily interpreted (see Results). Regardless of these limitations, these methods do allow an initial examination of major trends and patterns.

Results

From data in Table 19 (Growth and Life Cycles), I calculated seasonal overlap in growth for nine species. Values of overlap

ranged from 0.060 to 0.999 (Table 32). Mean overlap among all pairs of species was 0.422.

Dietary overlap was calculated for 20 species from data in Table 21. Values ranged from 0.138 to 1.000 (Table 33). Mean overlap among all species pairs was 0.764. I also calculated mean overlap for species within five different genera. Within genera, mean values were generally very high (0.923-0.973) with the exception of Drunella (0.742).

From data in Table 30, I determined habitat (substrate) overlap among 14 species. Habitat overlap ranged from zero to 1.000 (Table 34). Mean overlap among all pairs was 0.436. I also calculated mean overlap for species in two genera. For Caudatella, mean overlap was 0.350, whereas for Drunella it was 0.579.

Overlap of species among transect stations was calculated for the same 14 species considered for habitat (see Table 29 for data). The minimum value of overlap was zero, the maximum value was 1.000 (Table 35). Mean overlap was 0.278. Among only Caudatella species, mean overlap was 0.150. Among Drunella species, mean overlap was 0.541.

Of the four niche dimensions examined, ecological separation of species was greatest over the longitudinal gradient of small stream to river (mean overlap = 0.278) and least for diet (0.764). Seasonal and habitat overlap were intermediate and of approximately the same magnitude (0.422 and 0.402 respectively). Because species composition varied depending on the niche dimension examined (cf. Tables 32-35), I also calculated values of mean overlap among a consistent set of species for each resource axis (Table 36). Although values changed slightly depending on the number of species examined, the relative amount of separation on one axis relative to others was generally consistent. The only exception occurred for time relative to habitat, but for these two axes overlap values were similar.

Table 32. Overlap in timing of growth among nine species of Ephemerellidae. Values calculated with the equation of Pianka (1973) and can vary between 0 and 1.

	cascadia	hystrix	teresa	tibialis	infrequens	spinifera	doddsi	pelosa
C. cascadia								
C. hystrix	.668							
S. teresa	.177	.194						
S. tibialis	.070	.123	.473					
E. infrequens	.536	.976	.204	.126				
D. spinifera	.485	.705	.433	.251	.689			
D. doddsi	.998	.671	.110	.060	.539	.483		
D. pelosa	.419	.940	.162	.130	.990	.663	.416	
D. coloradensis	.089	.163	.999	.473	.174	.408	.082	.176

Table 33. Dietary overlap among 20 species of Ephemerellidae. Values calculated as in Table 32.

	cascadia	hystrix	edmundsi	hetero-caudata	teresa	tibialis	velmae	infre-quens	inermis	verruca	aurivilli	spinifera	doddsi	pelosa	colora-densis	grandis	delantata	margarita	lodi
C. cascadia																			
C. hystrix	.981																		
C. edmundsi	.930	.968																	
C. heterocaudata	.944	.976	.940																
S. teresa	.990	.957	.875	.921															
S. tibialis	.905	.890	.907	.874	.947														
S. velmae	.924	.964	.933	.922	.913	.908													
E. infrequens	.880	.825	.674	.794	.929	.951	.799												
E. inermis	.836	.774	.619	.731	.903	.957	.797	.956											
E. verruca	.861	.807	.660	.761	.922	.972	.829	.967	.995										
E. aurivilli	.698	.599	.408	.560	.791	.865	.609	.919	.962	.918									
U. spinifera	.561	.612	.509	.757	.583	.687	.572	.605	.533	.546	.457								
U. doddsi	.644	.771	.807	.843	.590	.605	.780	.428	.362	.405	.340	.757							
U. pelosa	.838	.919	.958	.882	.787	.743	.952	.598	.573	.619	.339	.491	.865						
U. coloradensis	.763	.866	.872	.916	.723	.740	.875	.594	.522	.564	.308	.778	.982	.913					
U. grandis	.810	.783	.626	.828	.868	.946	.763	.925	.913	.911	.864	.825	.563	.570	.600				
A. delantata	.704	.607	.417	.567	.796	.871	.617	.922	.963	.952	1.000	.461	.146	.349	.317	.866			
A. margarita	.830	.765	.605	.720	.899	.956	.783	.964	.996	.997	.970	.530	.344	.557	.507	.908	.973		
E. lodi	.698	.600	.408	.560	.791	.867	.609	.916	.961	.949	1.000	.457	.138	.340	.308	.853	1.000	.970	
T. hecuba	.940	.945	.870	.898	.955	.969	.978	.894	.902	.927	.761	.579	.669	.868	.792	.847	.768	.896	.761

Mean overlap:

```
        Total = 0.764
  Caudatella = 0.956
  Serratella = 0.923
 Ephemerella = 0.960
    Drunella = 0.742
   Attenella = 0.973
```

Table 34. Habitat overlap among 14 species of Ephemerellidae. Values calculated as in Table 32.

	cascadia	hystrix	edmundsi	hetero-caudata	teresa	tibialis	infre-quens	spinifera	doddsi	pelosa	colora-densis	delantala	margarita
C. cascadia													
C. hystrix	.915												
C. edmundsi	.648	.291											
C. heterocaudata	.075	.173	.000										
S. teresa	.640	.300	.987	.162									
S. tibialis	.000	.079	.000	.989	.163								
E. infrequens	.030	.076	.029	.668	.146	.747							
D. spinifera	.518	.280	.799	.589	.886	.600	.496						
D. doddsi	.017	.100	.000	.992	.163	1.000	.741	.599					
D. pelosa	.702	.900	.027	.523	.098	.433	.306	.280	.454				
D. coloradensis	.099	.190	.024	.995	.186	.994	.737	.615	.996	.531			
A. delantala	.000	.073	.000	.915	.154	.957	.908	.585	.954	.401	.947		
A. margarita	.000	.031	.000	.392	.075	.493	.946	.328	.484	.172	.479	.724	
T. hecuba	.000	.000	.000	.000	.012	.110	.000	.101	.098	.104	.742	.394	.919

Table 35. Station overlap among 14 species of Ephemerellidae. Values calculated as in Table 32.

	cascadia	hystrix	edmunds	hetero-caudata	teresa	tibialis	infre-quens	spinifera	doddsi	pelosa	colora-densis	delantala	margarita
C. cascadia													
C. hystrix	.042												
C. edmundsi	.000	.000											
C. heterocaudata	.000	.283	.572										
S. teresa	.609	.045	.000	.000									
S. tibialis	.000	.481	.000	.589	.000								
E. infrequens	.045	.257	.759	.920	.040	.419							
D. spinifera	.076	.182	.981	.607	.000	.079	.788						
D. doddsi	.386	.739	.083	.648	.000	.518	.587	.237					
D. pelosa	.042	.675	.000	.756	.000	.805	.564	.116	.849				
D. coloradensis	.032	.501	.179	.893	.000	.681	.728	.262	.830	.949			
A. delantala	.000	.006	.047	.108	.000	.012	.352	.047	.077	.073	.105		
A. margarita	.000	.000	1.000	.572	.000	.000	.759	.981	.083	.000	.179	.047	
T. hecuba	.000	.000	.000	.000	.000	.000	.000	.000	.000	.000	.036	.990	.000

Table 36. Mean overlap among species of Ephemerellidae for four different niche axes.

| | Nine Species* | | Fourteen species* | | | Total Speciest | | |
	All	Drunella	All	Drunella	Caudatella	All	Drunella	Caudatella
Time	.422	.371	--	--	--	.422	.371	--
Food	.769	.798	.768	.798	.957	.764	.742	.967
Habitat	.445	.579	.401	.579	.350	.401	.579	.350
Station	.349	.541	.278	.541	.150	.278	.541	.150

* Species composition is identical for each resource.
† Includes all species encountered. Species composition varies among resources.

Overall niche overlap rarely exceeded 0.700 (summation), or 0.100 (multiplicative)(Table 37). I point out that the ecological significance of these overall values is unclear. Mean values among species were very similar to values obtained when random values of O_{ij} for each species were assigned to each niche dimension. When values of O_{ij} are randomly assigned, the expected value of mean overlap is 0.500 (summation) and 0.0625 (multiplicative).

When all species pairs are considered, no relationships emerged between overlap along one dimension and overlap along another (Fig. 22). Specifically, there was little indication that overlap in one dimension was either positively or negatively correlated with overlap in another resource. When I considered only species within a genus, a few relationships emerged. Among species of Drunella, seasonal overlap was negatively related to dietary overlap ($r = -0.923$, $n = 6$, $P < 0.01$). For these same species, overlap in season also showed a tendency to be negatively correlated with both station overlap and habitat overlap, although these relationships were not significant ($r = -0.807$, station; $r = -0.799$, habitat; $n = 6$, $P = NS$). Dietary overlap showed a tendency to be positively related to both habitat overlap and station overlap indicating that diet was associated with spatial distribution in this genus (see Food Habits). Neither of these trends, however, were statistically significant. Habitat overlap and station overlap also were positively correlated, but only weakly so. Among species of Caudatella, no trends among overlap values were apparent as observed for species of Drunella.

I examined distributions of species along dimensions of food and habitat for evidence of guild structure. Neither graphs of mean overlaps nor standard deviations of overlaps indicated grouping in use of food. Both curves were smooth; mean overlap decreased and standard deviation increased harmonically with increasing rank. For habitat, the graph of mean overlap declined smoothly, but standard

Table 37. Overall niche overlap among nine species of Ephemerellidae. Numbers in top
half of matrix are multiplicative, numbers in bottom half of matrix are
summation values.

	cascadia	hystrix	teresa	tibialis	infre-quens	spinifera	doddsi	pelosa	colora-densis
C. cascadia		.025	.045	.000	.001	.011	.004	.010	.000
C. hystrix	.652		.003	.004	.016	.022	.038	.525	.013
S. teresa	.589	.374		.000	.001	.000	.000	.000	.000
S. tibialis	.244	.393	.396		.038	.008	.019	.034	.237
E. infrequens	.372	.534	.330	.561		.163	.100	.102	.055
D. spinifera	.377	.445	.476	.404	.645		.052	.011	.051
D. doddsi	.512	.570	.216	.546	.574	.519		.139	.067
D. pelosa	.500	.859	.262	.528	.614	.388	.646		.081
D. coloradensis	.246	.430	.477	.722	.556	.516	.723	.642	

Mean overlap	Summation	Multiplicative
Total =	0.495	0.052
Drunella =	0.572	0.067
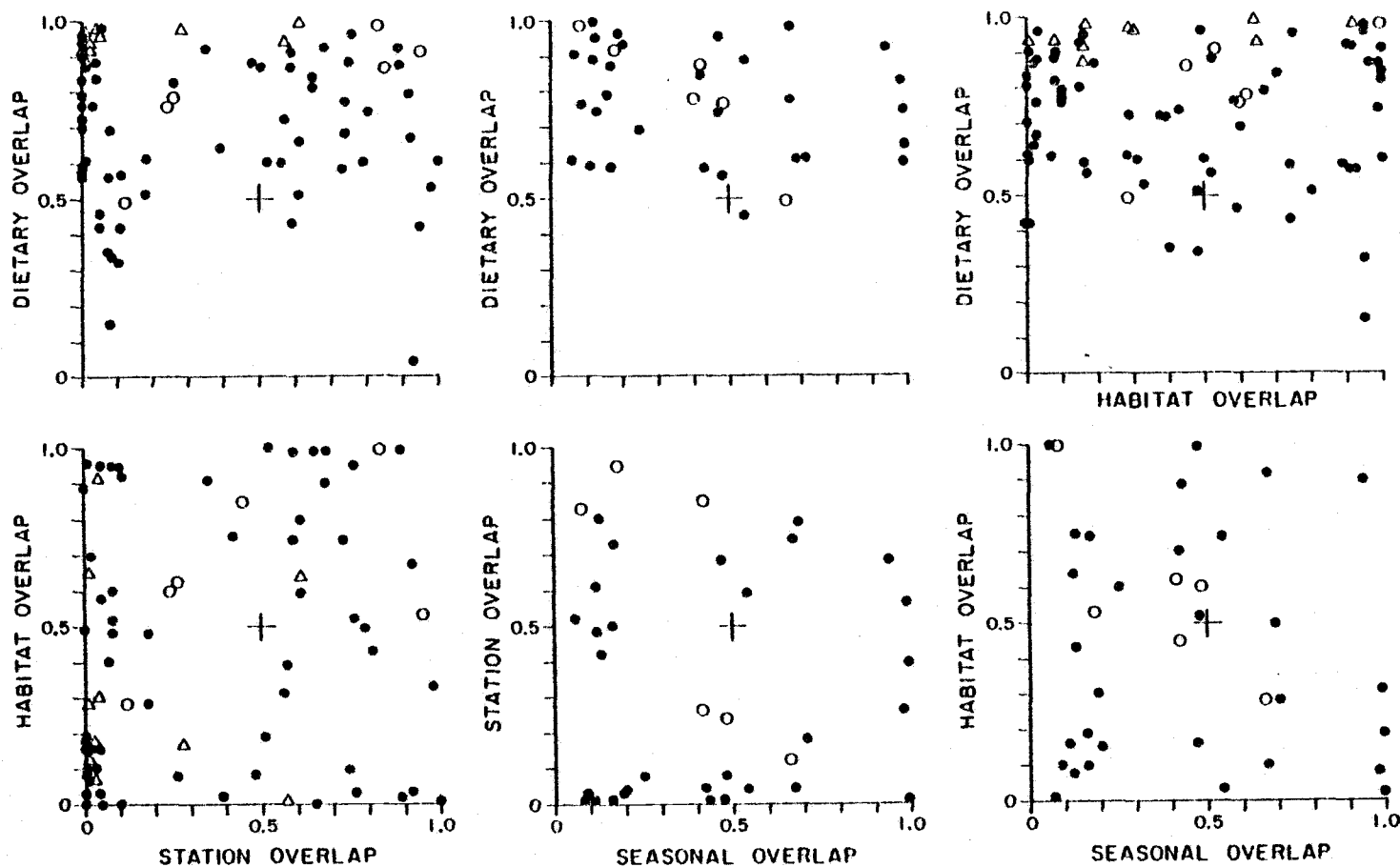
Figure 22. Pairwise species overlap on one niche dimension plotted against overlap between the same species on other niche dimensions. Open symbols are congeneric pairings: _Drunella_ (O) and _Caudatella_ (△).

deviations peaked suggesting some grouping of species may be occurring (Fig. 23). However, a graph of standard deviations based on observed values of habitat use randomly rearranged among habitats for each species also showed a peak. Although this peak is not as strong, its presence indicated that the observed peak for real data may be an artifact of the method rather than a reflection of true ecological groupings of species.

Discussion

Resource Axes and Separation of Species

Multidimensional patterns of resource use among closely related species of aquatic insects have not often been studied (Grant and Mackay 1969, Green 1974, Hildrew and Edington 1979). Neither are the data from these studies always in agreement with respect to the relative importance of different niche dimensions. For example, Grant and Mackay (1969) considered 13 pairs of species and concluded that time of occurrence was most important in segregating species, station (longitudinal gradient) next most important, and substrate least important. Green (1974) on the other hand observed herbivore-detritivore species to be more spatially (habitat) separated than temporally so, although he found carnivores to be more separated in time. Grant and Mackay's observation are in apparent contrast to the more extensive findings of Schoener (1974) who concluded after reviewing a large amount of literature on both terrestrial and aquatic animals that habitat dimensions are usually more important than temporal dimensions. Green's data are generally consistent with Schoener's conclusions. Schoener did note, however, a tendency for habitat to be less often the most important dimension for aquatic animals. Because neither Grant and Mackay nor Green considered food in their analyses, it is impossible to contrast the
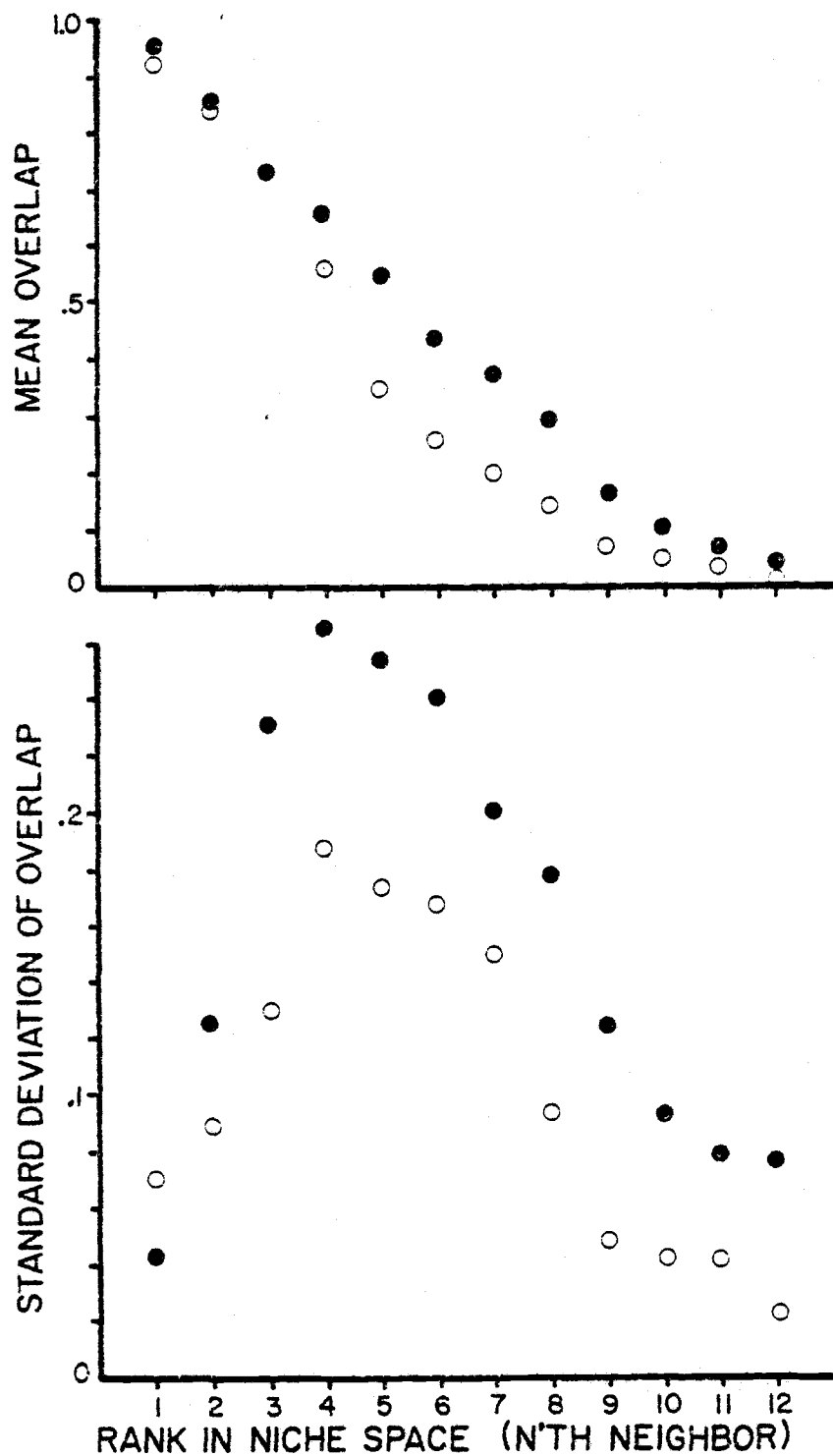
Figure 23. Inger-Colwell analysis for guild structure among
species of Ephemerellidae in habitat use. Dark circles
are observed data; open circles are randomized data.
See text for explanation of analysis.

importance of food relative to the other dimension that they did study. Schoener, however, observed that food partitioning was the second most important niche axis in separation of species.

My data are consistent in large part with the observations of both Green and Schoener. Segregation was most pronounced among stations, was intermediate for habitat and time of year, and was least for food. My observations differ from those of Schoener in that I found food to be less important than time. My data also support Green's observation that carnivores are most strongly separated by time (see Table 36, Drunella).

Schoener (1974) also provided many examples of complementarity between resource axes in separating species. For example, if two species overlapped strongly in habitat, they showed little overlap in diet. With exception the of species of Drunella, little evidence for complementarity was observed. Moreover, many species of Drunella were just as likely to show similar overlaps on two axes; that is, low overlap on one dimension was associated with low overlap on another dimension, and high overlaps were similarly associated. High overlaps on both axes (e.g. dietary and habitat, Fig. 22) were probably due in part to both resources being correlated and not completely independent of one another (see below).

Of the four niche axes used in this analysis (station, habitat, time, food), only food and habitat are direct measures of resources actually used by individuals or of environmental conditions that impinge on the activity of an individual. The gradient from headwater stream to river (stations) represents a complex shift in physical and biological features (Vannote et al. 1980) that can either singly or in combination influence the success of a species. At least five important environmental variables shift from small stream to river and are often correlated with one another: current (shear stress), substrate particle size, temperature, dissolved oxygen, and food. It should not be surprising then that mean

overlap was least among stations, in that differences in species
occurrence among stations are probably due to the integrated effects
of many factors.

Time of year also is an index to a number of important
variables, the most important of which are light, temperature (see
Fig. 3), current velocity, and food availability. The well
documented effect of temperature on growth rates of different
species (see section on Growth and Life Cycles) and the fact that
all species tend to show optimal temperatures for growth and
development strongly imply that seasonal segregation among species
is mainly an effect of adaptation to different temperatures.

Even where measures of a resource are more or less direct (e.g.
food and substrate), these resources often are components of a more
complex interacting milieu of variables that are inextricably
correlated with one another. Because adaptations of organisms are
almost always integrated to solve problems posed by a complex
environment (Ricklefs 1979), the interactive nature of component
variables within stream environments must always be considered when
comparing niche differences and patterns of adaptive radiation.
Some examples are useful to consider with respect to Ephemerellidae.

Adaptations and Niches

Species living on the tops or sides of boulders (e.g. pelosa,
doddsi, heterocaudata) and in moss (cascadia, edmundsi, spinifera)
must almost certainly cope with, among other factors, rapid current
commonly associated with these habitats. The morphological traits
of many species reflect adaptations to and even dependence on high
current (Dodds and Hisaw 1924). For example, D. doddsi and pelosa
both have profuse ventral setae (in doddsi as a suction disc, in
pelosa as a brush) that help them cling to smooth stone surfaces and
that reduce the likelihood of their being swept away by swift

current. These species also are either markedly flattened (pelosa)
or streamlined (doddsi), a further adaptation to swift current.
Neither species survived long when placed in still water (personal
observation) indicating strong respiratory dependence on the high
oxygen tension of flowing water.

Those species inhabiting moss in swift currents (cascadia,
edmundsi, spinifera) all have long, barbed dorsal tubercles. By
snaring strands of moss, these spines probably reduce the chance of
an individual being swept away by swift current. This argument is
strengthened by the fact that S. teresa, which inhabits moss in less
rapid water, does not have long tubercles. Caudatella hystrix, a
sister species to cascadia, is found less often in moss than
cascadia and has smaller tubercles than cascadia. Furthermore, C.
heterocaudata, a species not associated with moss, except weakly so
by food, has very small tubercles. Hynes (1961, 1970) developed
similar arguments for the adaptive value of spines in both
Ephemeroptera and Plecoptera that inhabit moss.

Those species that inhabit sand and gravel substrates show none
of the specialized features discussed above, but often show
adaptations clearly related to the slower currents associated with
deposition of small particles. Three species are rather clumsy
crawlers (infrequens, delantala, margarita) that inhabit either the
interstitial spaces between particles or the surface of small
substrates. None show marked streamlining. Timpanoga hecuba is the
only species among this group that shows extreme morphological
adaptations. It is dorso-ventrally flattened and has copious setae
over the entire body that presumably keep silt away from the gills
and body surface. It is worthwhile to note that those species
occurring in very slow valley streams and slow, sandy reaches of the
Willamette River are either more hairy than their upstream
counterparts (e.g. E. inermis cf. infrequens) or have operculate
gills that keep silt away from respiratory surfaces (Eurylophella
lodi).

The food habits of some species also tend to vary with their habitat preferences (cf. section on Food Habits). Species that inhabit tops and sides of boulders and cobbles consume diatoms, animals, or both. McIntire (1966, 1968) has shown that primary production and algal biomass are highest at relatively high current velocities, currents where boulders and cobble are dominant substrates. Moss dwellers consume significant quantities of moss. Those species that inhabit sand and gravel consume, largely if not entirely, detritus. In areas of slack curent where sand and gravel are found, detritus is deposited and is usually the most abundant food source.

As indicated earlier, the close relationship between food availability and physical habitat is probably responsible for the positive relationship between habitat overlap and dietary overlap observed for species of Drunella and to a lesser extent species of Caudatella (Fig. 22). A similar positive relationship was observed for species in these two genera in overlap in diet and station. On the other hand, overlap in diet was inversely related to timing of growth.

Patterns and Mechanisms

The mechanisms by which patterns arise and are maintained in communities are often frustratingly difficult to address. Examination of patterns can suggest mechanisms but cannot exclude all alternative explanations. It is not my intention at this point to attempt a critical appraisal of all hypotheses that may account for patterns. It is useful, however, to consider how likely some mechanisms may be relative to others.

Interspecific competition, either past or present, has often been invoked as a major, if not the most important, mechanism underlying patterns of abundance, distribution, and resource use

(see discussions by Pianka 1976, Connell 1975). Patterns generated
by competition may ostensibly be the result of either active
interactions maintaining separation (e.g. Thienemann 1912, Beauchamp
and Ullyot 1932, Lock and Reynoldson 1976) or the consequences of
either past or infrequent interactions (Connell 1980, Wiens 1977).
Unfortunately it is difficult to test competition hypotheses against
either null hypotheses (random patterns) or alternative explanations
(see discussions by Strong et al. 1979, Strong 1980, Grant and
Abbott 1980, Feinsinger et al. 1981, Lawton and Strong 1981, Diamond
and Gilpin 1982, Gilpin and Diamond 1982), and neither are the
ultimate effects of competition necessarily directly approachable
through experimentation (Connell 1980). Inferences concerning the
effects of competition are therefore often based on circumstantial
evidence, because competition is so difficult, and sometimes
impossible, to show.

By examination of my data, I can only assess how probable
competition may be as an important mechanism producing pattern among
ephemerellid speceies. Three species of Caudatella and Serratella
teresa are strongly associated with moss (Table 30). Another
species of Caudatella, heterocaudata, does not appear to be
associated with moss as a habitat, but its food habits link it to a
previous moss association (Table 21). Species of Caudatella show
strong longitudinal segregation (Fig. 20, mean overlap = 0.150).
The rather uniform distribution of species among sites implies that
competition may have been responsible for longitudinal zonation
among species (see Allan 1975b for another discussion of competition
and longitudinal distribution in stream insects).

Competition may have facilitated adaptive radiation within
species of Caudatella by gradually displacing populations
downstream. Populations displaced downstream would become less
dependent on moss as a resource. This interpretation is consistent
with observed patterns of resource use among species. The headwater

(cascadia) is strongly associated with moss for both food and habitat, as is S. teresa. In intermediate reaches of stream where moss is less common, hystrix shows a strong association with moss as food but a weaker association with moss as habitat. In the main channel of the McKenzie River, heterocaudata shows only a weak association (food) with moss. A fourth species (edmundsi) also occurs in the McKenzie River, but is again strongly associated with moss (Fontinalis) both for food and habitat. It is possible that because Fontinalis is both a predictable and abundant resource, a dependency on moss was reestablished by edmundsi. It may be, however, that this species is more typically a headwater species. I have also found it in small, Fontinalis-choked streams of the Oregon Coast Range. The occurrence of edmundsi in the McKenzie River may be due in part to the unusually stable discharge and temperature regimes of the upper and middle sections of this river that allow Fontinalis to persist. Species of Fontinalis do not generally occur in other rivers of this size in Oregon.

Drunella species do not show distinct longitudinal separation (Fig. 20), but do exhibit relatively low overlap in timing of growth and intermediate overlap in both habitat and station (Table 36). These species also may partition habitat more finely than I measured. For instance, D. pelosa is restricted to the tops of boulders and cobbles, doddsi occurs more on the sides of boulders and cobbles than the tops (see Linduska 1942), coloradensis also occurs on boulders and cobbles but usually under these substrates (Dodds and Hisaw 1924) or in slower currents (personal observation), and spinifera inhabits moss and lurks beneath boulders. Competitive pressures among species may have enhanced adaptive radiation in the use of habitat. Although compensatory reduction in overlap in habitats compared with stations is not evident, compensatory segregation between habitat and timing of growth was observed (Fig. 22).

For competition to be a viable hypothesis as an explanation of niche segregation, resources must be limiting often enough to produce differential survival of individuals within and among species. It is important to note that some ecologists maintain that density-independent factors are far more important in regulating populations than density-dependent mechanisms (e.g. Andrewartha and Birch 1954, Lawton and Strong 1981), a view that implies a minimal importance to competition in structuring communities (but see discussion in Price 1975, p. 170 for summary of different views). Comparison of individual growth rates in the laboratory and field and comparison of population densities between shaded and sunlit reaches of streams, strongly supports the contention that food is limiting in the stream reaches that I studied. If food limitation is generally true in these systems, competition must be considered as a probable and potentially major mechanism by which structure in stream communities evolved and is maintained.

A second biological force that may affect community patterns in stream ecosystems is predation. Although it is not clear how predation might act to initiate adaptive radiation among species, predation might maintain or reinforce existing patterns. To do so, predation must be capable of imposing significant mortality on prey populations. The evidence for such effects, however, is equivocal in stream systems. Although abundances of both invertebrate and vertebrate predators are probably dependent on abundance of prey in some Oregon streams (Hawkins and Sedell 1981, Murphy et al. 1981, Hawkins et al. 1982a,b), predators do not necessarily suppress prey populations. Also, although experimental studies of predation in the laboratory have shown that both invertebrate and vertebrate predators can depress initial populations of prey (e.g. Davis and Warren 1965, Ware 1972), the existence of such relationships in the field is just beginning to be examined.

Two field experiments have been done to examine effects of vertebrate predation on prey abundance. In one, Allan (1982) could not demonstrate any effect on prey abundance after removing trout to approximately one-fourth of their initial density. In another study, Griffiths (1981) showed that after increasing trout density to about four times normal levels, standing crop and production of some invertebrate taxa were reduced compared with a control section with no fish. From these two studies, it appears that unusually high densities of trout may differentially depress prey populations but that normal densities of trout have no or little effect relative to low densities. It should be noted that Peckarsky and Dodson (1980) have conducted cage experiments in the field that appear to show that invertebrate predators also can depress prey abundance.

There is some evidence that shows differential mortality of prey occurs depending on the habitat available to prey. Hildrew and Townsend (1977) have shown that prey individuals are less likely to be consumed by an invertebrate predator if prey are provided with the habitat that they prefer in the field. If predation on individuals occurring in marginal habitats is generally higher than predation in preferred habitats, the resulting differential mortality would act to maintain habitat specificity by prey species. The fact that invertebrate herbivore and detritivore species (prey) tend to be habitat specialists to a greater degree than invertebrate predators (Green 1974, also this study) lends support to a potential predator effect enhancing ecological separation among species.

With respect to both competition and predation, it is probable that these mechanisms, if important, have acted to facilitate ecological separation once initial separation occurred. In this sense, both factors may be important forces maintaining structure. Evaluation of the processes by which differences among species arise continues to be an important and active area of research (see Dobzhansky et al. 1977, Templeton 1981) and both allopatric and

sympatric speciation seem possible. Regardless of the details of speciation, it is useful to briefly consider the consequence of adaptive radiation for community patterns in the absence of biological interactions.

An alternative hypothesis to account for observed patterns among species is one that posits no biological interactions (competition or predation) among species. Pattern may be due to specialization of different populations on different resources with subsequent speciation during periods of geographic isolation. Thus, observed patterns may be merely a reflection of historical accident and present distribution of resources. Neither competition nor predation would have been important as an evolutionary force creating pattern, and may or may not be important in maintaining pattern.

In this model, species would be distributed in niche space individually and apparently randomly in much the same way that Whittaker (1975) describes plant distributions along elevation gradients. Considering that mean overall niche overlap among species was similar to random patterns, this hypothesis cannot be ignored. However, far more revealing methods are required (Thompson and Rusterholz 1982, Feinsinger et al. 1981) before pattern due to ecological and evolutionary processes can be adequately compared with random patterns.

To examine the general significance of these hypotheses, it would be necessary to consider in detail ecological separation of species in light of phylogenetic relationships. It would also be important to know what environmental conditions were like during periods of speciation. Such a comparison might sheld light on how cladogenesis is linked to ecological adaptation and adaptive radiation (Resh and Solem 1978). Unfortunately, little is known about the evolution of insects in fresh water (Wootton 1972, Resh and Solem 1978), especially with regard to the phylogenetic relationships within families of Ephemeroptera (Edmunds 1972, 1975).

For example, I know of no quantitative and detailed treatment of phylogentic relationships among species of any of the genera and species considered in this study.

It is highly probable that community patterns are the result of many mechanisms. Community structure may owe its origin to any number of factors in much the same manner as Mayr (1976) describes for entire faunas. Furthermore, as May (1976) points out, many interacting variables may produce pattern such that the importance of any single factor is obscured.

Guild Structure

The evidence for discrete guilds among species of Ephemerellidae is not strong. It may be that an analysis of the entire invertebrate fauna in streams would show patterns that are not apparent among the relatively few species that I examined. It is important to consider, however, what factors may act to form guilds within communities and how important these factors may be in stream ecosystems. Guilds may ostensibly arise by at least two means: 1) avoidance of diffuse competition and 2) specialization on resources that are discontinuous in space or time. Even though guilds are viewed as "arenas of intense interspecific competition" (Pianka 1980), it may be less difficult for a species to compete with a few very similar species than with many more or less similar species (Pianka 1974, Inger and Colwell 1977; see Jaksic 1981). This argument suggests that avoidance of diffuse competition may act to create small groups of ecologically similar species. Another means by which guilds may arise is if gaps exist in resource space (Pianka 1980). If gaps exist, species will converge in utilization of resource "islands." In this case, competition may be inconsequential either in forming groups or maintaining them.

My data indicate that if competition is important, it has acted to separate species rather than to concentrate them. I recognize that this inference may be rather myopic, since I cannot consider patterns in Ephemerellidae relative to all other taxa in the community. I also know of no instances of distinct discontinuity along major resource or environmental axes (substrate, current, temperature, oxygen) in stream systems. Rather, most factors (except perhaps food) change gradually in character over time and various scales of space. It is also interesting that overlap among species in diet (the most discontinuous resource considered) was higher, not lower, than for any other resource. For these reasons, I suspect that distinct clusters of similar species may not exist in stream communities.

Absence of true, well separated guilds in communities does not necessarily preclude valuable use of the concept, but definitions of guilds must therefore be arbitrary (see e.g. Table 28) and thus prone to the limitations of all arbitrary classifications. Certainly investigation of the interactions among similar species (discrete guild or not) defined a priori on the basis of natural history may lead us to more important insights concerning the actual mechanisms that structure communities.

ON MAYFLIES, EVOLUTION, AND STREAM ECOSYSTEMS:
SOME SPECULATIONS

'The waters wear the stones:'
The Book of Job, XIV, 19. A.V.

In three sections of this thesis I have attempted to describe
patterns of growth, abundance, and distribution of species of
Ephemerellidae in relation to temperature, food, and substrates. In
the previous chapter, I further attempted to compare the relative
importance of these three factors as determinants of community
structure. In this concluding section, I wish to consider in
greater breadth the manner in which environmental factors act as
templates (sensu Southwood 1977) upon which biological pattern may
arise. I will consider some general questions regarding the nature
of stream ecosystems and their invertebrate biota and attempt to
place observations on Ephemerellidae into a broader context. This
is done for two reasons. First, pattern, or lack thereof, among the
Ephemerellidae may not be representative of commmunity patterns in
general. Second, it is useful to consider some of the broad
implications of physical and biological phenomena in streams for
community structure in general. Also it is worthwhile speculating
about the relationships between structure and function as they are
influenced by different factors.

It is not my purpose here to provide a rigid or comprehensive
evaluation of stream ecosystems. Rather, following the example of
Smith (1975), I will speculate on the nature of some relationships
between stream biota and ecosystem structure and function. Toward
this end, I will attempt to describe how some major factors have
been responsible for the evolution of the ecology of stream
invertebrates, and conversely, consider the implications that the

suite of adaptive traits shown by invertebrates have for system-level phenomena. I will further point out areas that I believe deserve special study in the future.

Temperature

Annual temperature fluctuations are usually predictable and have relatively high amplitude in temperate streams (see Fig. 3). Temperature also varies in a consistent and predictable manner along either latitudinal or altitudinal gradients, both in amount of heat accumulated over time and in the temporal fluctuations at a specific location (see Vannote et al. 1980).

Because temperature has such a profound influence on metabolic rates, we ought to expect streams that differ in temperature regimes to show corresponding differences in biological structure. Ide (1935) and Vannote et al. (1980) ascribe the differences in biological diversity along altitudinal (longitudinal) gradients to differences in pattern and amount of temperature fluctuation. Specifically, they concluded that reaches with larger temperature fluctuations have higher biotic diversity than those with low fluctuations. Presumably, because species have different temperature optima for growth, more species can persist in a reach that varies in temperature than in one that varies little. The reduction of biological diversity in regulated streams where temperatures vary little (see Ward and Stanford 1982) lends evidence that temperature provides an important template for biological structure as does the relatively low seasonal overlap among species that I observed (see Niche section).

My data on Ephemerellidae do not support the contention that temperature is the major control of species richness. The number of species observed along the longitudinal transect of second- to seventh-order stream showed no clear pattern of increased species

richness as stream order increased (Fig. 20). Furthermore, species richness of Ephemerellidae was high at site VII, a section of the McKenzie River with relatively low temperature fluctuations (annual mean daily range of 4 to 13°, U.S. Geological Survey 1975). Also, Kalama Spring, a constant temperature system, had nine species (Thut 1967). When I considered only those samples taken for growth determinations, both Fawn Creek (2 to 20° annual mean daily range) and MAOG (0-14°) had ten species and the two sites shared nine species in common. The fact that species within Ephemerellidae show moderate to strong niche differentiation on all niche axes considered is further reason to doubt temperature as the primary determinant of species richness.

Neither is it clear that, over a latitudinal range, temperature plays an equivalent role in regulating life cycles and diversity as postulated for longitudinal and altitudinal gradients in temperate streams. Species richness in tropical streams is apparently higher than in temperate streams (Stout and Vandemeer 1975, G. W. Minshall, unpublished MS). Unfortunately too few data exist by which to compare overall (annual) species richness in tropical and temperate streams. It is possible that tropical streams show relatively high diversity at any one time, whereas these streams may show little seasonal change in faunal composition as occurs in temperate streams. Certainly a thorough comparison of how spatial and temporal heterogeneity in tropical and temperate streams is translated into biological structure would provide significant insight into the relative importance of temperature versus other factors.

The relationship between temperature and biological structure in streams, as elsewhere, is almost certainly asymmetric and unidirectional. Although biota are strongly influenced by their temperature environment, reciprocal effects are unlikely. Unlike some special systems (e.g. termite nests), the metabolic output of

stream animals is negligible compared with the overall heat budget of a stream. Community structure associated with temperature has no obvious implication for community function, except in the sense that overall metabolic rates and thus processing rates may be strongly temperature dependent.

Habitat Constraints

I argued in the section on habitat relationships that in addition to the effect of habitat complexity on biotic richness, temporal behavior of habitats also has strongly influenced life cycles. Both length and timing of life cycles have direct implication for community structure as well as ecosystem function.

Unlike marine and some lentic systems, lotic environments possess few sessile or long-lived invertebrates. The reason for the paucity of such species may be due to the catastrophic effect of occasional floods, desiccation, or both. In spite of the predictability of many stream hydrographs, the severity of physical disturbance in stream systems may prohibit the evolution of long life cycles. For example, floods can occasionally completely scour and rearrange stream beds. Also, it seems that mobile animals may have a higher chance of surviving the rolling and crushing of stream substrates than sessile animals, especially if they are small (Harker 1952). Interestingly, such unpredictable or irregular events may prevent any evolutionary tendency toward specialization to "most likely conditions," a possibility that, if true, requires stream ecologists to have a long-term perspective of environmental dynamics to adequately understand the nature of stream communities. It is likely that in the absence of devastating floods or desiccation, life cycles, morphology, and behavioral traits of more species would have evolved toward forms that are longer-lived and highly competitive for space, a characteristic that is highly developed in sessile organisms.

The fact that stream animals are generally not sessile has important consequences for community interaction and successional patterns and perhaps for system function as well. Although stream habitats change in nature seasonally due to changes in flow regimes, habitats are very similar from year to year for any one season at a particular location. The presence or absence of animals in streams does little to change the nature of the habitat. In some marine systems, long lived and sessile species, can extensively change the physical nature of habitats. As habitats are modified, new species can colonize and persist in the community. In fact, the entire composition of a community may change radically over ecological time. This kind of biological feedback or control is conspicuously lacking in stream systems.

The magnitude and variability of discharge in stream systems also may influence the degree to which energy inputs are efficiently used. If stream systems were highly stable, species within communities probably would not only be highly competitive but consumers would, as a consequence, be efficient exploiters of any available energy resource. Because demand would usually be greater than supply, the entire stream system would be characterized as an efficient processor of both energy and material. Predictability of resources in a stable system would also be greater compared with an unstable system, because organic resources would not be physically exported from a reach before consumers had sufficient time to use them. Also, as a result of intense biological demand and efficient use of resources, the qualitative nature of food sources generally available to consumers in stable systems would be much different than in more unpredictable systems or those periodically reset. Organic substrates would probably be dominated by highly refractile detritus that has been ingested and defecated many times. The digestive and feeding strategies of consumers would therefore be specialized toward efficient use of low nitrogen compounds (e.g.

cellulose) (see Mattson 1980) rather than having the facultative strategy of depending on resources of mixed origin and highly variable quality (detritus, algae, animal) as shown by Ephemerellidae. These speculations might be tested by examining the feeding and digestive strategies of invertebrates from streams, stable springs, and permanent lakes.

Trophic Structure and Trophic Stability

The most obvious and often examined link between community structure and ecosystem function is defined by relationships between consumers and their food resources (e.g. Cummins 1973). Consumers affect the nature of food resources by the processes of ingestion, mastication, digestion, and defecation. If consumers specialize either on food type (e.g. algae, detritus, animal) or on other distinguishable characterisitics (e.g. form, shape, size), abundance and distribution of animals should be correlated with abundance and distribution of their preferred food. This argument formed a major hypothesis of River Continuum predictions (see Vannote et al. 1980), and some recent studies have supported such a close relationship (see Wiggins and Mackay 1978, Hawkins and Sedell 1981).

My data for Ephemerellidae do not provide clear evidence for strong organization of communites around food sources. Such a conclusion may be misguided, though, because so few species were actually examined. It is useful therefore, to consider more extensive analyses of communities. In Table 38, I show examples of how number of genera in three different herbivore guilds differ depending on the type of aquatic environment. Data were taken from tables in Merritt and Cummins (1978). I consider only herbivore genera here because many Ephemerellidae show moderate to strong dependence on living plant material. Trends shown here are similar to those shown by Wiggins and Mackay (1978) for Trichoptera only.

Table 38. Number of genera in different herbivore* guilds in upstream, downstream, and lentic environments. Data taken from Merritt and Cummins (1978).

Site	Guild	Ephem- erptera	Plecop- tera	Trich- optera	Lepidop- tera	Hemip- tera	Coleop- tera	Diptera	Total
					Western				
Upstream	Scrapers	16	9	14	0	0	7	14	60
	Piercers	0	0	2	0	0	0	0	2
	Shredders	1	0	12	0	0	2	4	19
Downstream	Scrapers	9	0	11	2	0	2	5	29
	Piercers	0	0	5	0	1	5	0	11
	Shredders	1	0	12	0	0	5	7	25
Lentic	Scrapers	3	0	3	1	0	3	7	17
	Piercers	0	0	3	0	0	6	0	9
	Shredders	0	0	9	14	0	9	17	49
					Eastern				
Ustream	Scrapers	11	8	10	0	0	7	12	48
	Piercers	0	0	2	0	0	0	0	2
	Shredders	0	0	8	0	0	0	4	12
Downstream	Scrapers	9	0	11	1	0	0	5	26
	Piercers	0	0	5	0	1	4	0	10
	Shredders	0	0	4	0	0	3	8	15
Lentic	Scrapers	3	0	3	1	0	4	7	18
	Piercers	0	0	3	0	0	5	0	8
	Shredders	0	0	11	22	0	7	20	60

*includes genera in which living plant material constitutes a significant portion of the diet.

If food sources vary between these environments in such a way that periphyton is the dominant living plant found in headwater streams, and macrophytes are more important in slow lotic (downstream) and lentic systems, the distribution of genera among environments bears a close correspondence to the availability of different food types. Such a relationship implies that communties are strongly structured on the basis of trophic relationships.

Heatwole and Levins (1972) argued that terrestrial arthropod faunas show similar trophic structure on mangrove islands, although species composition varied significantly among islands. However, in a response to Heatwole and Levins's analysis, Simberloff (1976) denied that evidence for stable or predictable trophic structure had been shown. The trends shown in Table 38 and by Wiggins and Mackay (1978) are significant in that they too support the contention that communities are organized around trophic interactions and on a predictable basis. Unfortunately unequivocal conclusions regarding the relationships between community structure and food sources are difficult to defend, and these data are open to alternate explanations. Number of species or genera may merely be a reflection of differences in area of suitable habitat available to species rather than higher abundance of different types of food per se.

An examination of abundances ought to provide a better test of the relationship between community structure and food sources. In Table 39, I show data collected from ten pairs of shaded and open streams. Abundances were greatest in open reaches regardless of guild, including the three most abundant groups (collector-gatherers, scrapers, and shredders). Percent composition of different guilds fit expectations somewhat better. For example, shredders comprised a higher percentage of both density and biomass in the shaded reaches than the open ones. These trends were not so strong, however, to provide convincing evidence that communities are

Table 39. Densities, standing crops, and relative abundances of three
major guilds: collector-gatherers, scrapers, and detritus
shredders. Values are means of ten shaded and ten open
stream reaches.

Guild	Density (Number/m^2)		Biomass (mg/m^2)	
	Shaded	Open	Shaded	Open
Collector-gatherers	613	2066	72	117
Scrapers	271	511	30	164
Shredders	73	132	8	15
	Percent Density		Percent Biomass	
Collector-gatherers	64	76	65	50
Scrapers	28	19	27	46
Shredders	8	5	7	4

strongly influenced by availability of different types of food
resources. Consideration of data given by Malmquist et al. (1978)
also do not support a clear association between different guilds and
availability of different food sources.

These data indicate that the linkage between food sources and
community structure may not be a simple one, and although
methodological problems exist in defining guilds, the very nature of
adaptation may prohibit simple tests of how strongly community
structure is determined by differences in food sources. As argued
earlier (Niche section), organisms are adapted to a suite of
conditions. If food sources are changed independently of other
factors, any response in community structure is constrained by
adaptations and specificities to other factors (e.g. current,
substrate size) that make organisms successful in a particular
environment. In fact, manipulation of a single variable in a
complex environment may in large part evoke responses only from
trophic and habitat generalists instead of trophic specialists.
Such a response would be especially likely if trophic specialists
were also strongly associated with special habitats as well.

Understanding and analysis of community structure and dynamics
would be clearly facilitated if communities were organized around a
few functional roles. Indeed many analyses of community structure
either explicitly or implicitly assume such a substructure within
communities (e.g. see McIntire and Colby 1978). Different
functional roles are thought to represent a relatively few ways an
organism can make a living, and different species in the community
reflect minor variations around these few evolutionary themes or
"adaptive syndromes" (Root 1975). If such substructure exists in
communities, temporal variation in community organizaiton
(substructure) should be less than variation in species composition.
For example, although the abundances of species from year to year
may vary due to differences in several factors, compensatory changes

in the abundances of species within groups should maintain group
abundance at relatively stable levels if food resources to support
that functional role remain constant.

I used data from Illies (1975) and Hynes (1970) to examine
functional stability of invertebrate communities in streams. Over a
five year period, annual emergence of three different guilds varied
considerably both in absolute amount and relative to one another
(Table 40) as shown by my examination of the data of Illies from the
Breitenbach in Germany. Hynes (1970, p. 423) provided data on
spring collections of invertebrates in the River Derwent for nine
consecutuve years. I have reconstructed his data to show the number
of individuals of each taxon that he collected each year (Table 41).
Each species was assigned to a group (predator, shredder, scraper/
collector). I then compared variation over time in abundance of
species within a group with variation in abundance for each group as
a whole. The taxa collected by Hynes included no clear examples of
scrapers. Because of this, I lumped those species that both gather
fine detritus and loose algae as scraper/collectors. Two time
periods were examined. The first consisted of data for six years
only (1955-1960). In 1961 a major change occurred in community
structure (composition). According to Hynes, this change was not
associated with a change in temperature, discharge, or other obvious
factors. The second period examined included all nine years.

If groups were more stable than their component species, the
ratio of the sum of variances for individual species over variance
for the group should be greater than one and can be tested by an
F-test for equality of variance. For no group over either time
period was this ratio statistically greater than one (Table 42). In
fact the ratio was usually less than one.

I also examined correlations of abundances of species within
groups. There was no significant trend for taxa within guilds to be
either positively or negatively correlated with one another (Table

Table 40. Annual variation in biomass of three different guilds (scrapers, collector-gatherers, and detritus shredders) emerging from a small stream in Germany. Data from Illies (1975).

| Parameter | Guild | Year | | | | | $\overline{X}$ | CV |
		1969	1970	1971	1972	1973		
Biomass $(g \cdot m^{-2} \cdot y^{-1})$	Scrapers	3.0	9.7	2.5	0.2	1.0	3.3	115
	Collector-Gatherers	11.4	24.6	15.3	20.4	3.8	15.1	53
	Shredders	9.1	7.5	2.6	0.1	9.3	5.7	72
Percent of Total Biomass	Scrapers	13	23	12	1	8	11	70
	Collector-Gatherers	48	59	75	98	29	64	26
	Shredders	39	18	13	1	71	29	97
Ranking	Scrapers	3	2	3	2	3	3	
	Collector-Gatherers	1	1	1	1	2	1	
	Shredders	2	3	2	3	1	2	

Table 41. Temporal variations in the number of animals taken each spring from the River Derwent. Data taken from Hynes (1970).

Taxon	Guild*	1955	1956	1957	1958	1959	1960	1961	1962	1963
Polycelis felina	P	26	11	3	8	26	11	32	18	11
Protonemura meyeri	Sh	1	5	2	2	3	0	0	10	46
Nemoura (3 spp.)	Sh	2	9	6	3	23	1	11	2	32
Amphinemura sulcicollis	Sh	239	573	580	199	110	112	11	2	120
Brachyptera risi	Sc/Co	2	1	1	1	1	0	16	4	19
Leuctra (4 spp.)	Sh	65	18	162	12	49	2	2	0	5
Chloroperla (2 spp.)	P	60	70	39	25	32	21	0	2	3
Isoperla grammatica	P	110	308	113	70	90	109	5	0	0
Perlodes microcephala	P	15	5	3	13	3	11	0	2	1
Rhithrogena simicolorata	Sc/Co	743	494	512	415	203	160	2	2	3
Heptagenia lateralis	Sc/Co	0	5	0	1	3	0	2	0	5
Ecdyonurus venosus	Sc/Co	4	11	3	8	6	6	0	0	0
Baetis (2 spp.)	Sc/Co	168	115	1153	58	400	46	4448	1297	552
Hydropsyche (2 spp.)	F	0	18	117	99	206	202	0	0	7
Rhyacophila dorsalis	P	11	23	39	8	9	2	16	0	0
Polycentropus sp.	P	6	34	3	2	3	44	0	2	1
Sericostoma sp.	Sh	9	18	10	3	3	7	0	0	0
Stenophylax sp.	Sh	2	0	0	10	17	6	0	4	4
Esolus parallelopipedus	Sc/Co	254	54	107	16	357	165	482	351	133
Limnius volkmari	Sc/Co	9	16	6	2	70	14	42	97	47
Elmis maugetti	Sc/Co	6	0	6	2	15	22	37	28	32
Ceratopogonidae (1 spp.)	P	4	75	19	3	87	37	37	77	14
Orthocladinae spp.	Sc/Co	336	335	110	65	746	127	26	53	121
Tanypodinae spp.	P	1	5	2	1	6	12	11	6	12
Simulium spp.	F	0	9	84	0	386	5	0	0	5
Empididae (1 sp.)	P	0	0	3	0	12	1	5	2	0
Limnaea pereger	Sc/Co	0	5	0	3	0	5	0	2	1
Total Number of Animals		2073	2217	3058	1030	2866	1128	5185	1916	1174

* P = Predator, Sh = Shredder (detritus), Sc/Co = Scraper/collector, F = filterer.

Table 42. Variance in guild abundance and sum of variances for taxa within different guilds. Values calculated from data in Table 41. F calculated as sum of taxa S^2 divided by guild S^2. Analysis for the time period 1955-1960.

Guild	Guild S^2	Sum Taxa S^2	F
Predators	18	10	0.54
Shredders	65	51	0.79
Scraper/Collectors	360	310	0.86
Total	731	402	0.55
Predators	21	13	0.64
Shredders	65	51	0.78
Scraper/Collectors	1878	2123	1.13
Total	1715	2209	1.29

43). These data and those in Table 42 also suggest that there may
be no strong substructure within stream communities.

The analyses I performed were based on trophic guilds sensu
Cummins (1973). As such, any inferences are only as strong as the
accuracy of classifying species correctly into guilds. Certainly
our knowledge of feeding behavior in aquatic invertebrates is not
complete and this analysis may not detect real organization because
of improper classification. On the other hand, conclusions based on
this analysis are similar to those by Root (1973) for community
organization of terrestrial arthropods associated with collards.

These results together with the lack of evidence for strong
guild structure among species of Ephemerellidae indicate that we
would be wise to critically examine our concepts of community
structure and organization in stream ecosystems. In particular, we
should first consider what questions can be realistically tested
experimentally. Many of the questions that I have raised here
appear intractable to experimental manipulation. Lacking recourse
to experimental analysis, ecologists may still be well served by the
descriptive data of true naturalists. Certainly this approach
helped shape much of Darwin's (1859) thinking. A critical element
to such an approach, however, is the maintenance of a broad
perspective. Toward this end, I will conclude by suggesting that
stream ecologists may benefit greatly by consideration of the many
routes and reasons for adaptive radiation among benthic
invertebrates. The ecology of individuals, populations, species,
communities, and entire ecosystems must certainly reflect
evolutionary forces of the past. A truly holistic appreciation of
form and process in stream ecosystems will only occur once we
recognize both the multiple and interdependent forces that have
shaped the ecology of each species and the consequences of complex
adaptations for community structure and function. Clearly, the
conceptual constraints are as imposing as the study design and
sampling used to address such questions.

Table 43. Number of positive and negative correlations between abundances of different taxa within different guilds. Values calculated from data in Table 41.

Guild	Number of Correlations		P(K)	Critical Value
	Positive	Negative		
Predators	18	18	0.57	0.98
Shredders	9	6	0.85	0.98
Scraper/Collectors*	21	23	0.67	0.98
Filterers	1	0	--	--
Total*	193	157	0.65	0.98

* One correlation of zero.

It is the hope of all students that by brilliant design, unequivocal data, and incisive deduction that they will add something new and profound to their field of endeavor. During this study I came to recognize weakness in its design, became frustrated with ambiguous data, and struggled with matters of seemingly simple interpretation. As a consequence, my hope for magnificient achievement was clearly thwarted. On the other hand, I have become aware that there exist important questions regarding community structure and organization in stream ecosystems that are neither well understood nor easily addressed. Answering these questions ought to be a primary goal of future research.

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APPENDICES

Appendix A. Relationships between temperature at MACC, WYCO, COUG, and FAWN and temperature at MAOG. Predictive equations based on regressions of data shown in following figures are:

MACC I. $T = -0.806 + 1.210\ T_{MAOG}$, $r^2 = .966$, $n = 75$.
           temperatures $>5°$ only.

      II. $T = -0.161 + 0.916\ T_{MAOG}$, $r^2 = .887$
           temperatures $\leq 5°$ only.

WYCO $T = 1.917 + 0.886\ T_{MAOG}$, $r^2\ .960$, $n = 96$
           temperatures $\geq 3°$ only.

COUG $T = 1.705 + 0.895\ T_{MAOG}$, $r^2 = 0.960$, $n = 204$

FAWN $T = 2.308 + 1.377\ T_{MAOG}$, $r^2 = 0.935$, $n = 270$.

North Fork Wycof Creek

Cougar Creek

Fawn Creek
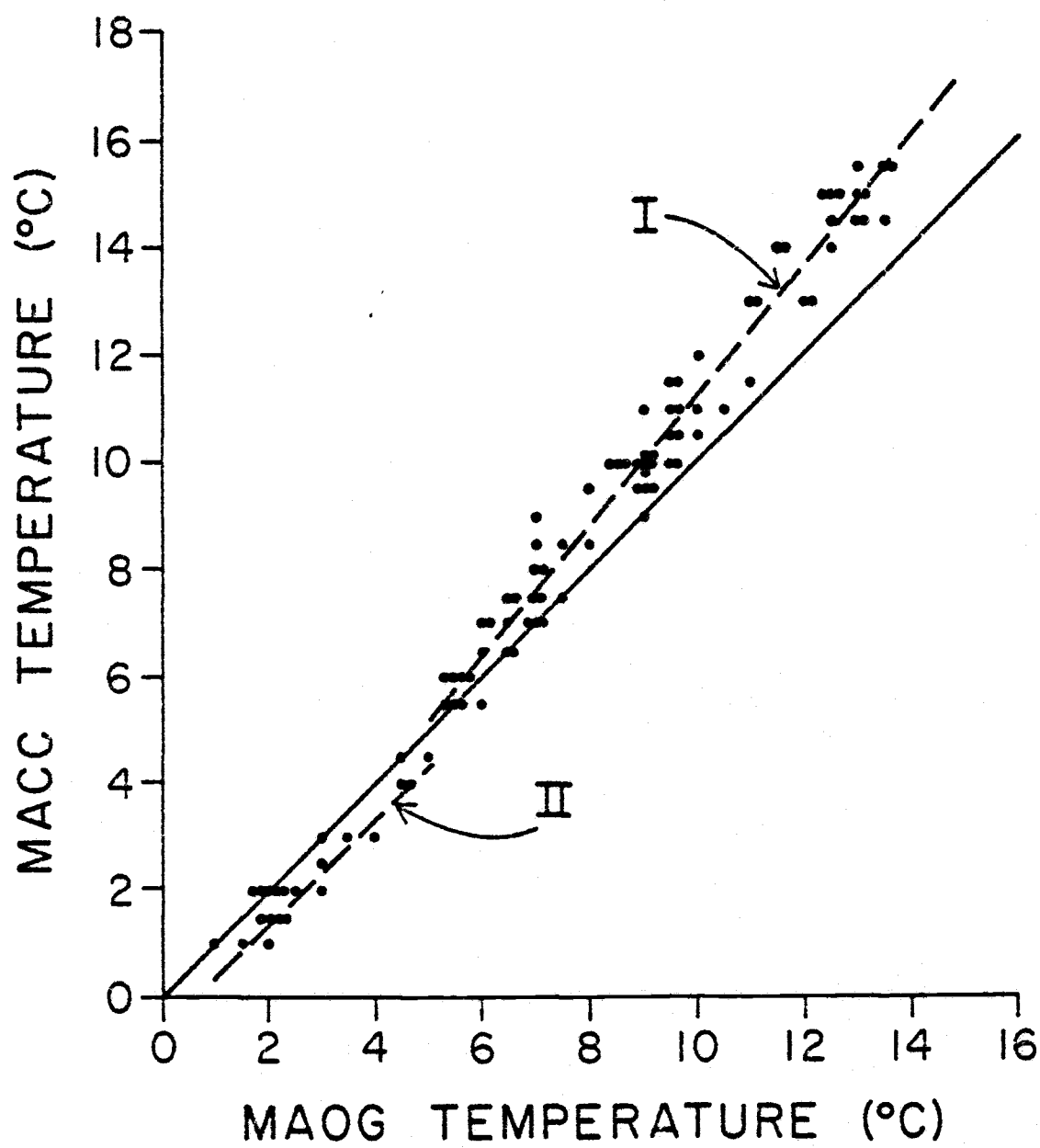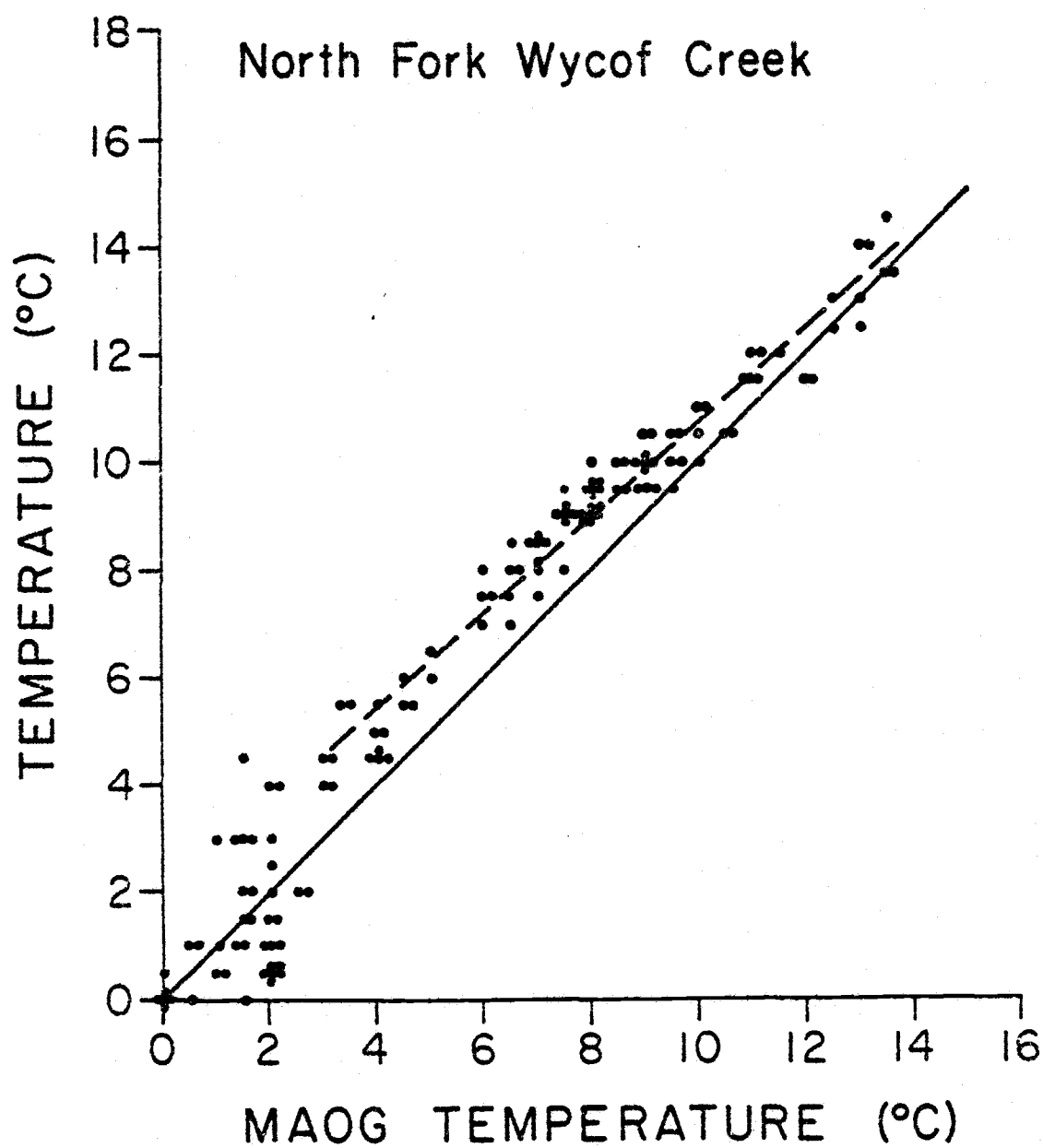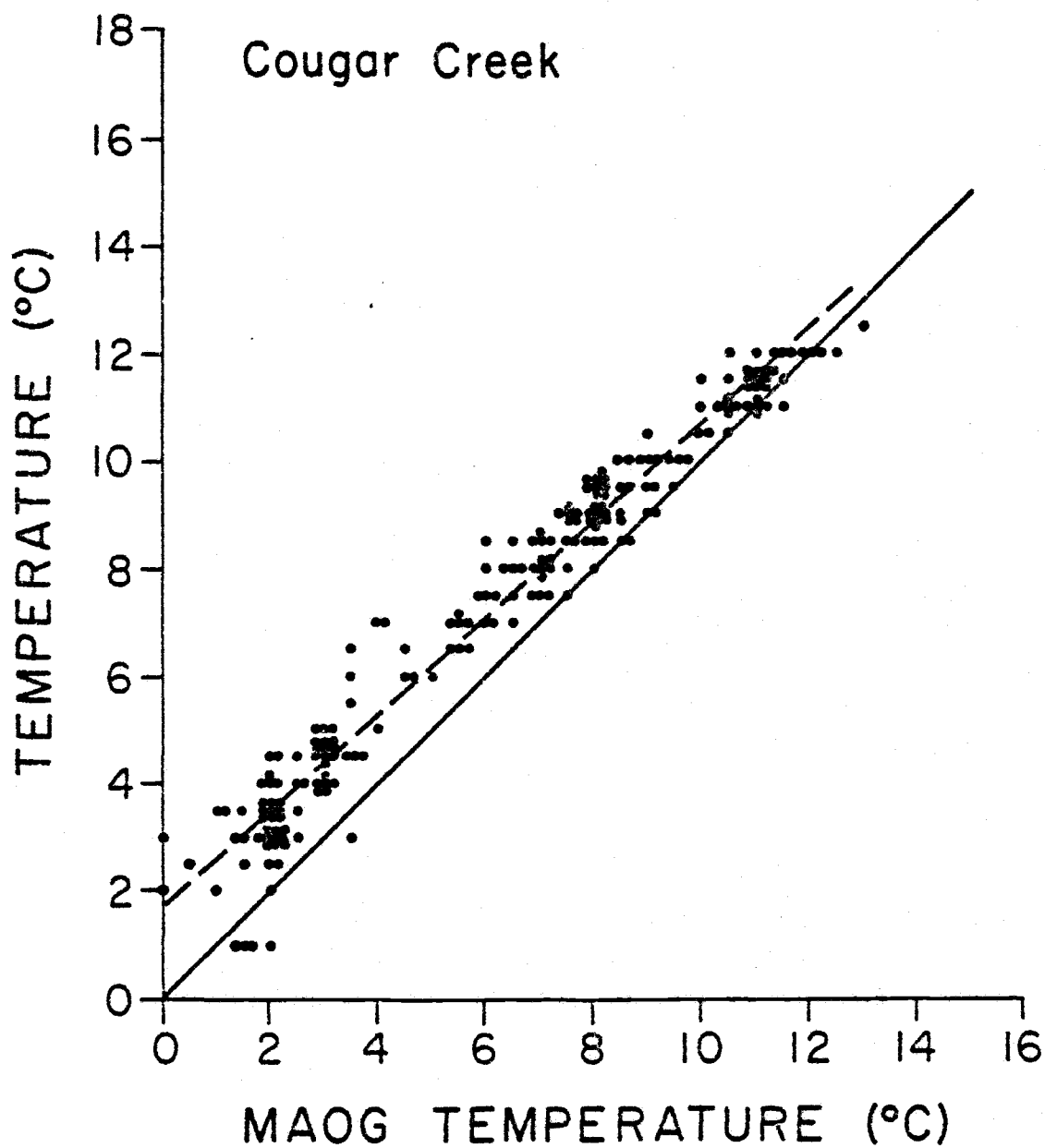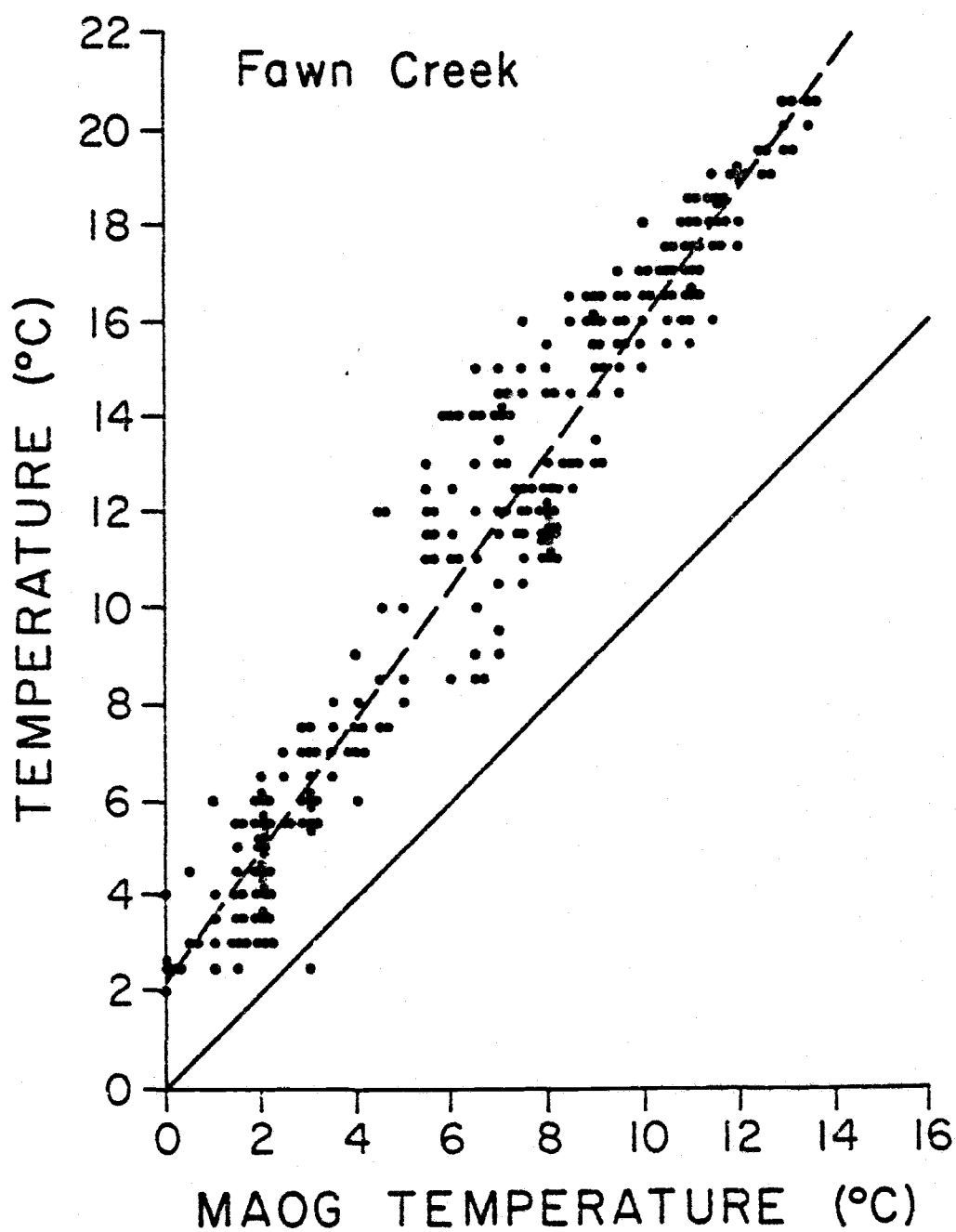
Appendix B. Estimates of different food sources at the six main study
sites.

Appendix B1. Quantity* of detritus taken from core samples during August and leaf litter standing crops for October and November. Detritus values are an average of three samples. Leaf litter estimates are from twelve quadrat samples, six from October and November respectively. Equal numbers (3) of riffle and pool samples were taken each month.

	High Gradient Sites			Low Gradient Sites		
	MAOG	WYCO	MACC	MILL	COUG	FAWN
Riffles						
VFPOM†	3.2	12.0	3.2	17.2	15.6	10.8
FPOM	14.0	16.8	16.4	55.6	50.0	57.2
CPOM§	6.0	19.6	19.2	26.4	19.2	22.0
Total	23.2	48.4	38.8	99.2	84.8	90.0
Pools						
VFPOM	7.6	45.6	8.0	73.2	47.2	40.4
FPOM	26.0	96.4	31.2	356.8	131.6	129.6
CPOM	112.0	144.8	90.4	256.0	222.4	122.4
Total	145.6	286.8	129.6	676.0	401.2	292.4
Leaf Litter	13.2	36.0	3.2	2.0	103.2	trace

* (AFDM)/m^2
† Very Fine Particulate Organic Matter: 0.45μ - 0.05 mm
  Fine Particulate Organic Matter: 0.05 mm - 1 mm
§ Coarse Particulate Organic Matter: 1 mm - 16 mm

Appendix B2. Organic matter (Aufwuchs) attached to rocks. Estimates are means of scrapings taken from three cobbles from riffles and pools respectively. Values are in g/AFDM/m^2.

	High Gradient Sites			Low Gradient Sites		
	MAOG	WYCO	MACC	MILL	COUG	FAWN
Riffles						
Jul	1.24	0.88	1.10	1.74	1.33	3.13
Aug	0.97	0.88	3.48	2.01	1.32	1.41
Sep	2.82	0.95	1.45	1.09	1.20	2.45
Oct	1.33	0.77	1.94	1.17	1.02	3.37
Dec	0.70	0.26	0.72	0.59	2.54	0.54
May	1.14	1.04	2.00	1.20	3.08	1.89
$\bar{X}$, months	1.37	0.80	1.78	1.30	1.75	2.13
SD	0.75	0.28	0.97	0.50	0.85	1.07
N	6	6	6	6	6	6
CV	55	35	55	38	49	50
$\bar{X}$, gradient		1.32			1.73	
SD		0.80			0.86	
N		18			18	
Pools						
Jul	0.79	0.68	1.89	1.55	2.27	4.05
Aug	0.58	0.77	7.13	2.07	1.57	3.09
Sep	0.94	0.60	9.21	1.66	1.55	1.13
Oct	0.98	0.95	1.38	3.72	1.83	4.96
Dec	0.94	0.20	0.63	4.63	1.37	0.61
May	2.06	1.39	2.14	1.51	2.09	1.68
$\bar{X}$, months	1.05	0.77	3.73	2.52	1.78	2.59
SD	0.52	0.39	3.54	1.33	0.35	1.73
N	6	6	6	6	6	6
CV	50	51	95	53	20	67
$\bar{X}$, gradient		1.85			2.30	
SD		2.39			1.25	
N		18			18	

Appendix B3. A) Chlorophyll pigments associated with VFPOM. Chlorophpyll a and pheophpytin a are summed. Values are in µg pigment/g AFDM. B) Estimated algal biomass (mg/g AFDM).

	High Gradient Sites			Low Gradient Sites		
	MAOG	WYCO	MACC	MILL	COUG	FAWN
Jul	99	91	308	112	44	347
Aug	45	81	492	38	23	210
Sep	84	64	1,623	72	73	120
Oct	trace	113	17	trace	39	92
Nov	169	316*	1,633	155	239*	435
Dec	92	202*	173	68	161*	77
Mar	49	162*	127	97	132*	74
May	143	141*	89	120	145*	305
Jun	244	302	381	79	105	587
X̄, months	103	164	538	82	107	250
SD	74	93	636	46	70	182
N	9	9	9	9	9	9
CV	72	57	118	56	66	73
X̄, gradient		268			146	
SD		409			134	
N		27			27	
Jul	5.3	4.9	23.1	6.0	2.4	26.0
Aug	2.4	4.4	36.9	2.1	1.2	15.8
Sep	4.5	3.5	121.7	3.9	3.9	9.0
Oct	trace	6.1	1.3	trace	2.1	6.9
Nov	9.1	23.7*	122.5	8.4	17.9*	32.6
Dec	5.0	15.2*	13.0	3.7	12.1*	5.8
Mar	2.6	12.2*	9.5	5.2	9.9*	5.6
May	7.7	10.6*	6.7	6.5	10.0*	22.9
Jun	13.2	16.3	28.6	28.6	5.7	44.0
X̄, months	5.6	10.7	40.4	4.4	7.3	18.7
SD	4.0	6.8	47.7	2.5	5.7	13.6
N	9	9	9	9	9	9
CV	72	63	118	56	77	73
X̄, gradient		18.9			10.2	
SD		31.0			10.4	
N		27			27	

* Open canopy due to leaf fall.

Appendix B4. Respiration of fine (FPOM) and very fine (VFPOM) organic
detritus. Data are mean respiration rate (μl O_2/g
AFDM/hr) of three subsamples taken from random grab
samples from each site. Respiration was measured at
ambient stream temperatures observed each month.
Temperature is reported as °C.

	High Gradient Sites			Low Gradient Sites			Temp
	MAOG	WYCO.	MACC	MILL	COUG	FAWN	
FPOM							
Jun	251	189	268	159	---	217	10
Jul	18	236	79	63	72	248	13
Aug	65	278	128	70	57	522	15
Sep	84	86	506	40	30	155	10
Oct	90	82	645	61	96	36	10
Nov	57	51	215	---	246	205	5
$\overline{X}$, months	94	154	307	79	100	231	
SD	81	94	223	46	85	161	
N	6	6	6	5	5	6	
CV	86	61	73	59	85	70	
$\overline{X}$, gradient		185			142		
SD		166			127		
N		18			16		
VFPOM							
Jun	225	256	393	281	---	404	10
Jul	19	202	174	46	48	428	13
Aug	56	561	312	126	74	774	15
Sep	136	138	669	26	---	161	10
Oct	164	---	347	---	---	---	10
Nov	116	110	361	91	147	117	5
$\overline{X}$, months	120	253	376	114	90	377	
SD	74	181	163	101	51	262	
N	6	5	6	5	3	5	
CV	62	72	43	89	57	70	
$\overline{X}$, gradient		249			209		
SD		175			214		
N		17			13		

Appendix B5. A) Chlorophyll pigments associated with attached organic matter (Aufwuchs) on rocks. B) Algal biomass associated with attached organic matter. Estimates based on scraping from six cobbles. Three from riffles and three from pools. Values are mg pigment or algal biomass/g AFDM.

		High Gradient Sites			Low Gradient Sites	
		MAOG	WYCO	MACC	MILL	COUG	FAWN
A	Jul	1.2	0.3	0.7	0.8	0.6	0.5
	Aug	1.0	0.6	0.5	1.1	0.8	0.5
	Sep	2.4	2.1	1.1	2.2	1.0	2.4
	Oct	2.5	1.3	1.8	1.5	1.2	1.7
	Nov	3.4	1.2*	1.8	1.5	0.7*	2.5
	Dec	0.2	0.4*	1.8	1.0	1.8*	0.6
	Mar	2.1	2.4*	2.2	0.9	1.1*	1.4
	May	1.4	1.0*	0.5	0.8	0.6*	0.6
	Jun	2.0	1.2	0.8	1.2	0.6	0.6
	$\overline{X}$, months	1.8	1.2	1.2	1.2	0.9	1.3
	SD	0.9	0.7	0.6	0.4	0.4	0.8
	N	9	9	9	9	9	9
	CV	52	63	52	36	40	62
	$\overline{X}$, gradient		1.4			1.1	
	SD		0.8			0.6	
	N		27			27	
B	Jul	67	16	49	44	33	38
	Aug	51	32	34	61	46	34
	Sep	129	114	79	117	54	179
	Oct	135	68	134	81	66	128
	Nov	182	92*	134	71	56*	187
	Dec	13	26*	136	54	132*	47
	Mar	116	181*	152	50	82*	108
	May	75	73*	37	42	46*	46
	Jun	110	65	63	62	34	97
	$\overline{X}$, months	98	74	91	65	61	96
	SD	51	51	48	23	31	60
	N	9	9	9	9	9	9
	CV	52	69	52	36	50	62
	$\overline{X}$, gradient		88			74	
	SD		49			42	
	N		27			27	

* Open canopy due to leaf fall.

Appendix B6. Chlorophyll pigments per m^2 of rock surface.
Estimates based on three rocks from both riffles and
pools. Values expressed in mg pigment/m^2.

	High Gradient Sites			Low Gradient Sites		
	MAOG	WYCO	MACC	MILL	COUG	FAWN
Riffles						
Jul	1.54	0.27	0.72	1.41	0.82	1.57
Aug	0.92	0.53	1.58	2.31	1.12	0.64
Sep	6.75	2.00	1.53	2.36	1.20	5.84
Oct	3.32	0.97	3.46	1.76	1.24	5.74
Dec	0.17	0.09*	1.29	0.59	4.46*	0.34
May	1.59	1.01*	0.99	0.92	1.90*	1.17
$\overline{X}$, months	2.38	0.81	1.60	1.59	1.79	2.55
SD	2.38	0.69	0.97	0.72	1.36	2.55
N	6	6	6	6	6	6
CV	100	85	61	45	76	100
$\overline{X}$, gradient		1.60			1.97	
SD		1.59			1.67	
N		18			18	
Pools						
Jul	0.99	0.21	1.24	1.26	1.40	2.03
Aug	0.55	0.47	3.24	2.35	1.33	1.39
Sep	2.25	1.27	9.77	3.59	1.55	2.70
Oct	2.46	1.21	2.47	5.61	2.23	8.46
Dec	0.23	0.70*	1.14	4.34	2.41*	0.38
May	2.87	1.35*	1.06	1.16	1.28*	1.04
$\overline{X}$, months	1.56	0.87	3.15	3.05	1.70	2.67
SD	1.11	0.48	3.36	1.78	0.49	2.95
N	6	6	6	6	6	6
CV	72	55	107	58	29	110
$\overline{X}$, gradient		1.86			2.47	
SD		2.17			1.97	
N		18			18	

* Open canopy due to leaf fall.

Appendix B7. Algal biomass per m^2 of rock surface. Values in mg algae/m^2.

	High Gradient Sites			Low Gradient Sites		
	MAOG	WYCO	MACC	MILL	COUG	FAWN
Riffles						
Jul	83	15	54	76	44	118
Aug	50	27	118	125	60	48
Sep	364	108	115	127	65	438
Oct	179	52	260	95	67	430
Dec	9	7*	97	32	334*	26
May	86	76*	74	50	142*	88
$\overline{X}$, months	129	47	120	84	119	191
SD	128	39	73	39	111	191
N	6	6	6	6	6	6
CV	100	83	61	46	93	100
$\overline{X}$, gradient		99			131	
SD		91			130	
N		18			18	
Pools						
Jul	54	11	93	68	76	152
Aug	30	25	243	127	72	104
Sep	122	69	733	194	84	202
Oct	133	65	185	303	120	634
Dec	12	52*	86	234	181*	28
May	155	101*	80	63	96*	78
$\overline{X}$, months	84	54	236	165	105	200
SD	60	32	252	96	41	221
N	6	6	6	6	6	6
CV	71	60	106	58	39	111
$\overline{X}$, gradient		125			156	
SD		164			139	
N		18			18	

* Open canopy due to leaf fall.

Appendix C1. Mean individual biomass (mg) observed for $\underline{E}$. infrequens at different dates and streams.

		Biomass (mg)							
Date	Day	MAOG	MACC	WYCO	MILL	FAWN	COUG	KALA	GORGE
28 DEC	0	0.07	0.12	0.41	0.11				
1 JAN	4							0.14	
1 FEB	35							0.33	
1 MAR	63							0.64	
10 MAR	73								0.14
20 MAR	82	0.19	0.19	1.58	0.46	0.36	0.20		
1 APR	93							1.39	
8 APR	100	0.53	0.39		1.51	0.71	0.29		0.19
21 APR	113	0.32							
1 MAY	123							3.62	
5 MAY	127								0.21
9 MAY	131	0.58	0.52	2.21	1.08	1.45	0.81		
26 MAY	148	0.81	0.36	4.55	1.03				
1 JUN	153							5.07	
2 JUN	154								0.28
6 JUN	158	0.71	1.08						
3 JUL	185								1.07
29 JUL	211								0.76
26 AUG	239								1.16
Degree-days (1 JAN - 1 MAY)		219	178	261	--	587	408	720	20

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Appendix C2. Mean individual biomass (mg) observed for D. coloradensis at different dates and streams.

		Biomass (mg)							
Date	Day	MAOG (78)	MAOG (79)	MACC (79)	PROVO	KALA	FAWN	WYCO (79)	GORGE
1 MAR	1				0.05	0.14			
20 MAR	20		0.07	0.09			0.23	0.10	
1 APR	32				0.10	0.38			
5 APR	36	0.25							
8 APR	39		0.18	0.15			0.30		
21 APR	52								
1 MAY	62				0.16	1.25			
5 MAY	66								0.04
9 MAY	70			0.92			1.55	1.03	
26 MAY	87		0.48	0.70			2.61	1.32	
1 JUN	93				0.36	4.85			
2 JUN	94								0.08
10 JUN	102	1.75							
21 JUN	113		0.89	1.80			3.96	3.10	
1 JUL	123				1.15	8.81			
3 JUL	125								1.16
12 JUL	134	3.37							
19 JUL	141	3.88							
29 JUL	151								6.40
1 AUG	154								
5 AUG	158				3.04				
12 AUG	165				3.21				
14 AUG	167								
19 AUG	172				3.58				
26 AUG	179				2.84				7.56
1 SEP	185				4.36				
Degree-days (1 MAR - 1 SEP)		1265	1193	1298	1084	1104	2177	1352	908

Appendix C3. Mean individual biomass (mg) observed for $\underline{D.}$ $\underline{doddsi}$ at different dates and streams.

				Biomass (mg)				
Date	Day	MAOG	MACC	WYCO	COUG	LUSK	KANA	KALA
28 DEC	1	2.78	3.58	4.79				
1 JAN	4		.					6.38
28 JAN	31					1.32		
20 FEB	54					1.64		
1 MAR	63							12.39
20 MAR	82	3.80	7.56		8.33			
25 MAR	87					4.17		
1 APR	94							22.81
8 APR	102	6.17		14.43	6.95			
21 APR	115					5.10	0.34	
1 MAY	125							33.57
9 MAY	133		14.24					
12 MAY	136					7.63	0.71	
26 MAY	150	16.31	15.25	25.36	16.97		2.58	
12 JUN	167					11.66		
21 JUN	176	17.65	20.06					
1 JUL	186						7.81	
15 AUG	231						18.49	
15 SEP	262						30.59	
Degree-days (1 JAN - 1 SEP)		1262	1350	1423	1543	719	680	1458

Appendix C4. Mean individual biomass (mg) observed for <u>D</u>. <u>doddsi</u> at different dates and streams.

		Biomass (mg)							
Date	Day	MAOG	MACC	MILL	FAWN	WYCO	LUSK	KANA	KALA
10 JUN	10	0.02	0.04	0.05		0.05			
1 Jul	31							7.81	0.02
8 JUL	38								
12 JUL	42	0.08							
19 JUL	49	0.11	0.16	0.27	0.07	0.11			
1 AUG	62								0.16
14 AUG	75	0.21	0.23	0.27	0.31	0.24		18.49	
								0.02	
15 AUG	76								
1 SEP	93								0.58
15 SEP	107						0.03		
20 SEP	112	0.63	0.84		0.59	0.55		30.59	
								0.12	
26 SEP	118	0.77							
10 OCT	132	1.47	2.23	1.15		1.25		0.13	
15 OCT	137						0.07		
1 NOV	154								1.73
10 NOV	164						0.15		
24 NOV	178	2.38	2.28	3.37		2.03			
13 DEC	197						0.40		
28 DEC	212	2.78	3.58			4.79			
1 JAN	216								6.38
Degree-days (1 JUN - 1 JAN)		1503	1616		2452	1653	726		1278

Appendix C5. Mean individual biomass (mg) observed for <u>D. spinifera</u> at different dates and streams.

Date	Day	Biomass (mg)			
		MAOG	MACC	MILL	COUG
1 SEP	1				
20 SEP	20		0.27	0.35	0.13
26 SEP	26	0.45			
10 OCT	40	0.59	0.70	0.37	0.43
24 NOV	85		1.15		0.40
13 DEC	104	0.97			
28 DEC	119		0.97		0.70
20 MAR	201		2.72	2.03	2.44
8 APR	220	2.72	3.58		2.66
9 MAY	251				5.35
26 MAY	268	3.10	8.07	7.68	7.07
21 JUN	294	4.36	8.60	12.72	
Degree-days (1 SEP - 1 JUL		1212	1208		1598

Appendix C6. Mean individual biomass (mg) observed for <u>D. pelosa</u> at different dates and streams.

Date	Day	Biomass (mg)			
		MAOG	MACC	WYCO	FAWN
24 NOV	1	0.01	0.01	0.02	0.01
28 DEC	35	0.02	0.02		0.02
20 MAR	117	0.10	0.13	0.29	0.35
8 APR	136	0.15	0.29		
9 MAY	167	0.58			
26 MAY	184			2.56	
21 JUN	210		1.42		
Degree-days (24 NOV - 21 JUN)		610	557	649	1384

Appendix C7. Mean individual biomass (mg) observed for S. tibialis at different dates and streams.

Date	Day	Biomass (mg)		
		MAOG	MACC	KALA
1 APR	1			0.004
1 MAY	31			0.020
1 JUN	62			0.116
10 JUN	71	0.02	0.04	
1 JUL	92			0.496
12 JUL	103	0.20		
19 JUL	110		0.26	
1 AUG	123			3.23
14 AUG	136		0.81	
20 SEP	173		1.72	
26 SEP	179	1.86		
Degree-Days (1 APR - 1 OCT)		1388	1492	1098

Appendix D1. Degree-days accumulated since 28 December (E. infrequens).

Degree-days

Date	MAOG	MACC	WYCO	FAWN	COUG	KALA	GORGE
28 DEC	0	0	0				
1 JAN						9	
1 FEB						195	
1 MAR						381	
10 MAR							0
20 MAR	113	90	119	348	240		
1 APR						561	
8 APR	163	132		464	315		0
21 APR	188						
1 MAY						747	
5 MAY							35
9 MAY	251	206	255	666	466		
26 MAY	343	305	375				
1 JUN						927	
2 JUN							128
6 JUN	416	388					
3 JUL							308
29 JUL							594
26 AUG							860

Appendix D2. Degree-days accumulated since 1 March (D. coloradensis).

Date	Degree-days							
	MAOG (78)	MAOG (79)	MACC (79)	FAWN	WYCO	PROVO	KALA	GORGE
1 MAR						0	0	
20 MAR		46	37	107	53			
1 APR						130	186	
5 APR	134							
8 APR		96	78	224				
21 APR								
1 MAY						263	366	
5 MAY								35
9 MAY			153	426	190			
26 MAY		275	252	627	310			
1 JUN						426	522	
2 JUN								128
10 JUN	447							
21 JUN		466	451	1003	522			
1 JUL						610	732	
3 JUL								308
12 JUL	721							
19 JUL	789							
29 JUL								594
1 AUG								
5 AUG						884		
12 AUG						936		
14 AUG								
19 AUG						989		
26 AUG						1041		860
1 SEP						1084		

Appendix D3. Degree-days accumulated since 28 December, except KANA where degree-days are calculated from 31 April (D. doddsi).

	Degree-days						
Date	MAOG	MACC	WYCO	COUG	LUSK	KANA	KALA
28 DEC	0	0	0				
1 JAN							9
28 JAN					33		
20 FEB					66		
1 MAR							354
20 MAR	113	91		244			
25 MAR					99		
1 APR							540
8 APR	163		191	319			
21 APR					152		
1 MAY							720
9 MAY		206					
12 MAY					214	45	
26 MAY	343	305	376	588		156	
12 JUN					325		
21 JUN	533	505					
1 JUL						245	
15 AUG						517	
15 SEP						749	

Appendix D4.   Accumulated degree-days since 1 June (D. doddsi).

	Degree-days					
Date	MAOG	MACC	FAWN	WYCO	LUSK	KALA
10 JUN	84	96		96		
1 JUL						186
8 JUL						
12 JUL	360					
19 JUL	428	471	703	477		
1 AUG						372
14 AUG	736	794	1189	794		
15 AUG						
1 SEP						552
15 SEP					505	
20 SEP	1066	1156	1726	1159		
26 SEP	1114					
10 OCT	1228	1362		1348		
15 OCT					609	
1 NOV						912
10 NOV					669	
24 NOV	1426	1564		1592		
13 DEC					713	
28 DEC	1503	1616		1653		
1 JAN						1278

Appendix D5. Accumulated degree-days since 1
September (D. spinifera).

	Degree-days		
Date	MAOG	MACC	COUG
1 SEP	0	0	0
20 SEP		180	187
26 SEP	210		
10 OCT	324	360	375
24 NOV		562	626
13 DEC	566		
28 DEC		614	724
20 MAR		704	964
8 APR	762	746	1039
9 MAY			1190
26 MAY	942	919	1308
21 JUN	1132	1118	

Appendix D6. Accumulated degree-days since 24
November (D. pelosa).

	Degree-days			
Date	MAOG	MACC	WYCO	COUG
24 NOV	0	0	0	0
28 DEC	76	52		141
20 MAR	190	143	180	489
8 APR	240	184		
9 MAY	328			
26 MAY			437	
21 JUN		557		

Appendix D7. Accumulated degree-days since 1
April (S. tibialis).

	Degree-days		
Date	MAOG	MACC	KALA
1 APR	0	0	0
1 MAY			180
1 JUN			366
10 JUN	326	318	
1 JUL			546
12 JUL	599		
19 JUL		692	
1 AUG			732
14 AUG		1040	
20 SEP		1402	
26 SEP	1353		

Appendix E1. Hours of daylight accumulated since 28 December (<u>E.</u> <u>infrequens</u>).

	Hours of Daylight							
Date	MAOG	MACC	WYCO	MILL	FAWN	COUG	KALA	GORGE
28 DEC	0	0	0	0				
1 JAN							27	
1 FEB							314	
1 MAR							606	
10 MAR								678
20 MAR	862	862	862	862	862	862		
1 APR							977	
8 APR	1076	1076		1076	1076	1076		1010
21 APR	1215							
1 MAY							1381	
5 MAY								1391
9 MAY	1506	1506	1506	1506	1506	1506		
26 MAY	1759	1759	1759	1759				
1 JUN							1841	
2 JUN								1825
6 JUN	1927	1927						
3 JUL								2328
29 JUL								2741
26 AUG								3164

Appendix E2.   Hours of daylight accumulated since 1 March (D. coloradensis).

Date	Hours of Daylight							
	MAOG 78	MAOG 79	MACC	FAWN	WYCO	PROVO	KALA	GORGE
1 MAR	0	0	0	0	0	0	0	0
20 MAR		221	221	221	221			
1 APR						360	371	
5 APR	422							
8 APR		435	435	435				
21 APR								
1 MAY						757	775	
5 MAY								842
9 MAY			865	865	865			
26 MAY		1118	1118	1118	1118			
1 JUN						1203	1235	
2 JUN								1276
10 JUN	1374							
21 JUN		1545	1545	1545	1545			
1 JUL						1651	1701	
3 JUL								1779
12 JUL	1871							
19 JUL	1977							
29 JUL								2192
1 AUG								
5 AUG						2162		
12 AUG						2260		
14 AUG								
19 AUG						2356		
26 AUG						2450		2615
1 SEP						2529		

Appendix F1. ANOVA tables for comparison of regression lines defining G based on days.

Species	Source of Variation	df	SS	MS	F	P
E. infrequens	Among G's	6	3.7941	0.6324	7.49	<0.001
	Weighted Error	22	1.8569	0.0844		
D. coloradensis	Among G's	7	8.9934	1.2848	11.06	<0.001
	Weighted Error	26	3.0207	0.1162		
D. doddsi (L)	Among G's	6	6.3066	1.0511	12.81	<0.001
	Weighted Error	18	1.5531	0.0863		
D. doddsi (S)	Among G's	7	6.3660	0.9094	4.39	<0.005
	Weighted Error	26	5.3899	0.2073		
D. spinifera	Among G's	3	2.7556	0.9185	13.41	<0.001
	Weighted Error	19	1.3018	0.0685		
D. pelosa	Among G's	3	0.9670	0.3223	4.84	<0.05
	Weighted Error	8	0.5322	0.0665		

Appendix F2. ANOVA tables for comparison of regression lines defining G based on degree-days.

Species	Source of Variation	df	SS	MS	F	P
E. infrequens	Among G's	6	5.5852	0.9309	6.76	<0.001
	Weighted Error	22	3.0311	0.1378		
D. coloradensis	Among G's	7	12.8645	1.8378	6.06	<0.001
	Weighted Error	26	7.8790	0.3030		
D. doddsi (L)	Among G's	6	4.4124	0.7354	5.24	<0.005
	Weighted Error	17	2.4013	0.1413		
D. doddsi (S)	Among G's	5	8.1758	1.6352	12.08	<0.001
	Weighted Error	23	3.1121	0.1353		
D. spinifera	Among G's	2	2.0262	1.0131	11.43	<0.001
	Weighted Error	16	1.4180	0.0886		
D. pelosa	Among G's	3	4.4898	1.4966	3.31	NS
	Weighted Error	8	3.6200	0.4525		

Appendix F3. ANOVA tables for comparison of regression lines defining
G̲ based on hours of daylight.

Species	Source of Variation	df	SS	MS	F	P
E. infrequens	Among G's	6	4.4599	0.7433	8.26	<0.001
	Weighted Error	22	1.9791	0.0900		
D. coloradensis	Among G's	7	8.0117	1.1445	9.01	<0.001
	Weighted Error	26	3.3010	0.1270		
D. doddsi (L)	Among G's	6	4.4351	0.7392	9.14	<0.001
	Weighted Error	18	1.4551	0.0808		

Appendix G.   Statistical test of Poole and Rathcke (1978) used to
determine pattern in timing of growth among species.

Sample Statistic: $P = \dfrac{\sum\limits_{i=0}^{k} y_{i+1} - y_i - [1/(k + 1)]^2}{k + 1}$

where P = sample variance of intervals between
dates describing growth for different
species. Dates are ordered from earliest
to latest and the length of the growing
season is normalized to one.

y_i = date describing timing of growth for
species i after normalization to one.

k = number of species.

Expected value of P: $E(P) = \dfrac{k}{(k + 1)^2 (k + 2)}$,

if timing of growth is random.

P/E(P) is a measure of uniformity, randomness, or aggregation and can be
tested by $X^2 = KP/E(P)$ with K degrees of freedom. A high value of
X^2 (P < 0.05) indicates aggregation; a low value (P > 0.95) indicates
uniformity; intermediate values indicate randomness.

Appendix H. Densities (Number/0.1 m²) of species at different stations on three dates. Mean (X̄) represents average of dates.

SITE	C. cascadia APR	JUN	FEB	X̄	C. hystrix APR	JUN	FEB	X̄	C. heterocaudata APR	JUN	FEB	X̄
I	1.8*	1.4	1.0	1.2	*	0.1	0	0.1	0	0	0	0
II	0.2*	0.1	0.7	0.4	*	0	0.5	0.2	0	0	0	0
III	0.7*	0.1	0.1	0.1	*	2.6	0.9	1.8	0	0	0	0
IV	0.6*	0	0	0	*	0.7	1.3	1.0	0	1.3	0.1	0.7
V	0.4*	--	--	--	*	--	--	--	0	--	--	***
VI	--	--	--	--	--	--	--	--	0	--	--	***
VII	--	0	0	0	--	0	0	0	0	1.3	0	0.6
VIII	--	0	--	0	--	0	--	0	--	0	--	0

SITE	C. edmundsi APR	JUN	FEB	X̄	C. teresa APR	JUN	FEB	X̄	S. tibialis APR	JUN	FEB	X̄
I	0	0	0	0	1.2	6.4	2.8	3.5	0	0	0	0
II	0	0	0	0	0	0	0	0	0	0	0	0
III	0	0	0	0	0	0	0	0	0	0	0	0
IV	0	0.1	0	<0.1	0	0	0	0	0	3.5	0	1.2
V	0	--	--	--	0	--	--	--	0	--	--	0
VI	0	--	--	--	--	--	--	--	0	--	--	0
VII	17.0	11.7	380.0**	15.0	0	0	0	0	0	<0.1	0	<0.1
VIII	--	0	--	--	--	0	--	-	--	0	--	0

SITE	D. pelosa APR	JUN	FEB	X̄	D. doddsi APR	JUN	FEB	X̄	D. coloradensis APR	JUN	FEB	X̄
I	0	0	0	0	C	0	0	0	0	0.1	0	<0.1
II	0.1	0	0.2	0.1	0.4	0.2	0.8	0.5	0	0.3	0	0.1
III	0.2	4.0	2.9	2.4	0.7	0.4	0.6	0.6	2.0	2.5	0.1	1.5
IV	6.2	4.5	6.6	5.8	0.3	0.9	0.6	0.6	3.3	9.6	2.4	5.1
V	3.5	--	--	3.6	0.6	--	--	0.6	5.1	--	--	5.1
VI	--	--	--	--	--	--	--	--	--	--	--	--
VII	--	0	0	0	--	0.2	0	0.1	--	1.3	0	0.6
VIII	--	0	--	0	--	0	--	--	--	0.3	--	0.13

SITE	D. spinifera APR	JUN	FEB	X̄	E. infrequens APR	JUN	FEB	X̄	A. delantala APR	JUN	FEB	X̄
I	0	0.1	0	<0.1	1.5	1.4	0.8	1.2	0	0	0	0
II	0.1	0	0.2	0.1	0.5	0.3	0.3	0.4	0	0	0	0
III	0.2	0.2	0.1	0.2	2.1	1.7	1.2	1.7	0	0	0	0
IV	0.1	0.1	0.2	0.1	9.7	7.7	14.3	10.6	0	0.2	0	0.1
V	0	--	--	0	10.5	--	--	10.5	0.8	--	--	0.8
VI	--	--	--	--	1.3	--	--	1.3	0	--	--	0
VII	2.0	0.6	1.0	1.2	16.3	9.9	31.0	19.1	0	1.0	0	0.3
VIII	--	0	--	0	--	6.4	--	6.4	--	6.3	--	5.3

SITE	A. margarita APR	JUN	FEB	X̄	T. hecuba APR	JUN	FEB	X̄
I	0	0	0	0	0	0	0	0
II	0	0	0	0	0	0	0	0
III	0	0	0	0	0	0	0	0
IV	0	0	0	0	0	0	0	0
V	0	--	--	0	0	--	--	0
VI	0	--	--	0	0	--	--	0
VII	0	0	1.0	0.3	0	0	0	0
VIII	--	0	--	0	--	0.7	--	0.2

-- No sample taken.
* C. cascadia and hystrix combined during April. Values not included in calculation of mean.
** Not included in calculation of X̄. Value based on one sample.
*** No mean calculated.

Appendix I. Percent habitat use on three dates by eleven species.

Species	April				June				February			
	Gravel	Cobble	Boulder	Moss	Gravel	Cobble	Boulder	Moss	Gravel	Cobble	Boulder	Moss
C. cascadia	*	*	*	*	0	0	0	100	0	0	8	92
C. hystrix	0	6	28	66	0	12	0	88	0	0	55	45
C. edmundsi	0	100	0	0	0	73	27	0	0	100	0	0
C. heterocaudata	0	0	0	100	0	0	0	100	0	0	0	100
S. teresa	0	40	0	60	1	3	0	96	0	0	0	100
D. pelosa	0	3	91	6	0	56	0	44	0	38	62	0
D. doddsi	5	95	0	0	0	76	24	0	23	72	5	0
D. coloradensis	24	63	8	5	1	79	20	0	0	95	5	0
D. spinifera	17	83	0	0	3	3	0	94	0	33	0	67
E. infrequens	63	28	2	7	5	35	0	60	78	21	1	0
A. delantala	100	0	0	0	--	--	--	--	--	--	--	--

* C. cascadia and hystrix combined during April.
-- No animals collected.