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VARIATION IN INDIVIDUAL GROWTH RATES AND POPULATION DENSITIES OF EPHEMERELLID MAYFLIES[1]

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Abstract. Individual growth and densities of six taxa of ephemerellid mayflies were examined in relation to differences in temperature and food among streams of western North America. For most taxa, growth rate was not a simple function of either temperature or food. Growth periods of taxa differed relative to seasonal changes in temperature. As a result of the interaction between size and temperature, growth rates and shapes of the growth curve varied among taxa. The significance of temperature for life history phenomena therefore cannot be easily generalized to explain phenological patterns among stream insects. Also, little evidence was found that implicated food as the cause for observed differences in growth rates among most sites. Growth rates in streams with high rates of algal production (open sites) were similar to growth rates in streams with low algal production (shaded sites). Only sites with long periods of ice cover, and presumably low availability of food, showed marked reduction in individual growth rates. Densities, however, varied strongly across sites: open streams had higher densities than shaded streams. These results imply that populations in streams may be near carrying capacity and that per capita food availability is similar among streams. The presence of such interactions between individual and population processes may help explain patterns at individual, population, and ecosystem levels of organization.

Key words: aquatic insects; Cascade Mountains, Oregon; densities; Ephemerellidae; food; growth rates; life histories; mayflies; streams; temperature.

INTRODUCTION

The two most important factors affecting individual growth in aquatic poikilotherms are temperature and food (review by Sweeney 1984). Growth rate usually increases with temperature up to a maximum, after which growth declines precipitously as near-lethal temperatures are reached (Precht et al. 1973). Although it is difficult to generalize among species with respect to specific growth-temperature relationships, several empirical studies in aquatic environments strongly suggest that temperature may be the most important single factor influencing growth rates (e.g., Brittain 1976, Mackey 1977, Humpesch 1979, 1981, Vannote and Sweeney 1980). However, many other studies have shown that quality or quantity of food also can affect growth rates of aquatic invertebrates (reviews by Monakov 1972, Cummins 1973, Anderson and Cummins 1979, Cummins and Klug 1979). Unfortunately, the separate effects and relative importance of food and temperature have been difficult to distinguish (Sweeney 1984). This is especially a problem outside of the laboratory where temperature and food availability may vary concomitantly and thereby confound interpretations of growth patterns.

The purpose of this study was to examine patterns of individual growth and abundance of several related mayfly species as a function of stream environment and location. The study was designed to test two contrasting hypotheses: (1) temperature is the most important variable affecting growth of aquatic invertebrates; (2) food is the most critical factor. In addition, the data were used to examine whether individual growth or population density was most sensitive to differences among sites in food availability. Based on the results of this study, I question whether simple relationships between food, temperature, and patterns of individual growth can be easily generalized to populations in nature. I believe that the reasons for this are that (1) timing of growth relative to temperature regime can obscure otherwise direct effects of temperature, and (2) population responses may minimize individual response to environmental differences in food.

STUDY SPECIES

Because the larval taxonomy of ephemerellid mayflies in North America has been relatively well documented, species in this family were chosen for study. The family Ephemerellidae is also a ubiquitous and ecologically diverse taxon found in most stream ecosystems in north temperate regions of the world (Allen 1980). Eighty species in eight genera are now recognized in North America (Edmunds et al. 1976). Thirty-two species occur in the western United States and Canada. In this study, I considered the following species: *Ephemerella infrequens* McDunnough, *E. inermis* Eaton, *Drunella coloradensis* Dodds, *D. flavilinea* McDunnough, *D. doddsi* Needham, *D. spinifera* Needham, *D. pelosa* Mayo, and *Serratella tibialis* McDunnough. Taxonomic uncertainty exists with respect to previously published accounts for two pairs of cognate species. *Ephemerella infrequens* and *E. iner-*

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TABLE 1. Food and habitat associations for the six study taxa. See Hawkins (1984, 1985) for detailed descriptions.

Species	Dominant food	Habitat
Ephemerella infrequens/inermis	detritus, diatoms	gravel, sand
Drunella coloradensis/flavilinea	diatoms, animals	cobble
Drunella doddsi	diatoms, animals	cobble
Drunella spinifera	animals, detritus	cobble, moss
Drunella pelosa	diatoms	boulders, cobble
Serratella tibialis	detritus, diatoms	cobble

mis were therefore combined in all analyses, as were *D. coloradensis* and *D. flavilinea.*

Because aspects of the general ecology of the different species are useful when interpreting some phenological and growth patterns, I have summarized data on food and habitat use (Table 1).

STUDY SITES

Six stream sites in the Cascade Mountains of Oregon were studied for over a year (1978–1980). These sites were chosen to represent a range of environmental conditions. All sites were similar in size (basin area = 4–8 km^2, minimum discharge = 0.002–0.09 m^3/s) but differed in degree of riparian shading and elevational gradient. I chose these sites to maximize differences in type and quantity of food available to consumers. All sites were part of the McKenzie River drainage.

Of the six sites, one drained an old-growth coniferous basin (Mack Creek), another traversed an experimental clear-cut lying below the old-growth section of Mack Creek, and a third, North Fork Wycoff Creek, was surrounded by a dense red alder (*Alnus rubra*) riparian canopy. These three stream reaches were of similar gradient (10%). Three other reaches were of lower gradient (1%). Mill Creek drained a largely coniferous basin, Fawn Creek drained a clear-cut basin, and Cougar Creek was bordered by a dense alder canopy. These six reaches were described in detail by Murphy et al. (1981).

Life-history data for some of the species that I collected were also available for sites in Alberta, Washington, California, and Utah, thereby providing a larger data set and a latitudinal gradient by which to make additional comparisons. Growth data for *E. infrequens/inermis* from streams in California (C. P. Hawkins, *personal observations*), Alberta (Hartland-Rowe 1964, Ciboroski and Clifford 1983), and Washington (R. N. Thut, *personal communication*) were included in some analyses. Similar data sets were available for both *D. coloradensis/flavilinea* (Hartland-Rowe 1964, and unpublished data of D. Sagaguchi and J. Barnes, *personal communication,* and R. N. Thut, *personal communication*) and *D. doddsi* (Radford and Hartland-Rowe 1971; R. N. Thut, *personal communication*). The locations and major environmental features of all sites are summarized in Table 2.

METHODS

Environmental data

I sampled a number of environmental variables at the six main sites at intervals over the study period. 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: the clear-cut section on Mack Creek, North Fork Wycoff Creek, Cougar Creek, and Fawn Creek. Temperature data for Oregon streams other than Mack (old-growth) were incomplete. For those sites and dates for which I did not have recorded data, I estimated temperatures using predictive equations that related mean daily temperature at Mack (old-growth) to mean daily temperature at other sites (r^2 = 0.89–0.97, n = 75–270). By using both recorded tem-

TABLE 2. Summary of physical characteristics of the study sites.

Site	Location	Latitude (N)	Elevation (m)	Temperature (°C)		Ice cover	Canopy
				Degree days	Mean daily		
Kananaskis River*	Alberta	51°	···	1100	3.0	Oct–Apr	Open
Lusk Creek*	Alberta	51°	···	1270	3.5	None	Shaded
Gorge Creek*	Alberta	51°	1500	1420	3.9	Oct–Apr	Shaded
Pembina River	Alberta	53°35′	···	2680	7.3	Oct–Apr	Open
Kalama Springs	Washington	46°10′	···	2190	6.0	None	Open
Mack Creek (OG)**	Oregon	44°15′	760	2020	5.5	None	Shaded
Mack Creek (CC)**	Oregon	44°15′	730	2120	5.8	None	Open
North Fork Wycoff Creek	Oregon	44°15′	500	2330	6.4	None	Shaded
Mill Creek	Oregon	44°15′	360	···	···	None	Shaded
Fawn Creek	Oregon	44°15′	500	3640	10.0	None	Open
Cougar Creek	Oregon	44°15′	500	2430	6.7	None	Shaded
North Fork Provo River	Utah	40°60′	2000	1880	5.2	None	Open
Weber Creek	California	38°40′	500	4240	11.6	None	Shaded

* Approximate latitude.
** OG = old-growth section; CC = clear-cut section.

peratures and estimated temperatures, I was able to describe the annual temperature regimes of all main sites with the exception of Mill Creek. Temperature data were also available for the other streams examined.

I also estimated the quantity and quality of food available to invertebrate consumers by measuring detritus standing crops, organic matter on stones (aufwuchs), microbial respiration associated with detritus, and chlorophyll associated with both aufwuchs and detritus.

Field collections

Animals were collected approximately monthly at each of the six Oregon sites. Larvae were collected with a standard D-frame kicknet (0.5-mm mesh) as they were dislodged from stones, vegetation, and other substrates. Most habitats were sampled in each reach (riffles, pools, alcoves, bedrock). Samples were preserved in 95% ethanol immediately after collection.

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 (milligrams) with empirically derived equations relating head width (or length) to dry mass. Equations were of the form mass = aX^b, where a and b are constants, mass is in milligrams, and X is either body length or head-capsule width (in millimetres). For *D. coloradensis, D. doddsi,* and *D. spinifera,* I used the following values of the constants a and b: for length measurements, $a = 1.85 \times 10^{-3}$, $b = 3.46$ ($n = 256$, $r^2 = 0.91$); for head-capsule measurements, $a = 0.434$, $b = 3.62$ ($n = 256$, $r^2 = 0.92$). For all other species; $a = 1.02 \times 10^{-3}$, $b = 3.58$ ($n = 122$, $r^2 = 0.92$) for length; $a = 0.310$, $b = 4.02$ ($n = 123$, $r^2 = 0.87$) for head-capsule width. These relationships were obtained from K. W. Cummins, Oregon State University (*personal communication*). I converted data on length or head-capsule width to dry mass to allow standardized comparisons with data from other sites. Calculations of mass from data in other studies may be less accurate than for my data, because mean lengths or head widths had to be estimated from graphed data.

Use of such equations may have resulted in biased estimates of mass, especially if length-mass relationships varied considerably among species. The taxa that I studied exhibited one of two body forms. *Drunella coloradensis, D. doddsi,* and *D. spinifera* were all robust forms, whereas all other taxa had similar, more slender shapes. Different equations were therefore used to estimate individual mass for species in each group. Even if bias existed in estimates of mass, analyses are still valid, because comparisons of growth rates were made within species, not among species.

Data on abundance were collected in order to determine whether population density and individual growth were associated. During spring, summer, and autumn of 1978, quantitative samples of the benthos were taken at Mack old-growth, Mack clear-cut, Mill, and Fawn creeks to estimate abundances (Murphy et al. 1981, Hawkins et al. 1982). I sampled these streams because the contrast between heavily shaded and open sites that were otherwise similar would allow a clear examination of the effect of food on both abundance and growth. Three riffle samples and three pool samples were collected from each site on five different dates. Samples were collected with a modified Surber sampler (mesh = 1 mm).

Additional data on abundance (mesh = 0.5 mm) were collected during April and June 1979 and February 1980 (Hawkins 1984). Data were collected from several sites within the McKenzie drainage. These data are more extensive than the other benthos data in that I collected more samples (206) over a larger number of specific habitats.

Although use of 1-mm and 0.5-mm mesh nets almost certainly underestimated densities, these data allow a meaningful comparison of abundance with growth rate. All species attain lengths of 10 mm or more, and 90% of individual growth is elaborated within the last 2 or 3 mo of the growth period. Although density estimates are biased, they are biased toward those individuals whose growth rates are compared in subsequent analyses.

Laboratory studies

A laboratory study was conducted to determine the potential influence of type of food on growth. This study was designed to indicate the range in growth rates that could be expected in the field as a consequence of different food inputs. Experiments were conducted only with *E. infrequens.*

Erlenmeyer flasks (2 L) were used to rear animals. To each flask was added a layer of gravel, one of five food treatments, and one of two size classes of animals, thereby providing 10 treatment combinations. Treatments were not replicated. 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 (*Alnus rubra*) leaves, ground and conditioned alder leaves (<0.5 mm), and ground and conditioned alder wood (<0.5 mm). Leaf and wood material were conditioned for several weeks by dripping stream water into separate containers holding these food sources. Food and water in each flask were changed weekly. Food was always added in excess quantity so that the weekly portion was never completely consumed.

Individuals of *E. infrequens* were separated into two size classes: 4.0–4.5 mm (0.18 mg) and 6–7 mm (0.83 mg) in length. Seventeen individuals were placed in each flask of aerated stream water. Flasks were partially

submerged in a flow-through water bath to regulate temperatures. Temperature within each flask varied with temperature (5°–15°C) of the natural stream source used to supply the water bath.

The experiment was terminated after 56 d for small larvae, and 51 d for larger larvae. Each individual was dried at 50° for 24 h and then weighed on a Cahn electrobalance to the nearest 0.001 mg.

Analyses

Growth curves for each population were constructed by graphing mean size at each collection against date. Variation in growth rates was evaluated by calculating specific rates of growth, G, (Waters 1977). Two methods were used to calculate G. Growth between two successive dates was calculated as:

$$G = \frac{\ln(W_t/W_0)}{t} \cdot 100 \qquad (1)$$

where W_0 = mean initial mass, W_t = mean final mass, and t = the time interval in days. This method allowed numerous estimates of G to be made for the same cohort, but was sensitive to error because only two data points were used.

G was also estimated by regression analysis. Data were fitted to the equation:

$$W_t = W_0 e^{kt} \qquad (2)$$

where W_0 = mean mass at time zero, W_t = mean mass at time t, and k = the instantaneous coefficient of growth. $G = 100k$. Calculation of G by regression allowed estimation of error associated with estimates of G and thereby allowed statistical comparison by analysis of variance (ANOVA) among two or more populations. Tests for differences in G assume that growth curves are exponential and that residual variance (error) is random. If growth curves are not exponential, residual variance will not be random and tests may be biased.

Most populations did not exhibit exponential growth over the entire growth curve. The following procedure was therefore adopted. For each population, only data points that exhibited near exponential growth (straight line on semilog plot) were used to calculate G by regression. Also, values based on less than five individuals were never used in calculations of G. For some populations, growth was not continuous, or different sections of the growth curve exhibited clearly different slopes. For these populations, separate estimates of G were calculated for each section. Under these constraints, the relationship between mean size and time usually fit an exponential model well.

Because individuals in a collection from the same date often varied in date of birth, error existed in estimation of mean age. Growth rates derived from such analyses are valid only if mean size adequately represents the response of a single individual. Davenport (1934) showed that care must be taken in interpreting such data, especially when significant variation in timing of growth exists among individuals within a population. Brink (1949) and Thorup (1973) 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 an underestimate of 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 mo, Sweeney and Vannote 1981), and study reaches were not in close proximity to contrasting reaches. Because study reaches were representative of rather long sections of stream (≥1000 m), mean growth rates were probably not biased by immigration and emigration even in those species that drift (e.g., *E. infrequens*). Also, estimates of G were made after hatching of eggs was completed in order to minimize bias due to internal recruitment.

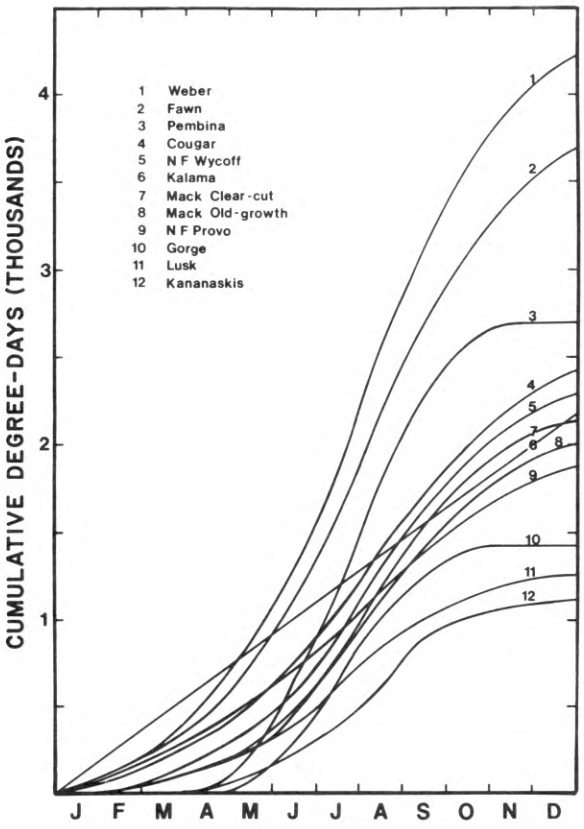

FIG. 1. Cumulative Celsius degree-days for each of the study sites.

Comparisons of G for each species were made among sites described above. Relationships between G, mean temperature during the growth interval, and median size were evaluated by correlation and regression analysis. I also examined whether G varied as a function of type of food available to consumers (i.e., open and shaded canopies) by applying analysis of variance to

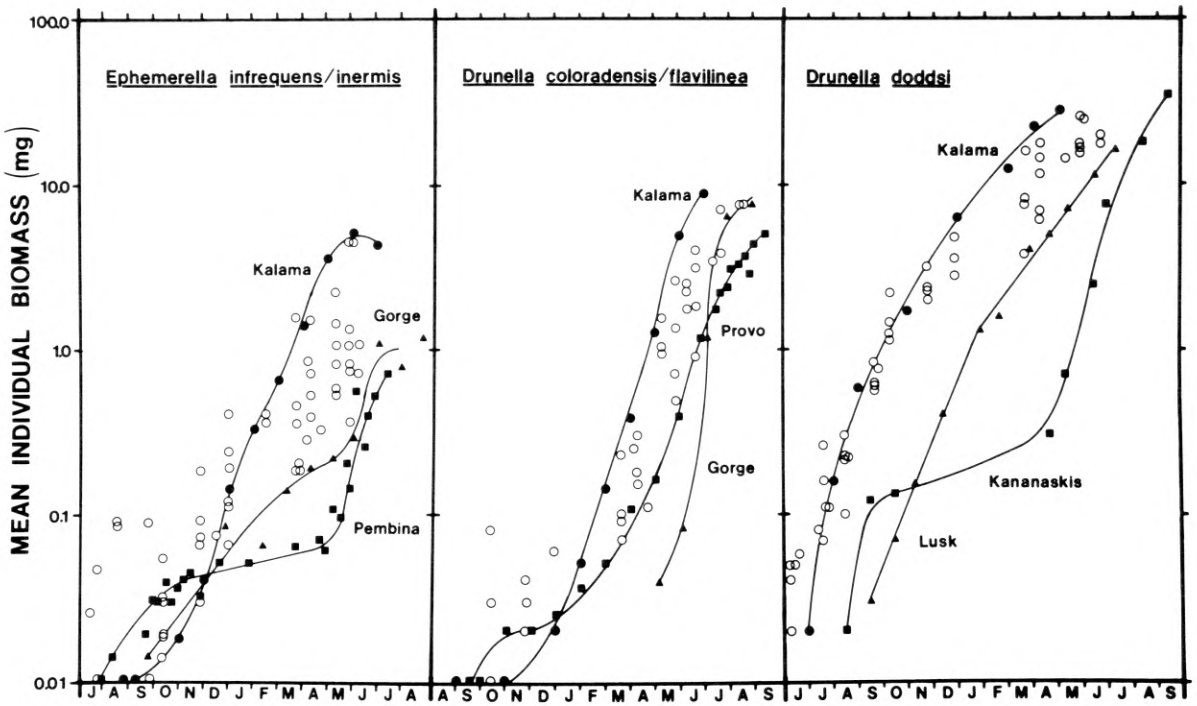

FIG. 2. Growth curves for *Ephemerella infrequens/inermis, Drunella coloradensis/flavilinea,* and *Drunella doddsi.* Data for other taxa were not graphed, because data were available only for the Oregon sites. Differences among Oregon sites were subtle and not easily distinguished visually. To facilitate comparisons among sites, lines were fitted to those growth curves that contrasted strongly with one another. Growth curves at Kalama Springs, the constant-temperature site, are shown, as are curves from the Alberta sites (Gorge Creek, Lusk Creek, Pembina River, and Kananaskis River) and the North Fork Provo River, Utah. Data from the Oregon sites (○) have been combined, because the overall shape of these curves was generally similar. Also, the growth pattern at the Oregon sites was generally intermediate to those at Kalama Springs and the Alberta sites.

data. I used correlation analysis to determine whether G varied with different measures of food quantity and quality.

Comparison of treatment effects in the laboratory study was made by two-factor ANOVA. For this analysis, multiple comparisons (Least Significant Difference, LSD) and ANOVA were applied to final masses of all larvae surviving at the end of the experiment.

Differences among sites in mean abundances were determined by t tests after $\log_{10}X + 1$ transformation of raw data. Data sets were sufficiently large to examine contrasts between streams with shaded and open canopies.

RESULTS

Environmental contrasts

The 12 sites exhibited distinct differences in both total accumulated heat (annual degree-days) and seasonal pattern of heating and cooling (Fig. 1). Total degree-days was a function of both latitude and altitude, and nearly a four-fold difference existed between the warmest (Weber Creek) and coolest (Kananaskis River) streams (Table 2). Among the Cascade Range streams, temperature patterns also were affected by shading. Heavily shaded streams were cooler than streams with open canopies. All streams exhibited typical seasonal patterns of summer warm and winter cold except Kalama Springs, which was 6°C all year. Gorge Creek, the Kananaskis River, and the Pembina River are covered by ice for ≈5 or 6 mo (October through April).

Both quantity and quality of food available to consumers differed among the Cascade sites (Hawkins et al. 1982). In general, open sites had higher standing crops of algae and higher rates of microbial respiration associated with detritus than did shaded sites. Gregory (1980) and McIntire and Colby (1978) also showed that open streams in the Pacific Northwest had higher rates of primary production than did shaded streams. In this study, low-gradient sites had higher detritus standing crops than high-gradient sites. Shaded sites had higher standing crops of leaves than open sites, but no difference existed between open and shaded sites in amount of total detritus. However, most of the detritus in these streams was of very low quality (wood and refractile fines). Standing crop of leaves is probably a better measure of food availability than total detritus. Open and shaded sites therefore provided a distinct contrast in food available to consumers.

TABLE 3. Growth statistics for six taxa of Ephemerellidae. Specific growth rate (G) is given for each site with number of data points (n) used to calculate G. The coefficient of determination (r^2) describes fit of data to the exponential model.

Site	*E. infrequens/ inermis*			*D. coloradensis/ flavilinea*			*D. doddsi* (small)			*D. doddsi* (large)		
	G	n	r^2	G	n	r^2	G	n	r^2	G	n	r^2
Open sites												
Mack (CC)*	1.18	6	0.78	3.28	5	0.93	2.26	7	0.92	1.00	5	1.00
Fawn	2.27	3	0.98	3.39	5	0.96	3.27	3	0.90	...	...	...
Kalama	2.48	6	0.99	3.55	5	0.99	2.87	5	0.92	1.40	4	0.99
North Fork Provo	...	...	...	2.52	10	0.99	...	...	...	...	...	...
Kananaskis	...	...	...	...	...	...	3.48	3	0.90	3.03	6	0.94
Pembina 1978	5.40	5	0.95	...	...	...	...	...	...	...	...	...
Pembina 1979	3.34	6	0.98	...	...	...	...	...	...	...	...	...
Pembina 1980	4.32	4	0.94	...	...	...	...	...	...	...	...	...
Shaded sites												
Weber (I)†	2.24	2	...	3.05	2	...	...	...	...	...	...	...
Weber (II)†	5.83	2	...	...	...	...	...	...	...	...	...	...
Mack (OG)* 1978	...	...	...	2.63	4	0.99	...	...	...	...	...	...
Mack (OG) 1979	1.62	7	0.92	2.57	4	0.97	2.48	9	0.93	1.17	5	0.89
Mill	1.64	5	0.81	...	...	...	2.36	5	0.97	...	...	...
North Fork Wycoff	1.50	4	0.96	3.67	4	0.98	2.28	7	0.99	1.11	3	1.00
Cougar	2.89	3	0.98	...	...	...	...	...	...	1.20	3	0.78
Gorge	1.37	7	0.89	5.31	5	0.94	...	...	...	...	...	...
Lusk	...	...	...	...	...	...	2.87	4	1.00	1.65	6	0.98
ANOVA‡ (H_0:G's equal)	$F = 7.49$, $P < .01$			$F = 11.06$, $P < .001$			$F = 4.39$, $P < .005$			$F = 12.18$, $P < .001$		

Site	*D. spinifera*			*D. pelosa*			*S. tibialis*		
	G	n	r^2	G	n	r^2	G	n	r^2
Open sites									
Mack (CC)	1.14	8	0.95	2.41	5	1.00	3.74	4	0.96
Fawn	...	...	...	3.14	3	0.99	...	...	...
Kalama	...	...	...	...	...	...	5.44	5	1.00
Shaded sites									
Mack (OG)	0.81	6	0.99	2.28	5	0.97	3.97	3	0.94
Mill	1.29	5	0.98	...	...	...	...	...	...
North Fork Wycoff	...	...	...	2.61	3	0.99	...	...	...
H_0:G's equal	$F = 13.41$, $P < .001$			$F = 4.84$, $P < .05$			$F = 6.97$, $P < .05$		

* CC = clear-cut; OG = old-growth.
† Two generations/yr present in Weber Creek.
‡ ANOVA of regression coefficients (G) used to test whether G varied significantly among all sites.

Growth

Initiation of growth was often associated with either latitude or elevation. For example, individuals of *D. doddsi* from Oregon sites began growth in June, whereas growth did not start until September for individuals in Lusk Creek, Alberta (Fig. 2). A similar trend was apparent for *D. coloradensis/flavilinea.* Growth was initiated first in the warmest Oregon site (Fawn Creek) and last in Lusk Creek, the coldest site from which this species was collected. However, for *E. infrequens/inermis,* a simple trend in onset of growth was not apparent. Individual growth for this taxon apparently starts as early as June in some of the relatively warm Oregon sites and as late as September for Gorge Creek, Alberta. However, no trend existed among Oregon sites for initiation of growth to vary with temperature. Also, onset of growth differed by as much as 4 mo (June–September, Fig. 2), even among sites that had similar temperatures (Fig. 1).

Shape of the growth curve also was extremely variable within taxa (Fig. 2). For streams that experienced ice cover during winter (Kananaskis River, Pembina River), growth was extremely low (*D. doddsi* and *E. infrequens/inermis,* respectively). Growth was continuous in other streams even though temperature was extremely low at some sites (Fig. 1). Subsequent to the breakup of ice, growth was very rapid; G was two to nearly four times greater than in other populations. Although winter samples were not available, this phenomenon of low winter growth and rapid summer growth apparently occurred in *D. coloradensis/flavilinea* in Gorge Creek as well.

Growth rates varied significantly among sites for all species examined (Table 3). This was true not only when all sites were considered, but also when the Oregon sites were considered separately. The highest rate within a taxon was as much as 4.7 times the lowest rate (*E. infrequens/inermis*). Because G is an exponen-

TABLE 4. Correlation coefficients (r) between instantaneous growth (G), mean temperature (T) and median mass (M) for the interval over which G was calculated. Correlations calculated from both two-sample incremental and regression data.

Species	Incremental data				Regression data			
	n	$G \times T$	$G \times M$	$M \times T$	n	$G \times T$	$G \times M$	$M \times T$
	Correlation coefficients (r)							
Ephemerella infrequens/inermis	36	0.47**	−0.10	−0.08	11	0.84**	−0.34	−0.29
Drunella coloradensis/flavilinea	34	−0.25	−0.40*	0.51**	9	0.09	−0.38	0.51
Drunella doddsi (large)	26	−0.10	−0.34	0.62**	7	0.44	−0.75*	−0.24
Drunella doddsi (small)	28	0.34	−0.44*	−0.53**	7	0.11	−0.84*	0.20
Drunella doddsi (all)	54	−0.16	−0.41*	0.29*	—†	—	—	—
Drunella spinifera	17	0.60*	−0.39	0.18	—	—	—	—
Drunella pelosa	12	0.22	0.28	0.81**	—	—	—	—
Serratella tibialis	9	−0.45	−0.37	0.08	—	—	—	—

* $P < .05$, ** $P < .01$.
† Dashes indicate cases where low number of sites prevented comparisons.

tial coefficient, such differences in G reflect large differences in absolute growth.

Taxa differed considerably with respect to the relationships between growth, mean temperature, and median mass (Table 4). Calculation of G by Eq. 1 provided sufficient data to examine the relationships between growth rate, temperature, and individual size for all taxa. Because of small samples size (i.e., number of sites), calculation of G based on regression restricted comparisons to only *E. infrequens/inermis, D. coloradensis/flavilinea,* and *D. doddsi.* Growth in two taxa (*E. infrequens/inermis* and *D. spinifera*) was positively correlated with temperature; other species exhibited no relationship between temperature and growth. However, for those species, mean size and temperature were usually positively correlated, e.g., *D. coloradensis/flavilinea* and *D. pelosa.* Growth of small larvae of *D. doddsi* was not correlated with temperature, but mean size and temperature were negatively correlated. For most species, size and G tended to be negatively correlated, although for only two species (*D. coloradensis/flavilinea* and *D. doddsi*) were correlations significant. *Serratella tibialis* was the only species to show no relationship between growth, size, and temperature.

Effect of food

Growth rate did not vary as a function of type or quantity of food entering the stream (Table 3: open vs. shaded). Values of G varied from low to high among both shaded and open streams for most species, and no significant differences in mean values of G between open and shaded sites were observed (t tests, $P > .05$) for any species. Correlation between G for *E. infrequens* and mean amount of chlorophyll in fine sediments (≤100 μm) was not significant ($r = -0.13$, $n = 6$), nor was correlation with either mean respiration rate of detritus ($r = -0.04$, $n = 6$) or mean quantity of aufwuchs ($r = 0.34$, $n = 6$). No significant correlations existed between these variables and growth rates of the other species, either.

Because effects of confounding variables such as temperature could possibly mask effects of food, growth rates for species collected in both the open and shaded sections of Mack Creek were compared by ANOVA of regression coefficients (i.e., G). These two sites were similar in temperature and other physical attributes (Fig. 1, Table 2, also Hawkins et al. 1982), but differed markedly in litter inputs and rates of primary production (Hawkins et al. 1982, Gregory 1980). Of six species, growth rate of only *D. spinifera,* a carnivore, differed significantly between the two sites ($P < .005$). It grew faster in the open section.

In the laboratory, however, differences in food resulted in significant differences ($P < .05$, LSD) in growth rates for *E. infrequens.* For small larvae, animals grew most rapidly on algae ($G = 5.25$). Tetramin and alder fines produced intermediate growth ($G = 4.51$ and 4.44), and growth was slowest on whole alder leaves and wood fines (2.52 and 0.79). Growth of larger larvae was highest on Tetramin and alder fines ($G = 2.52$ and 2.43), intermediate on algae and whole leaves ($G = 2.26$ and 2.15), and lowest on wood fines ($G = 0.67$).

Abundances

Comparison of densities of animals collected in 1978 in two shaded sites (Mack Creek and Mill Creek) and two open sites (Mack Creek and Fawn Creek) showed that the four most commonly encountered ephemerellid species (*E. infrequens, D. coloradensis, D. doddsi,* and *S. tibialis*) were all most abundant in open sites (Fig. 3). Comparison of densities of animals collected in 1979–1980 from these and other sites showed that *E. infrequens, D. pelosa,* and *D. coloradensis* were most abundant in open sites. *Drunella spinifera* was the only species to show no evidence of preference for either open or shaded sites.

DISCUSSION

Temperature and growth

The influence of temperature on life histories of these species is most clearly apparent in the variation among populations of *D. doddsi* and *D. coloradensis/flavilinea* in onset of growth (Fig. 2). The trend for growth to

begin earlier in warmer sites and later in cooler streams is probably a reflection of the inverse relationship between egg development and temperature observed for many aquatic invertebrates (e.g., Humpesch and Elliott 1980). However, much of the extensive variation among growth curves for populations of *E. infrequens/inermis* could not be completely explained by temperature differences among sites.

The variation observed in growth curves for *E. infrequens/inermis* is probably a consequence of latitudinal variation in voltinism in this taxon. Allen and Edmunds (1965) noted that numerous broods of *E. inermis* occurred throughout the summer months in many streams. In Weber Creek, California, *E. inermis* was bivoltine; one cohort emerged in May and the second emerged in August (C. P. Hawkins, *personal observation*). In some of the Oregon streams I studied, a weak but separate cohort of individuals that could not be distinguished from *E. infrequens* was present. These individuals were larger than other individuals during winter, and had emerged by May. R. N. Thut (*personal communication*) noted in 1967 that similar individuals were present in Kalama Springs. I did not include these individuals in my analyses and comparisons.

Although it is possible that these individuals are an undescribed sibling species (Allen and Edmunds 1965), they may simply be individuals that hatched from eggs laid late in the year (e.g., September). At this time temperatures were declining rapidly in most streams (Fig. 1), and egg development could have been retarded to such an extent that larvae did not hatch until February or March (see below for a discussion of size–temperature effects). Such individuals would probably not have sufficient time to complete development by summer in cooler streams. Instead they would have to grow through the following autumn and winter and emerge in early spring. This is exactly the pattern that R. N. Thut (*personal communication*) reported for the unknown *Ephemerella* sp. that he observed. In sufficiently warm streams, (e.g., Weber Creek) eggs laid by this cohort in May would probably have time to develop by August or September, thereby maintaining truly bivoltine populations. If cohort strength varied among streams, some of the unexplained variation among populations in timing of growth may therefore be an artifact of comparing different cohorts. Growth patterns would therefore not appear to vary with temperature. The effect of temperature on onset of growth would be apparent only when examined for each cohort separately.

The pattern for larval growth to slow in those streams with winter ice cover may be attributable to extremely low temperature. However, because ice cover also reduces primary production, lack of high-quality food may also reduce growth rates (see Food and Growth). Regardless of the reasons why growth slows in ice-covered streams, temperature and size appear to interact to influence the subsequent shape of the growth curve. Rapid growth (high G) was observed in *E. infrequens/inermis, D. doddsi,* and *D. coloradensis/flavilinea* following spring thaw. High rates of growth are in part attributable to rapidly warming water in these streams (e.g., Pembina River). However, the high growth rate for *D. doddsi* in the Kananaskis River cannot be explained by rapid warming, because this stream warms no more rapidly than other streams examined (Fig. 1). High growth rates for *D. doddsi* (Kananaskis River), *D. coloradensis/flavilinea* (Gorge Creek), and *E. infrequens/inermis* (Pembina River, Weber Creek–generation II) are probably manifested through an interaction of temperature and size on growth. For a unit change in temperature, growth changes more for small individuals than larger ones (Brody 1927), that is, Q_{10} for growth is greater for small than large individuals. Growth rates were much lower in streams where growth was continuous during winter, and larvae therefore were larger when streams began to warm (Table 3).

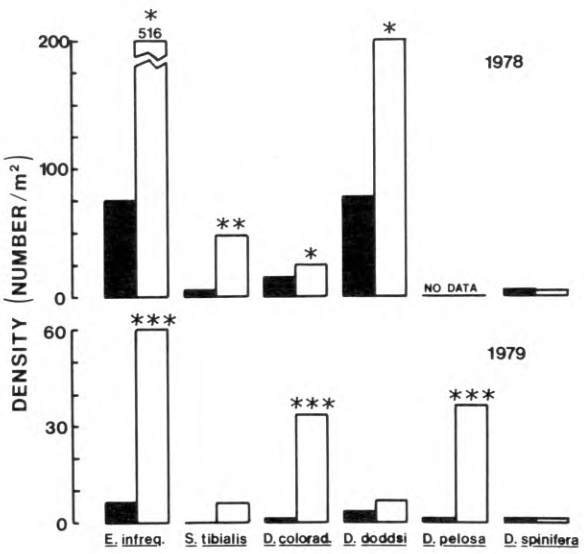

FIG. 3. Mean densities of six species of Ephemerellidae (*Ephemerella infrequens, Serratella tibialis, Drunella coloradensis, D. doddsi, D. pelosa, D. spinifera*) in Oregon streams with shaded (black bars) and open (open bars) canopies. Data given for two years. See Methods: Field Collections for explanation of differences in sampling between years. Significant differences between shaded and unshaded streams (t tests): $P < .05$ = *, $P < .01$ = **, $P < .001$ = ***.

Correlations between field growth rates and stream temperature were not consistent among taxa. For both *E. infrequens/inermis* and *D. spinifera,* growth rate was positively related to temperature over both short time periods (incremental data) and long time periods (regression data, Table 4). This type of pattern has been observed frequently (Brittain 1976, Mackey 1977, Humpesch 1979, 1981, Wise 1980, Markarian 1980, Vannote and Sweeney 1980), especially in laboratory studies. Because metabolic rates of most poikilotherms

are strongly influenced by temperature (Precht et al. 1973, Taylor 1981), such a positive relationship might be expected in the field.

Three taxa, however, showed no apparent relationship between temperature and growth (Table 4). Lack of a correlation between field growth rate and temperature does not necessarily imply that growth rate is truly independent of temperature. In the laboratory, animals exposed to different temperature regimes usually exhibit temperature-dependent growth responses. In natural settings, however, several physical and biological attributes may change concomitantly over time to obscure simple effects of temperature. For example, mean daily temperature usually exhibits cyclic changes on a seasonal basis, whereas individuals progressively increase in size with time. Two factors that can influence growth rate, temperature and size, can vary independently of each other.

Vannote (1978) hypothesized that in some stream insects, growth is timed such that a quasi-equilibrium exists between the positive effect of increasing temperature and the negative effect of increasing size on mass-specific metabolism (Minot's Law, Minot 1908, Sutcliffe et al. 1981, Robinson et al. 1983). Hence as streams warm in spring and summer and individuals increase in size, G should remain nearly constant. Growth in *D. coloradensis/flavilinea,* large *D. doddsi,* and *D. pelosa* apparently fits Vannote's model. For these species, there is a tendency, although not always strong, for G to decrease with increasing mass and for size to increase as temperature increases (Table 4).

Vannote's hypothesis, however, cannot be applied as a general model to explain the evolution of phenological pattern in all species of western Ephemerellidae. Three of the taxa studied did not fit the model: *E. infrequens/inermis, D. spinifera,* and *S. tibialis.* Also, small and large larvae of *D. doddsi* showed opposite relationships between individual mass and temperature. Such correlations would occur as a simple consequence of positive growth during the course of a thermal regime that falls and rises over the growth period. These exceptions lead me to believe that constant rates of G (i.e., a quasi-equilibrium) may be simply a coincidental effect of timing of growth. Selective factors other than temperature may therefore have been more important in the evolution of the phenologies of these species. For example, because these species exhibit strong habitat segregation and moderate separation based on food (Table 1, Hawkins 1984, 1985), the dynamics of habitat or food availability may have shaped life history patterns (e.g., Georgian and Wallace 1983).

Food and growth

This study provided little evidence that food, except under severe conditions, was responsible for much of the variation observed in field growth rates. Depression of growth rates in streams with ice cover was the only example of possible food-limited growth. Because winter temperatures in some streams without ice cover were as low as those streams with ice, these patterns presumably cannot be due to temperature differences. Ice cover in Alberta streams can be 60 cm thick (Ciborowski and Clifford 1983). Algal production and detrital inputs could therefore be very close to zero for up to 6 mo of the year in these streams. Under these severe conditions, food may very likely limit individual growth.

Results for streams without ice cover apparently contradict a large literature that implicates food (either quantity or quality) as a factor that commonly affects individual growth in aquatic and terrestrial invertebrates (reviewed by Waldbauer 1968, Monakov 1972, Cummins 1973, Anderson and Cummins 1979, Cummins and Klug 1979, Scriber and Slansky 1981, Sweeney 1984). Most of this literature describes responses of animals to laboratory experiments, whereas only one study of stream invertebrates of which I am aware has unequivocally related growth of uncaged individuals in the field to differences in food sources (Peterson et al. 1985). McMahon et al. (1974) reported significant correlations between growth of snails and limpets in the field with aufwuchs quality, but did not report possible effects of temperature. Anderson and Cummins (1979) also reported a significant correlation between food, as measured by P/R ratio of aufwuchs on stream sediments, and individual mass attained as prepupae for *Glossosoma nigrior* ($r^2 = 0.95$, $n = 4$, as determined from data in Table 3 of their paper). It is impossible, however, to determine whether growth was influenced by food or temperature, because biomass of prepupae was also correlated with degree-days ($r^2 = 0.95$, $n = 4$) for these same data. Peterson et al. (1985) increased food availability to invertebrate consumers by adding phosphorus to a stream. Over a 6-wk period, growth rates of the blackfly, *Prosimulium* sp., increased relative to upstream controls. The response observed by Peterson et al., however, may have been temporary, because population densities can change over time, thereby reducing per capita food availability to original levels (see Growth–Abundance Relationships).

Although rates of growth in the field and gross measures of food availability were not related, populations may still have been food limited. Laboratory results showed that growth of *E. infrequens/inermis* can be strongly influenced by food quality. Also, densities of most species were higher in open sites with high primary production than in shaded sites. These results indicate that densities may be food limited, even if individual growth is not. Other recent studies have also shown that food may limit stream invertebrate densities. Hart (1981) showed that food (aufwuchs) limited density of the stream caddisfly *Discosmoecus gilvipes.* Also, larvae of the caddisfly *Glossosoma* sp. (McAuliffe 1984) and a pleurocerid snail (C. P. Hawkins and J. K. Furnish, *personal observations*) can depress both

algal standing crops and abundances of other grazers. Indirect evidence for food limitation was 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 six of the Cascade streams considered here, Murphy et al. (1981) and Hawkins et al. (1982, 1983) showed sites open to sunlight to have significantly greater abundances of most taxa than similar but shaded sites. Other studies cited by Murphy et al. (1981) have shown similar differences between open and shaded streams.

Growth–abundance relationships

The differences in densities observed among sites appear to be a reflection of differences among sites in carrying capacity. If densities in streams are generally near carrying capacity, per capita food availability among streams may differ very little. This interpretation is consistent with the following observations. Densities of most invertebrates in the Oregon streams were positively correlated with food availability (cf. Fig. 3 and Hawkins et al. 1982), whereas individual growth was not. Densities in open systems like streams may seldom reach high enough levels to cause extreme depression of growth rates. Individuals that would otherwise be in excess of the carrying capacity for a reach or stream can be lost by drifting or active dispersal (Waters 1969). Increased drift rates in relation to low food supply have been observed by Hildebrand (1974), Bohle (1978), and others. Several other studies have noted that density can vary with resource level in streams, whereas growth rates are similar. Cummins et al. (1980) observed that the detritus shredder *Tipula* increased in density with addition of leaf litter to a stream, but they did not detect any change in individual growth.

The foraging and dispersal behavior of individuals should promote differences in densities while maintaining similar growth rates. For example, Fretwell (1972) predicted that dispersive organisms should exhibit an "ideal free distribution." An "ideal free distribution" is an equilibrium that obtains when individuals invade high-quality habitats in high densities and low-quality habitats in low densities such that individual fitness (i.e., growth rate) is similar across habitats.

Because many stream invertebrates are highly dispersive (Waters 1969, Sheldon 1984), rapid colonization of undersaturated localities is possible. Distributions similar to that predicted by Fretwell could therefore arise. Fraser and Sise (1980) and Power (1984) noted that some stream fishes conform to this distribution. The prediction of an "ideal free distribution" is probably most applicable to invertebrate taxa that are vagile, particularly those prone to drift. Up to 20% of benthic densities per day can disperse to other habitats by drift (Sheldon 1984). Of the taxa considered in this study, *D. spinifera* was the only species that was never collected in drift samples (C. P. Hawkins, *personal observation*). It was also the only species to show differences in individual growth rates but no differences in densities between open and shaded sites.

The assumptions of Fretwell's model, that individuals can (1) instantaneously disperse to any habitat patch, and (2) choose the best patch, rigidly constrain its application to many ecological systems. However, the more general idea that populations may maintain dynamic equilibrium densities by balancing recruitment and emigration is ecologically appealing. Such equilibria may occur over several spatial scales (e.g., among habitat patches, heterogeneous reaches, or entire drainages) and therefore lead to similar individual growth rates among habitats, reaches, or streams.

Conclusions

Based on the results of this work, it is evident that care must be taken when generalizing about the factors that control individual growth in natural stream ecosystems. Simple relationships derived from laboratory or field studies may lead to specious conclusions regarding the importance of single factors, unless they are studied in the context of both the complex interactions and patterns of life history adaptation exhibited in natural systems. For example, the laboratory and field studies would have led to different conclusions regarding the importance of food to individual growth. Such apparently contradictory results can be reconciled, however, if activity of individuals (e.g., growth) is interpreted in the context of factors affecting entire populations. Similarly, the effect of temperature on individual growth may not necessarily be manifested in nature in the simple manner that laboratory studies or metabolic considerations would suggest. The particular juxtaposition of growth periods with respect to changing thermal regimes can obscure and confound otherwise direct effects of temperature.

Temperature has often been viewed as a major, if not the dominant physical template (sensu Southwood 1977) upon which phenological patterns evolved (reviewed by Ward and Stanford 1982). Vannote's (1978) model explicitly suggests that timing of growth is a selected trait, and hence adaptive, in which individual growth has been timed to maintain homeostasis of metabolic output. My results indicate that no general patterns of timing in relation to temperature existed among these six taxa. A general pattern may not have emerged for several reasons. Among these are: (1) taxa may differ in degree of tolerance to temperature, i.e., some taxa may be eurythermal and others stenothermal, (2) timing of growth relative to temperature may not necessarily be as adaptive (cf. Butler 1984) as commonly suggested, and (3) other factors may have played an equally important or more important role in the evolution of timing of life histories.

Results derived from this study also have important implications for ecosystem-level processes as well as life history phenomena. If individual growth and density responses in streams are strongly linked, certain predictions can be made regarding the sensitivity of parameters that affect energy flow through consumers. For example, production can be measured as the product of individual growth rate and mean biomass ($P = GB$, instantaneous growth model, Benke 1984). If populations conform to an "ideal free distribution," differences in production among sites of similar temperature but different quality (quantity and quality of food) should mainly reflect differences in densities (biomass distribution) rather than individual growth. This is exactly what Behmer and Hawkins (1986) observed for invertebrates in a Utah stream. For populations that are less dispersive and do not conform to the "ideal free distribution," production may be equally or more influenced by individual growth than by density (e.g., O'Hop et al. 1984). Although these predictions are clearly limited because other factors such as temperature may affect G and perhaps density, it is only through the construction of models that incorporate life history and population phenomena that a general and explanatory theory of secondary production will emerge.

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