

RELATIONSHIPS BETWEEN HABITAT DYNAMICS FOOD AVAILABILITY, AND GROWTH PATTERNS OF EPHEMERELLID MAYFLIES FROM WESTERN NORTH AMERICA

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ABSTRACT

I examined whether variation in timing and length of the growth period for 11 species of EphemereLLidae was a function of either microhabitat stability or food availability. My data indicate that the growth patterns of these related species may be broadly constrained by taxonomic affinities. However, the final 90% of growth for each species almost always occurred during periods of maximum stability of preferred habitats. In addition, length of the growth period apparently varied directly with durational stability of preferred habitats, although this relationship is not exceptionally strong. For some species, timing of growth may also be influenced by predictable seasonal variation in availability of food. In general, hypotheses based on single factors are inadequate to explain all observed patterns. Also, comparison of my results with other studies indicates that the relative importance of different selective factors probably varies with geographic location.

INTRODUCTION

Within most groups of aquatic insects, species exhibit distinct phenological patterns of growth and emergence. Presumably, for any species, timing of individual growth represents an adaptive solution to seasonal variation in either resource availability or habitat suitability (e.g. Butler 1984). Unfortunately, it is usually not clear what specific selective forces operated in the past to produce present patterns. Moreover, because present patterns may be "ghosts of conditions past" (*sensu* Connell 1980) and may not reflect present day interactions, experimental investigation of causal mechanisms is nearly impossible. Nonetheless, it is important to understand the life-history dynamics of different species if aquatic ecology is to be an explanatory science. Hence, a number of hypotheses have been offered to explain differences in life-history patterns among related species. These

include:

1. life-history patterns have evolved to avoid or minimize interspecific competition (Grant and Mackay 1969, Hynes 1976, Sweeney and Vannote 1981, Georgian and Wallace 1983),
2. timing of growth and emergence periods maintain reproductive isolation (Price 1975),
3. growth periods take advantage of abundant or required food sources (Georgian and Wallace 1983), and
4. life-history patterns are not related to either past or present environments – i.e. they are random with respect to the environment and other species.

The first three hypotheses are intuitively reason-

able and ecologically plausible. However, few empirical and no experimental data exist by which to test them. Distinguishing the veracity of these hypotheses of "ultimate" cause is further hampered, because seasonal changes in temperature or photoperiod are apparently used by many species as "proximate" cues to initiate and end growth and development (*cf.* Butler 1984, Sweeney 1984).

In this paper, I present an alternative hypothesis to explain species specific differences in growth patterns. This hypothesis predicts that timing and length of growth are adaptations to seasonal changes in physical suitability of preferred habitats. A similar hypothesis was advanced by Southwood (1977). He argued that life-history strategies of species should vary in relation to the "durational stability" of the habitats each species exploited. For example, only species with short life cycles or high vagility should exploit habitats of low stability. Conversely, species with either short or long life cycles can exploit habitats of high stability, although long lived species may have a competitive advantage in such habitats. In Fig. 1, I show how length of the life cycle or growth period should theoretically vary with habitat stability.

In this paper, I use life-history data for several species of ephemereid mayflies from western

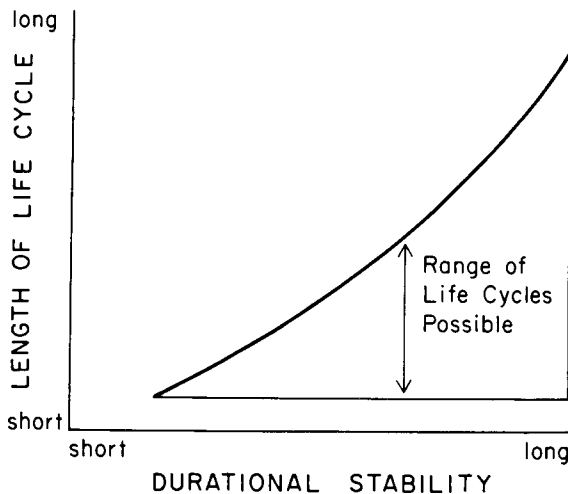


Fig. 1. Predicted relationships between habitat persistence (durational stability) and length of the life cycle or growth period for different species.

North America to evaluate the explanatory power of the habitat stability hypothesis compared to others. Ephemerellid mayfly larvae from this region exhibit extensive adaptive radiation in resource use. Niche overlap among species is lowest along the longitudinal gradient of small to large streams, intermediate for both timing of growth and use of microhabitat, and greatest for diet (Hawkins 1982). Observed values of mean niche overlap among 20 species were 0.28, 0.42, 0.40, and 0.76 for the resource axes mentioned above respectively, where values could theoretically (Schoener 1968) vary between 0 (no overlap) and 1 (complete overlap). The fact that overlap was extremely low along the longitudinal gradient studied was not surprising considering that several single environmental factors (e.g. temperature, substrate, and food) vary simultaneously along such gradients (Hynes 1970). With respect to single factors, these results imply that adaptive radiation among these species may have been largely facilitated by ecological partitioning of microhabitat use and time of year that growth occurs. However, if availabilities of different microhabitats in streams vary over the year, differences in growth may largely reflect adaptation to the seasonal dynamics of specific microhabitats.

METHODS

Life-history data for ephemereid mayflies were collected at several sites in the Cascade Mountains of Oregon (Fig. 2). At the same time, data on habitat use and diet were collected. Because details of sampling were reported previously (Hawkins 1984, 1985, 1986), only a brief summary is provided here. Animals were collected monthly with a D-frame kick-net (0.5 mm mesh) from several habitat units at each site. Habitat units were distinguished based on substrate size and location (e.g. sand, gravel, cobble, top of boulder, bottom of boulder, moss).

In the laboratory, lengths (L) and head-capsule widths (HCW) of larvae from each sample were measured to the nearest 0.5 mm and 0.03 mm for L and HCW respectively. Dry mass of individuals

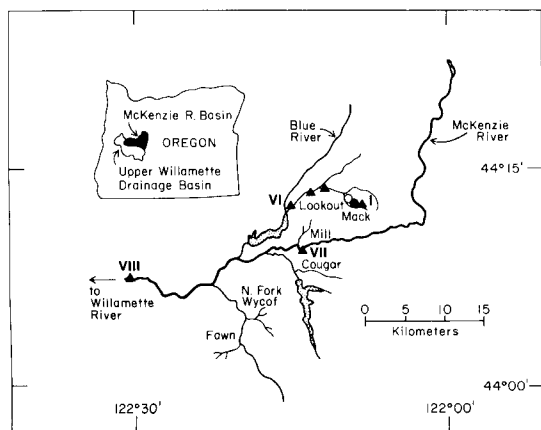


Fig. 2. Map of the McKenzie River drainage in Oregon. Sampling locations are shown with symbols.

was then estimated with length-mass or HCW-mass equations. Growth curves in terms of dry mass were constructed from these data. Analyses of diet, habitat preferences, and intraspecific variation in growth rates were reported elsewhere (Hawkins 1984, 1985, 1986). However, general aspects of these analyses will be incorporated into this paper when appropriate.

Growth and habitat persistence

For each species, I compared length of the growth period and timing of growth to estimates of habitat persistence of preferred habitats. Qualitative estimates of habitat persistence were made by considering the probable effects of changing flow regime on different habitat units. Sand-gravel (SG) patches were considered to be persistent for only 4 months (late spring – late summer). During other periods, small substrates are vulnerable to scour and movement by storm flows. Persistence of cobble (C) patches was estimated as 6 months (mid-spring – mid-autumn), because high flows can move cobble particles during seasons of high flow. Tops of boulders are exposed to torrential flows from late autumn through early spring. Conversely, tops of boulders are likely to be exposed to air in late summer as water levels decline to summer base flows. I therefore considered this habitat to be suitable for only 4 months – the period of moderate flows from mid-spring to early

summer. The bottoms of boulders and all substrates with moss cover were considered to be stable habitats all year (12 mo). Boulders are not likely to move except during flows of extremely high magnitude that occur rarely (e.g. > 50 yr). Because interstitial spaces beneath most boulders are wetted all year, they should therefore be extremely stable habitats. Patches of moss were also considered to be very stable, because mosses in these streams live for many years. They are stable by virtue of their presence.

Cast of characters

Fourteen species were collected during the course of the study at these sites. Sufficiently complete data were collected to quantify growth patterns of nine species. Less complete data were collected for two other species. The species used in the following analyses were: *Attenella margarita* Needham, *A. delantala* Mayo, *Ephemerella infrequens* McDunnough, *Drunella pelosa* Mayo, *D. coloradensis* Dodds, *D. doddsi* Needham, *D. spinifera* Needham, *Serratella tibialis* McDunnough, *S. nr. teresa* Traver, *Caudatella cascadia* Allen and Edmunds, and *C. hystrix* Traver. In this paper, I have followed the taxonomic divisions proposed by Allen (1980).

RESULTS AND DISCUSSION

The monthly contribution to growth as percent of individual mass attained at maturity varied considerably among species (Fig. 3). All species were univoltine and growth of individuals within species was highly synchronous. Although all species completed development in either spring or summer, it is apparent that relatively little overlap occurred among species in timing of growth (*cf.* values of niche overlap). Low temporal overlap is especially apparent when periods to complete the final 90% of growth are compared. The time required to complete growth (egg hatch to emergence) varied between 5 and 12 months. Time to complete the final 90% of growth varied between 2 and 7 months. In general size at maturity was

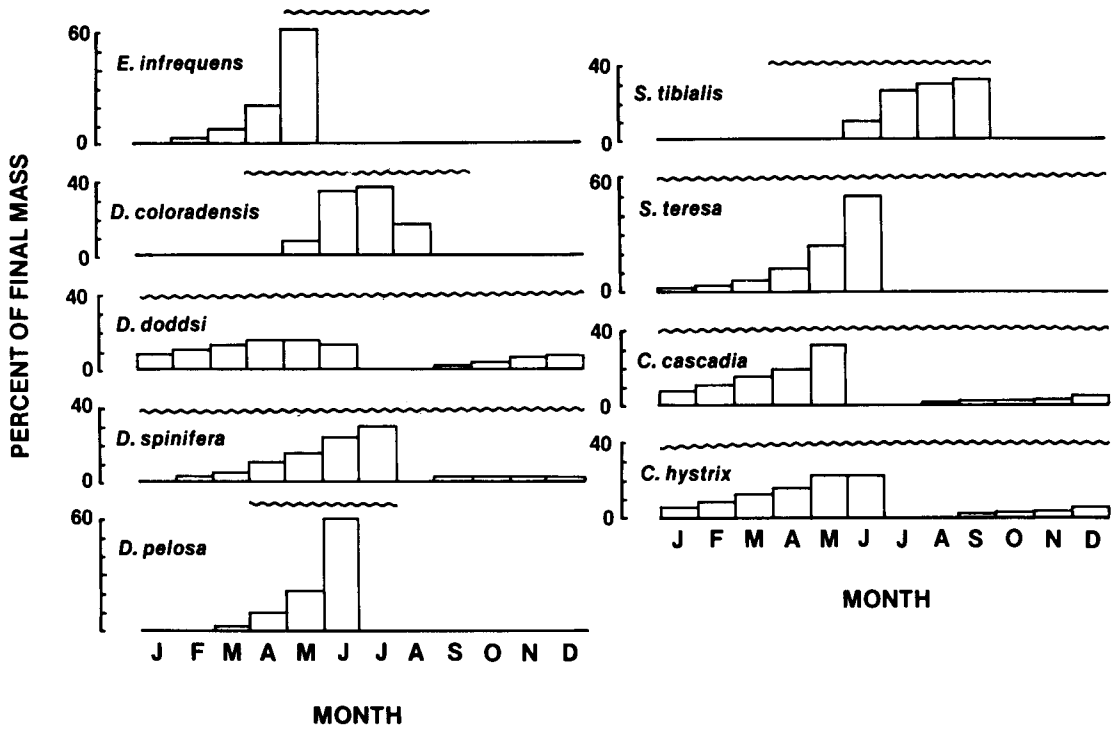


Fig. 3. Percent of total growth (dry mass) elaborated each month for nine sympatric species of Ephemereillidae. Wavy lines above histograms show period of time preferred habitats were estimated to be stable.

Table 1. Time to complete 100% and final 90% of growth, size at maturity, habitat preferences, and diet for 11 species of Ephemereillidae. Habitats are ranked from least to most stable

Species	Month of complete growth		Final size (mgDW)	Habitat*	Food
	100%	90%			
<i>A. margarita</i>	<5	<2	<2	G	detritus
<i>A. delantala</i>	<6	<3	<2	G, C	detritus
<i>E. infrequens</i>	10	4	4.5	G, C	detritus, diatoms
<i>D. pelosa</i>	8	3	2.5	TB, C	diatoms
<i>S. tibialis</i>	5	3	2.5	C	detritus, diatoms
<i>D. coloradensis</i>	11	6	7.5	C	diatoms, animals
<i>D. doddsi</i>	12	6	24.9	C, BB	diatoms, animals
<i>C. cascadia</i>	11	6	3.7	M, TB	detritus, diatoms, moss
<i>C. hystrix</i>	11	7	1.8	TB, M	diatoms, detritus, moss
<i>D. spinifera</i>	12	3	13.9.5	M, BB	animals, detritus
<i>S. teresa</i>	6		2.2	M	detritus, diatoms, moss

* Abbreviations are:

G = sand and gravel, C = cobble, TB = top of boulder, BB = bottom of boulder, M = moss.

directly related to length of the growth period (Table 1).

For these species, both length of the growth period and timing of growth appeared to be related to the seasonal dynamics of microhabitats. However, this relationship was more apparent when time to complete 90% of growth was compared rather than time for 100% of growth. All species completed the last 90% of growth within the time period that habitat units were stable – note that data points fall below the diagonal line in Fig. 4. This was not true for time to complete 100% of growth.

The relationship between habitat persistence and length of the growth period was not a simple linear one. Species that occupied sand-gravel habitats and the tops of boulders generally completed growth more rapidly than species which lived in more persistent habitats (moss or under boulders). However, although all species in short persistence habitats had short growth periods, a

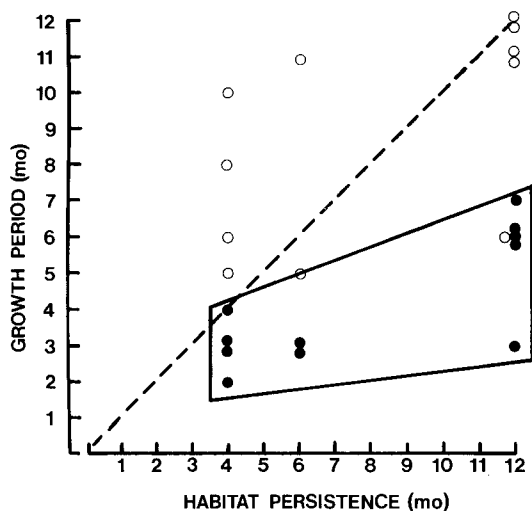


Fig. 4. Relationship between habitat persistence and length of the larval growth period for 11 species of Ephemeroidea. Solid dots indicate time to complete final 90% of growth. Open circles indicate time to complete 100% of growth. The diagonal line describes the relationship expected between habitat persistence and length of growth period if growth periods exactly tracked habitat persistence. The trapezoid describes the apparent range in length of the growth period (final 90%) possible in habitats of different persistence.

wider range of growth patterns occurred in stable habitats (Fig. 4). Inspection of Fig. 3 and Table 1 also shows that the main pulse of growth (i.e. 90%) in each species occurred during the time of year that preferred habitats were stable.

My results therefore tentatively support the contention that the dynamics of habitat units may be related to growth patterns of different species of ephemeroidea mayflies. However, other information is necessary to evaluate which of several hypotheses most efficiently explains patterns. Comparison of the growth patterns of each species in context of as many factors as possible may provide insight regarding the relative importance of different factors. Unless otherwise specified, the following ecological descriptions are based on data presented in Hawkins (1982, 1984, 1985, 1986).

Ephemera infrequens prefers gravel and cobble substrates in slow to moderate current. Although it is a feeding generalist, its diet consists mainly of detritus. However, individuals in the laboratory grow more rapidly on algae than detritus of terrestrial origin. Also, it is most abundant in streams with high levels of algal production. Availability of algae therefore is apparently important for this species. Either habitat stability or availability of high-quality food may be related to its growth pattern. Little growth occurs during autumn and winter when its preferred habitat is most susceptible to scour. However, algal production is low during these times as well. Most individual growth occurs in this species just after gravel substrates are stable and just prior to maximum algal production.

Drunella coloradensis strongly prefers cobble substrates. Its diet is dominated by diatoms during early instars and animal material (mostly chironomid midge larvae) during later stages. Most growth is elaborated from late spring through mid-summer. Food availability in terms of both algae and chironomid midges is highest at this time (Hawkins *et al.* 1982). Because cobble substrates offer stable habitat at other times of the year, food availability is the factor most clearly associated with the growth period of *D. coloradensis*.

Drunella doddsi is similar to *C. coloradensis* in both habitat use and diet, although it tends to occur on and under larger substrates (boulders) and consumes more animal matter. The greater stability of large substrates during high flows may be the reason *D. doddsi* grows during autumn and winter, whereas *D. coloradensis* does not. Although *D. doddsi* elaborates less relative growth than *D. coloradensis* during its later instars, final absolute size of *D. doddsi* is greater. Because fecundity is positively related to size in mayflies (Clifford and Boerger 1974), the ability of *D. doddsi* to grow during winter may increase its fitness relative to *D. coloradensis*. Evidently, timing of growth is not closely linked to seasonal variation in abundance of preferred food items. Emergence occurs well before the mid-summer peak in availability of algae and midge larvae.

D. spinifera inhabits moss substrates and interstitial spaces beneath cobbles and boulders. Like *D. doddsi*, it has a long growth period but elaborates a greater percent of final mass during the last two months than does *D. doddsi*. Animal matter (mostly midge and *Baetis* larvae) is the most conspicuous item in the diet of this species, especially in late instars. Like *D. doddsi*, *D. spinifera* emerges before the mid-summer peak in availability of food.

Drunella pelosa is largely restricted to the tops of boulders in rapid current. Its diet consists mostly of diatoms. Most of this species' growth occurs during May and June, and eggs apparently do not hatch until March. The growth pattern of this species seems to track both food availability and flow dynamics over boulder substrates. *D. pelosa* occupies tops of boulders during the time of year when flows are sufficient to cover most boulders and algae production is relatively high. Other times of the year appear to be unsuitable. During summer, tops of many boulders are exposed. During late autumn and winter, torrential flows make such habitats extremely harsh environments. The relatively short, rapid growth exhibited by this species allows it to exploit this habitat during relatively benign periods. Presumably as a consequence of the short growth period, final size of this species is smaller than for any other species of *Drunella*.

Serratella tibialis occurs mainly on cobble substrates. Its diet is similar to that of *E. infrequens*, although *S. tibialis* consumes slightly more diatoms. It too is more abundant in streams with high algal abundance, and most growth occurs during peak algal abundance. Availability of algal food sources is apparently important for this species. Like *D. coloradensis*, it occupies a habitat that is stable longer than its growth period.

Serratella nr *teresa* is strongly associated with moss, and is most abundant in small, shaded streams with abundant moss habitat. Moss in small to medium size streams in the northwestern United States occurs on the surface of boulders and bedrock. Unlike the tops of boulders, however, moss habitats are a relatively benign environment during autumn and winter, because they provide a refuge from the shear stress of high flows. However, long habitat persistence is apparently of little importance to the growth pattern of this species. Essentially all growth occurs during April, May, and June. The diet of *S. teresa* consists mainly of detritus and diatoms, although small amounts of moss are ingested. Moss provides surfaces for periphyton growth and traps detritus as well, but it is unknown how food availability changes with season in moss habitats. At this time, no obvious relationship is apparent between the growth pattern of this species and food availability.

The fact that the growth patterns of *S. tibialis* and *S. teresa* are very different indicates that one or both have diverged from some ancestral pattern. In this case, divergence may have occurred as a result of interspecific competition, although several additional assumptions must be true before this explanation can be accepted. If moss was the ancestral habitat of *Serratella* species, *S. tibialis* may have escaped interspecific competition with *S. teresa* by shifting to cobble habitats. Presumably, the growth periods of the two species would have been similar prior to divergence. Because cobble habitats are stable during the period *S. teresa* grows, a change in growth pattern would not be necessary to accommodate the shift in habitat use. However, *E. infrequens* occupies the same streams as *S. tibialis* and has a growth

pattern similar to *S. teresa*. Interspecific pressures from *E. infrequens* may have forced *S. tibialis* to shift its growth pattern away from the ancestral one. The result of these interactions would be a *Serratella* species that occupies a different habitat and grows at a different time than other *Serratella* species. This explanation is clearly speculative, and data on other species of *Serratella* are necessary to evaluate ancestral patterns of habitat use and growth. However, at least two other *Serratella* species (*S. levis* and *velmae*) also occur in moss habitats, and both appear to have growth patterns similar to *S. teresa*. Preliminary data therefore supports the contention that *S. tibialis* has diverged from ancestral patterns of both growth and habitat use.

Caudatella cascadia and *C. hystrix* are both associated with moss habitats. Diets of both consist of diatoms and detritus with a moderate amount of moss. Growth patterns are similar to that of *S. teresa*, another moss inhabitant. Growth in both of these species occurs over approximately 10 m, and length of the growth period may be related to stability of moss habitats. It is not clear whether food availability is associated with growth periods.

OVERVIEW

The interpretations of growth patterns given here are rather posthoc and can be criticized as either circular or contrived. If species are diet generalists (Cummins 1973) and shift diet with changing availabilities, inferences regarding timing of growth as a function of the abundance of specific types of food are weakened. It is important to note that although diet does shift for these species with both locality and size, such shifts are not sufficient to mask clear differences among species (Hawkins 1985). The same argument can be applied if species are habitat generalists. For these species, almost all specialize on relatively few of the available habitats (Hawkins 1984).

The most likely alternative interpretation of the patterns observed is that all patterns are derived from an ancestral ephemereleid life-history pattern

that reflects adaptation to those factors (e.g. temperature tolerances, constraints on adult emergence and behaviour) important to Ephemerellidae in general. Variation among species may be merely happenstance or represent minor adjustments to food, habitat, other species, etc.

Data given by Sweeney and Vannote (1981) for six species of Ephemerellidae from eastern North America allow interesting comparisons with these western species. Taken together, growth and emergence patterns for these six species are similar to those observed for the species examined here. Patterns for all species in the family are apparently constrained by the necessity for adults to emerge in spring or summer. Substantial variation exists however in the period when most growth occurs for both groups of species.

Periods of maximum growth among the six eastern species are apparently more uniformly staggered than for the nine western species. Also, there was little tendency for timing of growth, diet, and maximum availability of preferred food to show the correspondence that seems to exist for some western species. However, with one exception, all species studied by Sweeney and Vannote prefer similar habitats (riffles). If few opportunities existed for these species to radiate in habitat use (i.e. low habitat diversity), temporal separation may have been the only avenue available to avoid resource overlap. The competition hypothesis offered by Sweeney and Vannote (1981) to explain life-history separation in these six species may indeed be an accurate explanation (but see Towns 1983).

Conversely, in stream systems that exhibit higher habitat diversity or different temporal dynamics, life-history patterns of both single species and groups of species may reflect adaptive radiation in use of habitat or food to a greater extent than observed in streams with low resource diversity. Certainly, if stream ecosystems vary in the magnitude and importance of different environmental factors, we should expect life-history patterns to reflect biological adjustments to the specific mixture of conditions that characterize a given stream. It follows that any one hypothesis offered to explain life-history patterns in general and

growth patterns in particular must surely be an incomplete representation of reality, for the relative importance of single factors will vary from location to location.

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