16 Emergence of lotic mayflies (Ephemeroptera) in the Cascade Range of Oregon

F. Harper[1], N.H. Anderson[2] and P.P. Harper[1]
[1]Département de sciences biologiques, Université de Montréal, C.P. 6128, Succ. A, Montréal, PQ Canada H3C 3J7 and [2]Department of Entomology, Oregon State University, Corvallis, OR 97331-2907 USA

*Mayfly emergence was monitored in three third-order streams in the western Cascade Range of Oregon in 1982-1983. The streams represented three points along a secondary succession gradient: Grasshopper Creek flowed through a recently clear-cut area, Quartz Creek through a 40-year old regrowth deciduous forest and Mack Creek through an old-growth (ca. 450 years) coniferous forest. The mayfly communities in the streams differed not so much in their species lists and total numbers of taxa as in species dominance and total abundance. Grasshopper Creek supported the largest (733 individuals/m^2, 726 mg/m^2) mayfly community, but also the least diversified; Baetidae accounted for more than half of the mass of the emergence. In Quartz Creek, the community was smaller (411/m^2, 415 mg/m^2) and was dominated by detritivores (*Paraleptophlebia*); diversity was maximum. Density, biomass and diversity in the undisturbed Mack Creek were slightly lower (358/m^2, 377 mg/m^2), and opportunistic groups dominated (*Baetis, Cinygmula*). Emergence began earlier and the succession of species was more spread out in the warmer Quartz Creek; yet, emergence patterns of individual species were similar in all streams. There was a clear replacement of species in most genera and emergence patterns followed the usual "synchronous" and "dispersed" types despite a rather narrow annual range of water temperatures in these cold mountain streams.*

Introduction

As part of a study of the impact of riparian vegetation on stream ecosystems in the Western Coniferous Forest Biome, emergence of aquatic insects was monitored in 1982-1983 over a full emergence season in three streams in the Cascade Range of Oregon. The Trichoptera have been studied by Anderson et al. (1984); this paper reports on the Ephemeroptera.

The objectives of this investigation were two-fold: (1) to compare species composition of mayfly communities in three stream systems, with completely different riparian vegetation, along a secondary succession gradient and (2) to provide information on the phenology of western North American mayflies.

Study Sites and Methods

Collecting stations and methods have been described elsewhere (Anderson et al. 1984), and only a short summary is given here. Mack Creek, Quartz Creek and Grasshopper Creek are third-order streams in the McKenzie River drainage of the western Cascade Range (44°N, 122°W) of Oregon, U.S.A. At the time of data collection (1982-1983), Mack Creek flowed through an old-growth coniferous forest, ca. 450 years old, at an elevation of 800 m, Quartz Creek through a regrowth deciduous forest, ca. 40 years old, primarily of red alder (*Alnus rubra*) at an elevation of 490 m, and Grasshopper Creek through a recent, five- to six-year-old, clear-cut area at an elevation of 880 m.

Water temperature in all three streams peaked in August (Table 1). Temperatures were lowest at Grasshopper Creek where monthly means ranged from about 0.5°C in December to 10°C in August, for an accumulation of degree-days (above 0°C) of the order of 1450-1460. They were highest at Quartz Creek (1.7°C in December to 11.6°C in August; 2100-2300 degree-days). Corresponding values for Mack Creek were 2-3°C in December to 10.6°C in August (1825-1950 degree-days). The climate of the region is maritime with a dry summer; 90 per cent of the precipitation occurs from October to April.

Four large screen cages, each covering 3.34 m^2 (36 ft^2), were set up in each of the three streams, two over riffles and two over pools or drop zones. Each cage (mesh size 536 µm) was supported on a frame of plastic pipe and anchored at the corners. One edge of a trap was in contact with the stream bank. Traps were repositioned when water levels decreased.

Cages were installed in Mack and Grasshopper creeks in early May 1982 and in Quartz Creek in mid-June. They were removed in late October or early November after fall freshets knocked them down. Cages were reinstalled in late March 1983 and operated long enough to obtain a complete year of emergence. At Quartz Creek, the only site where a significant part of the emergence season was missed in 1982, the cages were operated until June 20, 1983, and Fig. 4 integrates both years. At Mack and Grasshopper creeks, less than five mayflies per m^2 were obtained in the five weeks of collecting in 1983; these few specimens were not included in Figs. 2-3.

Table 1. **Mean monthly water temperatures (°C) at the three sampling stations in 1982 (upper line) and 1983 (lower line). Temperatures are the averages of the day and night mean monthly temperatures. Asterisks (*) indicate months in which more than five days of data are missing.**

	J	F	M	A	M	J	J	A	S	O	N	D
Mack	1.6	2.1	2.1	2.0	3.8	7.8	9.8	10.7	9.1	6.4	3.3	2.9
Creek	2.9	2.8	3.5*	-	5.9*	7.5	8.4	10.6	8.3	6.8	4.3	2.1
Quartz	-	-	-	-	-	-	-	12.2*	10.3*	7.1	3.7	3.7*
Creek	-	-	3.9*	3.4*	6.3	8.1	8.6	11.6	9.6	7.8	5.6	1.7
Grasshopper		-	-	-	-	-	-	-	-	4.9*	2.0*	-
Creek	-	-	1.7*	2.6*	3.3	6.0	7.2	10.0	7.8	5.3	2.3	0.5*

Large cages were used in this study to encompass the array of microhabitats that occur in mountain streams where channel morphology is controlled by bedrock, boulders and large woody debris. Although individual cages covered areas with a range of current velocity and substrate types, the designations of "riffle" (R) and "drop zone" (D) make a distinction between erosional and depositional areas of the stream.

The cages were serviced every three to four days during the spring and summer and about weekly in the fall when emergence began to decline. Most of the insects were collected with a small vacuum cleaner powered by a 12-volt battery. The larger specimens were hand-picked and preserved in 70 per cent ethanol. Some subimagines were held in vials to complete the final moult. Collections are underestimates of actual emergence because some adults dropped into the water and drifted out of the traps. We also noted smaller collections during rainy weather and on a few very hot days, presumably due to weather-related mortality between collection intervals. Mean daily emergence for each site was calculated by summing the emergence from all traps and dividing by the number of days since the previous collection.

Material Collected

Some 20,000 mayflies were collected from the three sites representing five families, 15 genera and at least 44 species (Table 2). Specimens marked "sp." are unidentifiable subimaginal females. Problems of identification were encountered in three groups.

1. In the Baetidae, the *Baetis* spp. could not consistently be separated to species. Both *Baetis tricaudatus* Dodds and *B. bicaudatus* Dodds occurred at all the sites, as indicated by the presence of larvae; these species cannot presently be distinguished as adults (Morihara and McCafferty 1979) and other species may also be involved.
2. In Siphlonuridae, some of the *Ameletus* spp. seemed to differ significantly from existing descriptions and are marked with cf. *Ameletus* sp. A, represented by many imagines, did not agree with any known description and is probably undescribed. *Ameletus* sp. B also appeared distinct but only one subimago was available.
3. In Ephemerellidae, two species of *Drunella* were not identified because no imagines were available. An unknown species of *Ephemerella* (sp. A), was present both at Mack and Grasshopper creeks.

Results

Species Composition and Site Differences

The traps on Mack Creek yielded 4789 mayflies (358/m^2; 377 mg/m^2 dry biomass), on Quartz Creek 5497 (411/m^2; 415 mg/m^2) and on Grasshopper Creek 9794 (733/m^2; 726 mg/m^2) (Table 2, Fig. 1; Anderson 1992). The family Ephemerellidae was underrepresented in our trap data compared with results from benthos collections (Hawkins 1982).

Despite the altitude range of approximately 400 m and the differing riparian settings, the species list was similar at all three sites (Sorensen indices: similarity of 82.19 per cent between Mack and Grasshopper creeks, 82.86 per cent, between Grasshopper and Quartz creeks, 74.63 per cent between Mack and Quartz creeks). Of the 44 species recognized, 23 were present at all sites and 38 occurred in at least two. Diversity indices, however, indicated major differences between sites. The ranking for decreasing diversity (Shannon index, base *e*) and evenness is: Quartz (H = 2.242, E = 0.65), Mack (H = 2.036, E = 0.57) and Grasshopper (H = 1.310, E = 0.36).

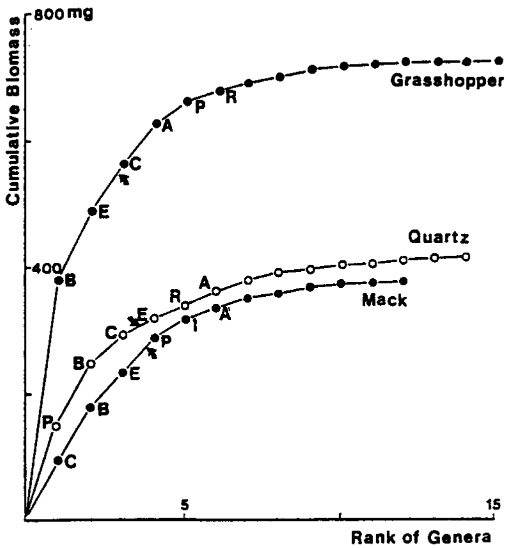
Table 2. Number of specimens emerged in riffle (R) and drop (D) zones in the three streams over a one-year period.

	Mack Creek		Grass. Creek		Quartz Creek	
	R	D	R	D	R	D
Siphlonuridae						
Ameletus amador Mayo	6	4	14	18	1	10
Ameletus cf. cooki McD.	4	85	7	185	0	58
Ameletus cf. dissitus Traver	7	3	3	1	0	5
Ameletus exquisitus Eaton	1	2	2	4	0	0
Ameletus suffusus McD.	5	13	39	116	1	11
Ameletus validus McD.	0	0	5	1	0	14
Ameletus vancouverensis McD.	0	1	0	0	0	0
Ameletus cf. velox Dodds	2	12	2	1	0	0
Ameletus sp. A	3	2	20	10	0	40
Ameletus sp. B	0	0	1	0	0	0
	3.13%		4.38%		2.58%	
Baetidae						
Baetis spp.	1314	606	5304	1612	1166	398
Centroptilum sp.	0	0	0	4	0	0
Diphetor hageni (Eaton)	112	133	19	51	111	218
	45.21%		71.37%		34.42%	
Heptageniidae						
Cinygma dimicki McD.	20	37	5	34	3	38
Cinygma integrum Eaton	0	20	0	2	0	1
Cinygmula par (Eaton)	1	0	0	0	0	0
Cinygmula ramaleyi (Dodds)	4	0	27	1	0	0
Cinygmula reticulata McD.	523	407	302	156	281	190
Cinygmula uniformis McD.	52	20	37	3	24	69
Epeorus (Iron) deceptivus McD	476	58	779	52	107	12
E. (Iron) hesperus (Banks)	0	0	4	0	4	0

Table 2. (continued)

E. (Iron) longimanus (Eaton)	74	9	273	41	39	10
E. (Ironopsis) grandis McD.	20	2	3	6	0	6
Ironodes nitidus (Eaton)	41	13	12	1	47	3
Nixe (Akkarion) rosea (Traver)	0	0	1	5	4	43
Rhithrogena robusta (Dodds)	22	6	9	13	14	17
	37.69%		18.03%		16.58%	
Leptophlebiidae						
Paraleptophlebia						
aquilina Harper & Harper	139	90	31	53	195	624
P. debilis (Walker)	0	6	0	0	5	257
P. gregalis (Eaton)	6	98	0	0	6	48
P. sculleni Traver	1	17	3	133	4	251
P. temporalis (McD.)	101	161	39	250	68	1015
P. vaciva (Eaton)	6	18	3	0	0	0
	13.43%		5.22%		44.97%	
Ephemerellidae						
Caudatella heterocaudata (McD)	1	0	1	0	0	0
Caudatella hystrix (Traver)	0	0	1	0	1	0
Drunella coloradensis (Dodds)	2	0	6	4	0	0
Drunella doddsi (Needham)	0	0	0	0	6	0
Drunella flavilinea (McD.)	1	0	3	0	0	2
Drunella sp. A	1	0	1	0	1	0
Drunella sp. B	1	1	0	0	0	0
Drunella sp.	9	3	5	4	2	1
Ephemerella infrequens McD.	0	2	0	4	20	21
Ephemerella sp. A	1	2	5	0	0	0
Ephemerella sp.	1	1	7	4	0	0
Serratella teresa (Traver)	0	0	0	1	2	0
Serratella tibialis (McD.)	0	0	48	3	23	0
	0.54%		0.99%		1.45%	
TOTAL	4789		9794		5497	

Figure 1. Contribution of genera to total biomass of emergence at the three sites, 1982-1983. Cumulative curves are marked at 75% with arrows. A: *Ameletus*; B: *Baetis*; C: *Cinygmula*; E: *Epeorus*; I: *Ironodes*; P: *Paraleptophlebia*; R: *Rhithrogena*.



The proportional composition also differed markedly between streams, both in numbers (Table 2) and in biomass (Fig. 1). Baetidae (45 per cent of total numbers) and Heptageniidae (38 per cent) were the most common families at Mack Creek, with four genera, *Cinygmula* (25.1 per cent), *Baetis* (22.5 per cent), *Epeorus* (16.6 per cent) and *Paraleptophlebia* (12.4 per cent), contributing collectively 76.6 per cent of the emergence biomass. At Quartz Creek, the Leptophlebiidae were the dominant group (45 per cent in total numbers), followed by Baetidae (34 per cent); the same four genera, but in different order (*Paraleptophlebia* 38.2 per cent, *Baetis* 21.4 per cent, *Cinygmula* 10.5 per cent and *Epeorus* 6.8 per cent), furnished 76.9 per cent of the biomass. At Grasshopper Creek, the predominance of Baetidae was extreme (71 per cent of total numbers) and baetid abundance was higher than the total mayfly emergences at each of the other two sites. The four dominant genera were *Baetis* (52.8 per cent), *Epeorus* (14.8 per cent), *Cinygmula* (10.3 per cent) and *Ameletus* (8.4 per cent), and their joint contribution to the biomass equalled 86.3 per cent.

The number of individuals emerging from riffle areas was much greater than from drop zones at Mack and Grasshopper creeks (1.6:1 and 2.5:1, respectively), but the reverse was true at Quartz Creek (1:1.6) (Table 2). This difference was due to the dominance of baetids and heptageniids at the former two sites and of *Paraleptophlebia* spp. at Quartz Creek.

The preference for slow or fast water conditions at emergence is evident for many species despite the fact that individual traps encompassed a range of flow conditions and drop-zone traps probably accumulated some emergents from riffles via drift. Taxa that emerged predominantly from quiet sections of the streams included: *Ameletus* spp., *Diphetor hageni*, *Centroptilum* sp., *Cinygma* spp., *Nixe rosea* and *Paraleptophlebia* spp. Fast water emergers were: *Baetis* spp., *Epeorus* spp., *Ironodes nitidus* and the Ephemerellidae. *Cinygmula* spp. and *Rhithrogena robusta* did not exhibit clear patterns of emergence with respect to the riffle or drop zone traps.

Phenology

There was a succession of species at all streams, with *Baetis* spp. as the earliest emergers (Figs. 2-4). A precise relationship between temperature and the onset of emergence cannot be established because a few *Baetis* were collected at Quartz Creek on the earliest date that the traps were emptied (March 28, 1983), while at Mack and Grasshopper creeks the recording thermometers were inoperative during the first days of emergence (late April, 1983). However, from available data at all sites we infer that emergence began when daily maximum water temperature reached 4-5°C on sunny days when air temperature was >10°C.

Despite differences in stream temperature and riparian vegetation, the emergence dynamics were similar in all three streams. Emergence began earlier at Quartz Creek, which is located at a lower elevation (490 m) than the other two sites (800-880 m) and, consequently, has higher water temperatures. There was a continuous succession of species in the streams. Mack and Grasshopper creek species followed one another from May to October, with about half of the species first appearing in June. In Quartz Creek the onsets of emergence were widely spaced, with a maximum between April and June. Seventy-two per cent of the species in Quartz Creek began to emerge before 1 July (vs. only 63 per cent in both other streams).

Several species appeared within a few days of the onset of the emergence season (Figs. 2-4). Combining data from the three streams for the 20 most abundant taxa, the following were early-season emergers: *Baetis* spp., *Diphetor hageni*, *Cinygmula reticulata*, *Epeorus deceptivus*, *E. longimanus*, *Ironodes nitidus*, *Rhithrogena robusta*, *Paraleptophlebia temporalis*, *Ameletus suffusus* and *A. amador*. All appeared to be univoltine except *Baetis* and *Diphetor*. *Diphetor hageni* produced a second generation at Quartz Creek, and polyvoltinism was undoubtedly involved in the emergence of *Baetis* spp., although the patterns were not clear.

Figure 2. Emergence of mayflies at Mack Creek, 1982. Species are listed by chronological order of first emergence. Kite diagrams show emergence of males (upper graph) and females (lower graph). Numbers on right of each diagram represent total numbers of males/females collected.

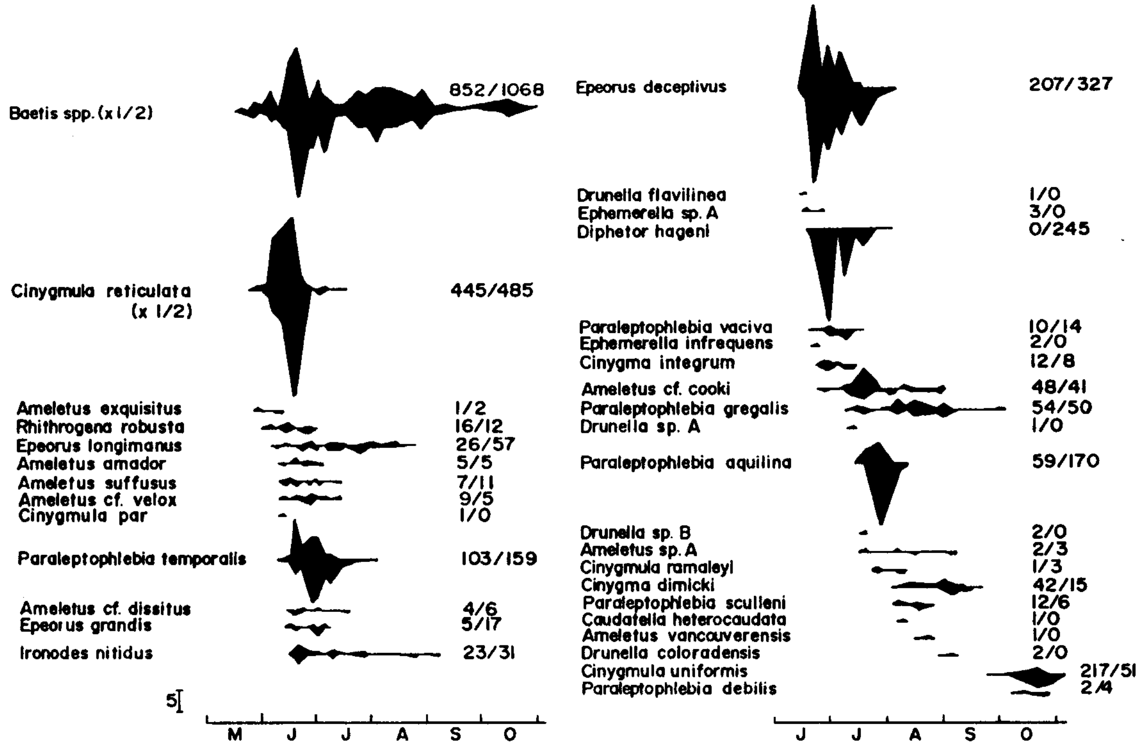


Figure 3. Emergence of mayflies at Quartz Creek, 1982-1983. Data to late-June is from 1983, afterwards from 1982. See legend on Figure 2.

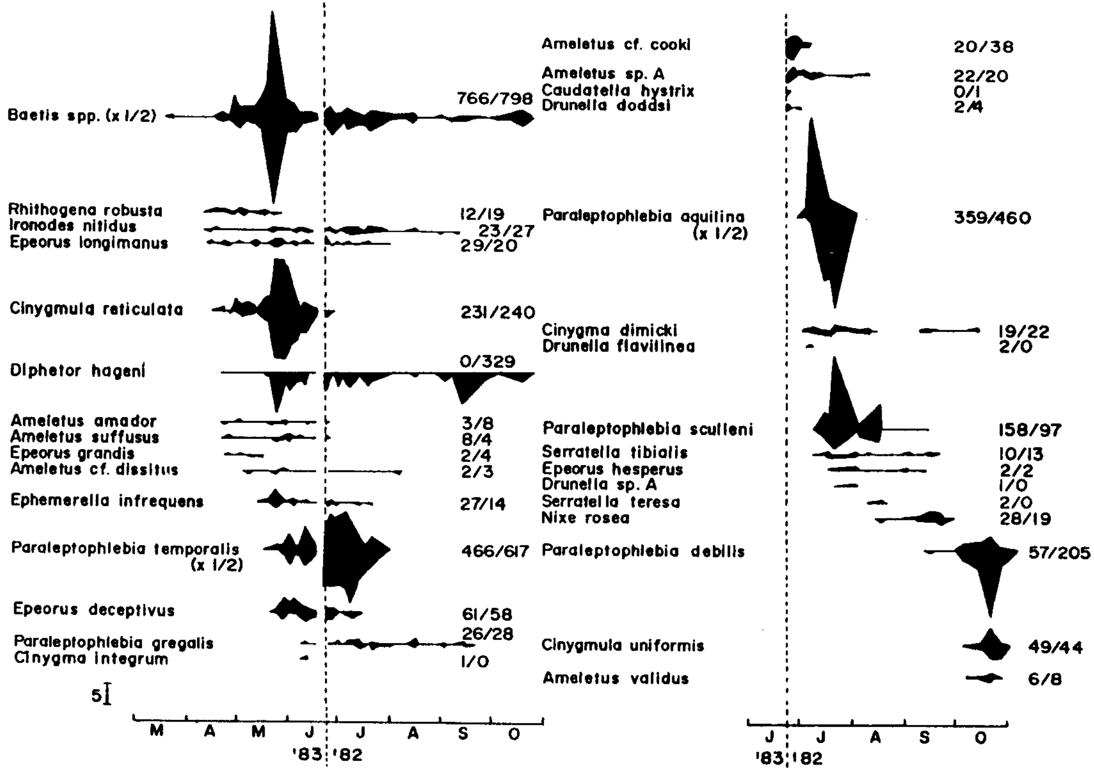
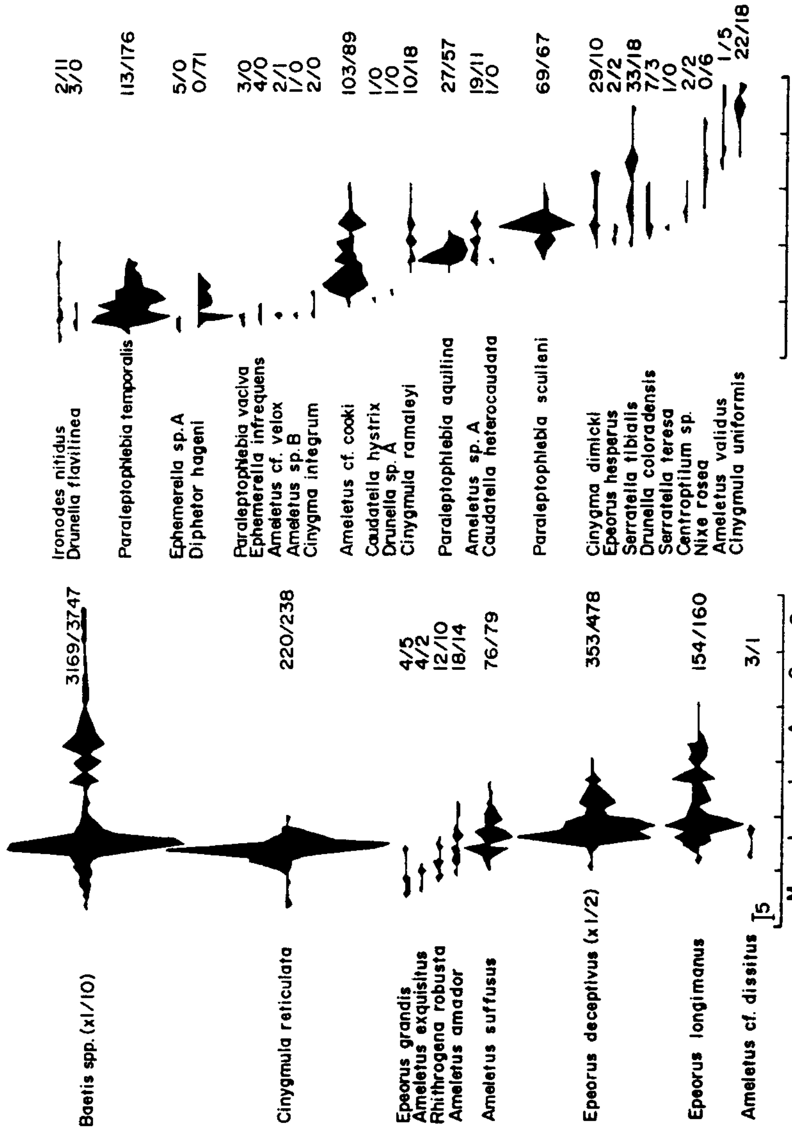


Figure 4. Emergence of mayflies at Grasshopper Creek, 1982. See legend on Figure 2.



Eight of the 20 most abundant species started to emerge when the water neared its maximum temperature. Their emergence peaked after the summer solstice and in most cases had ended before the water cooled in October. These species were *Paraleptophlebia aquilina*, *P. sculleni*, *P. gregalis*, *Ameletus* cf. *cooki*, *A.* sp. A, *Cinygma dimicki*, *Nixe rosea* and *Serratella tibialis*.

Only *Paraleptophlebia debilis*, *Cinygmula uniformis* and *Ameletus validus* were limited to late-season emergence. Emergence of *Baetis* spp. and *D. hageni* also extended into late fall.

Discussion

Density and Species Composition

Annual emergence at the three sites ranged from 358/m^2 at Mack Creek to 733/m^2 at Grasshopper Creek. These densities fall within the average range of 300-1500/m^2 for stream mayfly communities in North America and Europe, as summarized by Harper and Harper (1982), but are much lower than the 6000-6500/m^2 reported for some Ontario and Quebec streams (Ide 1940; Harper and Magnin 1971).

As the riparian setting for Mack Creek is a 450-year-old conifer stand, this may be considered as an example of a "prototype" stream (*sensu* Cummins et al. 1984) with only limited human impacts since aboriginal times. It follows that the biotic associations at Mack Creek may be representative of the expected conditions for an undisturbed western montane stream. The mayfly community was dominated by Baetidae (45 per cent of the adults) and Heptageniidae (38 per cent), with species richness being greatest in the heptageniids (11) and siphlonurids (eight species of *Ameletus*).

The other sites differed from Mack Creek in species patterns that appear to be responses to riparian alterations. The dominance of *Paraleptophlebia* spp. (45 per cent) at Quartz Creek is probably linked to their detritivorous feeding habits (Hamilton and Clifford 1983), and this site has a regrowth deciduous canopy. The prevalence of *Paraleptophlebia* could also be related to the lower gradient of the stream (5 per cent) relative to the two others (9-10 per cent) (Anderson et al. 1984). The extreme abundance of *Baetis* (71 per cent) in the clear-cut areas at Grasshopper Creek is in accord with their known preference for open areas (Thorup 1964). Wallace and Gurtz (1986) related the increase in abundance of *Baetis* after logging to greater autochthonous primary production associated with light, nutrient and temperature changes caused by removal of riparian vegetation.

When mayfly emergence is compared to the total insect emergence in the streams (Anderson 1992), the contribution of mayflies to the emergence production decreases from Grasshopper Creek (21.0 per cent of density, 44.1 per cent of biomass), to Quartz Creek (8.7 per cent and 27.2 per cent respectively), to Mack Creek (6.2 per cent and 22.8 per cent).

The changes in total emergence of mayflies, in species composition, and in the relative importance of mayflies in the total emergence appear to follow a pattern probably related to secondary ecological succession. Grasshopper Creek represents a first stage, when mayflies constitute a major element of the insect fauna and are dominated by grazers (*Baetis*, *Cinygmula*) able to exploit the growths of Aufwuchs on the stream bottom made possible by the absence of overhanging vegetation. Quartz Creek represents a successional stage where the presence of deciduous riparian trees supports a greater proportion of shredder-collectors (*Paraleptophlebia*) and high taxonomic diversity, but a reduced mayfly community in terms of numbers and mass. Mack Creek shows the mature stage with the climax of coniferous forest, which results in still fewer mayflies, a reduction of the proportion of shredders and slightly lower diversity. The dominant taxa are the opportunistic species able to exploit a variety of food sources, such as *Cinygmula* and *Baetis* (Brown 1961; Chapman and Demory 1963; Gilpin and Brusven 1970). Such a picture must remain very tentative as only three data sets are available, and the patterns observed may be due to other causes.

Phenology

Water temperature influenced both the onset and the dynamics of the emergence. Emergence began earlier and was more spread out at the warmer and lower Quartz Creek. There was, however, little effect on the emergence patterns of individual species, which were similar in all streams.

Harper and Magnin (1971) suggested that mayfly emergence patterns could be classified as either well "synchronized" or else "dispersed" over a long period. In our streams (Figs. 2-4), there are clear instances of synchronized emergences: *C. reticulata*, *P. temporalis*, *P. aquilina* and the first generation of *D. hageni*. The emergence of *E. deceptivus* was very synchronized at Mack and Grasshopper creeks, but its pattern is less clear for Quartz Creek because the graph covers two different years. The synchrony of *P. sculleni*, *P. debilis* and *C. uniformis* at Quartz Creek is also evident. Many of these species emerge in spring and early summer; increasing water temperature is thought to be the cue that allows such a synchrony (Harper and Harper 1982). However, this is not always the case; the last three species mentioned emerged when water temperature had peaked (*P. sculleni*) or was decreasing (*P. debilis*, *C. uniformis*).

Brittain (1982) pointed out that males often emerge before the females in the more synchronized emergences. This was true for *C. reticulata* at both Mack and

Grasshopper creeks, for *P. temporalis* at Mack Creek and for *P. aquilina* in all three streams.

The emergence was dispersed in *E. longimanus, A. suffusus, I. nitidus, A.* cf. *cooki, P. gregalis, C. ramaleyi, C. dimicki, S. tibialis* and *N. rosea* in all the streams where they occurred.

The existence of the synchronous/dispersed types of emergence in these streams is somewhat surprising. The distinction had originally been made in continental aquatic systems where a pronounced seasonal difference occurs in water temperature (Harper and Magnin 1971). In these Oregon montane streams the annual range of stream temperature is only about 10°C, and yet many of the early emerging species are synchronized to the same extent as in streams where the temperature range is of about 20-25°C and where spring heating is very rapid (Harper and Harper 1982, 1984). What is more unexpected is that a few mid-summer (July-August) and autumn species also exhibit synchronous emergence. As Harper and Harper (1982) indicated, little data are available on the dynamics of the life cycles of late-summer species, and these observations indicate that efficient seasonal regulation also occurs late in the emergence season.

The sequence in which species emerge is generally thought to be constant from year to year, whatever the temperature regime (Ward and Stanford 1982). In a given region, the peaks of the major species are usually segregated in time particularly within the same genus (Brittain 1982). In our streams there was a clear succession of species within the genus *Paraleptophlebia* in the following order: *P. temporalis, P. vaciva, P. gregalis, P. aquilina, P. sculleni* and *P. debilis*. All were synchronous except *P. gregalis*.

In *Cinygmula, C. reticulata* was the first to appear, followed by *C. par* (one specimen at Mack Creek), then in the summer by *C. ramaleyi*, and in the fall by *C. uniformis*. Where the two species of *Cinygma* coexisted, *C. integrum* emerged before *C. dimicki*. A succession also occurred in *Drunella*, with *D. flavilinea* and *D. doddsi* emerging at the same time, *D.* sp. A and sp. B emerging together later, and *D. coloradensis* later still. The pattern is not so clear in the other genera. Five species of *Ameletus* started emerging within a few days of one another in the spring. Later on the succession became more evident, with *A.* cf. *cooki*, followed by *A.* sp. A, *A. vancouverensis* and *A. validus*. The three species of *Epeorus* (*E. longimanus, E. deceptivus* and *E. grandis*) did not follow the same order at all three streams and seemed to emerge more or less together; *E. hesperus* emerged later than the others.

Predictably, the flying season of individual mayfly species in the three mountain streams is later and shorter than in lowland systems in Oregon such as Berry Creek (Kraft 1963), Oak Creek (Lehmkuhl 1968; Lehmkuhl and Anderson 1970, 1971) and the Metolius River (Lehmkuhl and Anderson 1970, 1971). The flight periods are similar to those at higher latitudes, such as Alberta (Hartland-Rowe 1964; Clifford et al. 1973).

Acknowledgements

We especially wish to thank Dr. C.P. Hawkins, Department of Fisheries and Wildlife, Utah State University, Logan, for developing the emergence program and for his comments and help. We are grateful to Dr. Greg Courtney and the many members of the Stream Team at Oregon State University for their assistance in the field work. This study was supported by National Science Foundation (U.S.A.) grants BSR 8112455 and DEB 8022190 (field work), and a Natural Sciences and Engineering Research Council of Canada grant (laboratory work). This is Technical Paper No. 9974 of the Oregon Agriculture Experiment Station.

References

Anderson, N.H. 1992. Influence of disturbance on insect communities in Pacific Northwest streams. *Hydrobiologia* 248:79-92.

Anderson, N.H., R.W. Wisseman and G.W. Courtney. 1984. Emergence trap collections of lotic Trichoptera in the Cascade Range of Oregon, U.S.A. P. 13-19 in J.C. Morse (Ed.), *Fourth International Symposium on Trichoptera, Ser. Entomol.* 30.

Brittain, J.E. 1982. Biology of mayflies. *Annu. Rev. Entomol.* 27: 119-147.

Brown, D.S. 1961. The food of the larvae of *Chloëon dipterum* L. and *Baetis rhodani* (Pictet). *J. Anim. Ecol.* 30: 55-75.

Chapman, D.W. and R.L. Demory. 1963. Seasonal changes in the food ingested by aquatic insect larvae and nymphs in two Oregon streams. *Ecology* 44: 140-146.

Clifford, H.F., M.R. Robertson and K.A. Zelt. 1973. Life cycle patterns of mayflies (Ephemeroptera) from some streams of Alberta, Canada. P. 122-131 in W.G. Peters and J.G. Peters (Eds.), *Proceedings of the First International Conference on Ephemeroptera.* Brill, Leiden.

Cummins, K.W., G.W. Minshall, J.R. Sedell, C.E. Cushing and R.C. Petersen. 1984. Stream ecosystem theory. *Verh. Internat. Verein. Limnol.* 22: 1818-1827.

Gilpin, B.R. and M.A. Brusven. 1970. Food habits and ecology of mayflies of the St. Mary's River in Idaho. *Melanderia* 4: 19-40.

Hamilton, H.R. and H.F. Clifford. 1983. The seasonal food habits of mayfly (Ephemeroptera) nymphs from three Alberta, Canada, streams, with special reference to absolute volume and size of particles ingested. *Arch. Hydrobiol. Suppl.* 65: 197-234.

Harper, F. and P.P. Harper. 1984. Phenology and distribution of mayflies in a southern Ontario lowland stream. P. 243-251 in V. Landa, T. Soldán and M. Tanner (Eds.), *Proceedings of the Fourth International Conference on Ephemeroptera.* Czechoslov. Acad. Sci., Ceské Budejovice.

Harper, F. and É. Magnin. 1971. Émergence saisonnière de quelques Éphéméroptères d'un ruisseau des Laurentides. *Can. J. Zool.* 49: 1209-1221.

Harper, P.P. and F. Harper. 1982. Mayfly communities in a Laurentian watershed (Insecta; Ephemeroptera). *Can. J. Zool.* 60: 2828-2840.

Hartland-Rowe, R. 1964. Factors influencing the life-histories of some stream insects in Alberta. *Verh. Internat. Verein. Limnol.* 15: 917-925.

Hawkins, C.P. 1982. Ecological relationships among western Ephemerellidae: growth, life cycles, food habits, and habitat relationships. Ph.D. Thesis, Oregon State University, Corvallis.

Ide, F.P. 1940. Quantitative determination of the insect fauna of rapid water. *Univ. Toronto Stud. Biol. Ser.* 47: 7-20.

Kraft, G.F. 1963. Seasonal occurrence and distribution of aquatic insects in Berry Creek. Ph.D. Thesis, Oregon State University, Corvallis.

Lehmkuhl, D.M. 1968. Observations on the life histories of four species of *Epeorus* in western Oregon (Ephemeroptera: Heptageniidae). *Pan-Pacif. Entomol.* 44: 129-137.

Lehmkuhl, D.M. and N.H. Anderson. 1970. Observations on the biology of *Cinygmula reticulata* McDunnough in Oregon (Ephemeroptera: Heptageniidae). *Pan-Pacif. Entomol.* 46: 268-274.

Lehmkuhl, D.M. and N.H. Anderson. 1971. Contributions to the biology and taxonomy of the *Paraleptophlebia* of Oregon (Ephemeroptera: Leptophlebiidae). *Pan-Pacif. Entomol.* 47: 85-93.

Morihara, D.K. and W.P. McCafferty. 1979. The *Baetis* larvae of North America. *Trans. Amer. Entomol. Soc.* 105: 139-221.

Thorup, J. 1964. Substrate type and its value as a basis for the delimitation of bottom fauna communities in running waters. P. 59-74 in K.W. Cummins, C.A. Tryon and R.T. Hartman (Eds.), Organism-substrate Relationships in Streams. *Spec. Publ. Pymatuning Lab. Ecol.* 4.

Wallace, J.B. and M.E. Gurtz. 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. *Amer. Midl. Nat.* 115: 25-41.

Ward, J.V. and J.A. Stanford. 1982. Thermal responses in the evolutionary ecology of aquatic insects. *Annu. Rev. Entomol.* 27: 97-117.