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COMPOSITION AND ABUNDANCE OF PERIPHYTON AND AQUATIC INSECTS IN A SIERRA NEVADA, CALIFORNIA, STREAM

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ABSTRACT.—The species composition of periphyton and benthic insect communities and abundances of common taxa (>0.1% of individuals) were examined during snow-free months in Convict Creek, a permanent snowmelt- and spring-fed stream in the Sierra Nevada of California. The communities were highly diverse. The most abundant taxa in the periphyton were diatoms (*Achnanthes minutissima, Cocconeis placentula lineata, Cymbella microcephala, C. sinuata, Fragilaria construens, F. crotonensis, Navicula* spp., *Synedra acus*, and *S. rumpens*), except in late spring and summer when several seasonal blue-green algae (*Chamaesiphon incrustans, Lyngbya* spp. and *Oscillatoria* spp.) are at their maximum densities. Most common periphyton taxa vary systematically in abundance with season, but relative abundances of taxa also appear to be influenced by streambed scouring and by concentrations of ambient nutrients.

Data on population densities and length frequencies of larval and nymphal stages of common benthic insects and occurrences of pupal and adult stages were examined to determine life history patterns. Taxa hatching in winter and spring and abundant as immatures in late spring include ephemeropterans (*Epeorus longimanus, Drunella flavilinea*, and *Caudatella heterocaudata*), plecopterans (*Calineuria californica, Doroneuria baumanni*, and *Pteronarcys princeps*) and dipterans (*Cryptolabis* sp.). Common taxa hatching in late spring or summer are the plecopteran *Malenka* (*californica?*) and the trichopterans *Arctopsyche grandis* and *Rhyacophila acropedes*. Several bivoltine and multivoltine ephemeropterans (*Baetis devinctus* and *B. tricaudatus*) and dipterans (*Simulium* spp. and Chironomidae) have summer cohorts. Taxa hatching in late summer or autumn and most abundant in autumn include ephemeropterans (*Baetis* spp., *Ephemerella infrequens, Epeorus dulciana, Ironodes lepidus*, and *Paraleptophlebia pallipes*), trichopterans (*Hydropsyche oslari, Lepidostoma* spp., *Glossosoma califica, Micrasema* sp., *Brachycentrus americanus, Neophylax* sp., and *Rhyacophila vaccua*) and dipterans (*Antocha monticola, Pericoma* sp., and Chironomidae). Major recurring events that may influence life history patterns and structure of the benthic insect community are (1) near-freezing, nighttime winter water temperatures and occasional anchor ice, (2) a prolonged period of high discharge in late spring and early summer (3) a brief summer, and (4) a prolonged period of moderate stream discharge in autumn when the substratum is stable and food is abundant.

Despite early biogeographical research on aquatic insects of the Sierra Nevada in California (see Usinger 1956), phenological data and information on structure of benthic insect communities in streams of this range are very limited. There is a similar lack of information on production of stream fauna and on the species composition and seasonality of stream periphyton. We report results of a four-year investigation of Convict Creek, a permanent snowmelt- and spring-fed stream draining a 41 km^2 watershed on the steep eastern escarpment of the Sierra Nevada. The study area includes both mesic and xeric terrestrial vegetation (Orr 1981). Objectives of this study were to determine (1) the species composition of periphyton and benthic insect communities of Convict Creek, (2) the temporal variation in population densities of common taxa, (3) basic life histories and annual production of the common benthic insects, and (4) effects of hydrologic extremes on community structure. The ecology of Convict Creek is compared to that of other streams at comparable altitudes in mountain ranges bordering the Great Basin of the western United States.

Study Area

Convict Creek (Lat. 37° 37′ N, Long. 118° 50′ W) is in the Inyo National Forest in Mono County, California. The study area lies within Convict Creek basin at an altitude of 2,185 m in the reserve of the Sierra Nevada Aquatic Research Laboratory. The geology of the upper part of the basin is unusual for the Sierra Nevada in that metamorphic rather than granitic rocks predominate. The lower part of the basin, including the study area, is composed of alluvium and morainal materials from erosion and glaciation of the area above. The metamorphic rock is of two major types,

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siliceous hornfels and siliceous calc-hornfels (Rinehart and Ross 1964). The granitic rock is primarily quartz monzonite and granodiorite. Sandstones in the vicinity of Convict Creek are primarily quartz sandstone and calcareous quartz sandstone. Mineralogic analyses of fine sand and silt (fraction <74 μm) in the sediments of Convict Creek indicate an abundance of feldspar, quartz, and calcite.

A Great Basin sagebrush community dominated by big sagebrush, *Artemisia tridentata* Nutt., rabbit brush, *Chrysothamnus nauseosus* (Pall.) Britt., and antelope bitterbrush, *Purshia tridentata* (Pursh) DC., covers much of the study area (Orr 1981). High desert riparian woodland occurs along the stream; dominant species of this community are quaking aspen, *Populus tremuloides* Michx., water birch, *Betula fontinalis* Sarg. and willows, *Salix* spp. Riparian meadow vegetation characterized by sedges, *Carex* spp., rushes, *Juncus* spp., and various grasses occur along the banks in low-lying areas of poorly drained soils.

Convict Creek is a perennial riffle-pool stream. Fluctuations in discharge are moderated by Convict Lake 4 km upstream and a bypass channel permitting diversion of flood water around the study area. The streambed is rocky, ranging primarily from coarse sand and pebbles to cobbles. The water is clear; suspended sediment concentrations are typically < 1 mg/liter. The stream is oligotrophic, with nitrate concentrations typically less than 10 μg/liter NO_3-N and ortho-phosphate concentrations not exceeding 0.2 μg/liter $PO_4^{3-}-P$ (Leland and Carter 1985). Silica concentrations range from 7.1 to 8.3 mg/liter SiO_2. The water is alkaline (pH 7.9 to 8.5) and always at or near saturation with respect to dissolved oxygen. Major ionic constituents (in mg/liter) determined during a period of base flow were: Ca^{2+}, 23; Mg^{2+}, 0.3; K^+, 0.7; Na^+, 1.4; SO_4^{2-}, 11; and Cl^-, 0.2.

The study area is the 340 m reach of Convict Creek that was used as a control section in experimental studies of Leland and Carter (1984, 1985) and Leland et al. (1986). For a map of the area, see Leland and Carter (1984).

MATERIALS AND METHODS

Water temperature and stream discharge in the study area were monitored continuously. The temperature sensor was located 5 cm below the surface of the streambed. A water stage servo-manometer with nitrogen-purge system (bubble gage—U.S. Geological Survey 1962) was used to determine discharge from 1978 through 1980. Stream discharge in 1977 was estimated from records maintained by the Los Angeles Department of Water and Power at a site approximately 2 km upstream of the study area. Degree-day estimates were calculated from 1 January.

Samples of benthic algae were scraped from 5 x 5 cm delineated areas of the upper surfaces of three separate cobbles (approximately 8 to 12 cm diameter) from the middle of the stream in unshaded riffles. Six samples (three per site) were taken from the same two riffles (each approximately 3 m by 30 m) each date. Sampling was approximately monthly from June through November in 1979 and 1980. Only algae with chloroplasts and intact cell walls were included in the counts (Leland and Carter 1984). Numbers of individuals recorded for each taxon were cells for free and colonial species and filament fragments for filamentous forms (according to the methods of Greeson et al. 1977, section 7.3). Most diatoms were identified to species, whereas green and blue-green algae were identified to genus.

Sampling of aquatic insects was conducted monthly to bimonthly from late spring through autumn of the years 1977 through 1980. The same riffle (approximately 3 m by 50 m) was sampled each date. An invertebrate box sampler (Ellis-Rutter)[2] with a net of 0.35 mm mesh and sampling area of 0.1 m^2 was used. Sampling was from the middle of the stream and included both upstream and downstream areas of the riffle. Three samples were taken each sampling date to permit estimation of mean population densities. Samples were preserved in 70% ethanol and sorted in the laboratory with the aid of sugar flotation (Anderson 1959). All aquatic insects were identified to the lowest taxonomic level practical (genus or species). Observations on time of adult emergence, composition of the drift, and rearing of later instars were conducted to provide additional life history information.

Abundance data are expressed as population densities (individuals/cm^2 of benthic algae and individuals/0.1 m^2 of benthic insects).

[2]Use of brand names is for identification only and does not constitute endorsement by the U.S. Geological Survey.

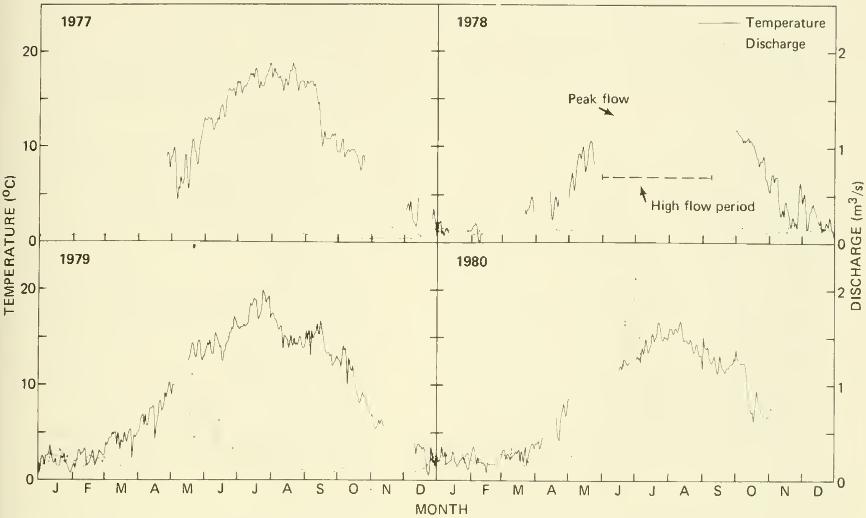

Fig. 1. Mean daily water temperature and mean daily discharge of Convict Creek.

Abundant taxa are defined as those with densities greater than about 2% of the individuals of all taxa. Common taxa are those with densities greater than 0.1% of the individuals of all taxa.

Secondary production was estimated using the size-frequency method (Hynes and Coleman 1968, Hamilton 1969, Benke 1979, Krueger and Martin 1980), with computations based on body lengths and dry weights of common taxa. Cohort production intervals, in days from hatching to the attainment of the largest aquatic size class, were determined from life history and abundance data summarized in Figure 4. Sampling began in August 1979 and continued until June 1980. Intervals between samples were 24, 38, 41, 166, and 39 days.

Results and Discussion

Environmental Variables

Continuous records of stream discharge and water temperature were obtained for most of 1977 through 1980 (Fig. 1). Convict Creek is typically at or near base flow in winter (December to mid-March). The stream discharge increases in late spring due to snowmelt higher in the basin. This annual period of high discharge begins in May or June and lasts one or two months. Peak discharge (in m^3/s) was 0.50 in 1977, 1.30 in 1978, 1.15 in 1979, and 2.14 in 1980. A second high discharge period occurred in early September 1978 due to unseasonably heavy rains accompanying Hurricane Norman. Stream discharge generally declines during late summer and autumn and reaches baseflow in October.

Mean daily water temperatures in winter ranged from 0.6 to 3.6 C in 1979 and 1980 (Fig. 1). Winter air temperatures were generally lower in 1978 and 1979 than in 1977 (a mild winter) or in 1980 (when an exceptionally heavy snow cover was present). Anchor ice formed more frequently during the winters of 1978 and 1979 than during the other two years. Mean daily water temperatures during summer (July-August) were higher in 1977 and 1979 than in 1980. Daily means in October did not vary substantially among years.

Periphyton

Community Composition.—The periphyton of Convict Creek is highly diverse (Table 1). A total of 30 genera (at least 104 species) of diatoms, 24 genera of green algae, and 29 genera of blue-green algae were identified

TABLE 1. Benthic algae of Convict Creek

CHLOROPHYTA
- *Ankistrodesmus falcatus* (Corda) Ralfs
- *Carteria* spp.
- *Chaetophora* spp.
- *Characium* spp.
- *Cladophora* spp.
- *Closterium* spp.
- *Coelastrum* spp.
- *Coleochaete* spp.
- *Cylindrocapsa* spp.
- *Dictyosphaerium* spp.
- *Draparnaldia* spp.
- *Elakatothrix* spp.
- *Gloeocystis* spp.
- *Mougeotia* spp.
- *Oedogonium* spp.
- *Oocystis* spp.
- *Pediastrum* spp.
- *Protoderma* spp.
- *Rhizoclonium* spp.
- *Spirogyra grantiana* Transeau
- *Stigeoclonium* spp.
- *Ulothrix* spp.
- *Zygnema* spp.

EUGLENOPHYTA
- *Euglena* spp.
- *Trachelomonas* spp.

PYRROPHYTA
- *Ceratium hirundinella* (O.F. Mull) Dujardin

CHRYSOPHYTA

Xanthophyceae
- *Vaucheria* spp.

Chrysophyceae
- *Dinobryon cylindricum* Imhof *ex* Ahlstrom
- *D. sertularia* Ehr.

Bacillariophyceae
- *Achnanthes bergiani* Cleve-Euler
- *A. exigua* Grun.
- *A. lanceolata* Breb. *ex* Kutz.
- *A. linearis* (W. Sm.) Grun.
- *A. minutissima* Kutz.
- *Amphora ovalis* (Kutz.) Kutz.
- *A. perpusilla* (Grun.) Grun.
- *Amphipleura pellucida* Kutz.
- *Asterionella formosa* Hass.
- *Ceratoneis* (= Hannaea) *arcus* Ehr. Kutz.
- *Cocconeis pediculus* Ehr.
- *C. placentula euglypta* (Ehr.) Cl.
- *C. placentula lineata* (Ehr.) V.H.
- *Cyclotella comta* (Ehr.) Kutz.
- *C. kutzingiana* Thwaites
- *C. stelligera* Cl. and Grun.
- *Cymbella affinis* Kutz.
- *C. brehmii* Hust.
- *C. lanceolata* (Ag.) Ag.
- *C. mexicana* (Ehr.) Cl.
- *C. microcephala* Grun.
- *C. minuta minuta* Hilse *ex* Rabh.
- *C. perpusilla* Cl.
- *C. prostrata* (Berk.) Cl.
- *C. sinuata* Greg.
- *C. tumida* (Breb *ex* Kutz.) V.H.

Table 1 continued.
- *Denticula* spp.
- *Diatoma hiemale* (Lyngb.) Heib.
- *D. vulgare* Bory
- *Diploneis ovalis oblongella* (Naeg.) Cl.
- *Epithemia adnata adnata* (Kutz.) Breb.
- *E. sorex* Kutz.
- *E. turgida* (Ehr.) Kutz.
- *E. turgida granulata* (Ehr.) Brun
- *Fragilaria brevistriata inflata* (Pant.) Hust.
- *F. construens* (Ehr.) Grun.
- *F. construens binodis* (Ehr.) Grun.
- *F. crotonensis* Kitton
- *F. leptostauron* (Ehr.) Hust.
- *F. pinnata* Ehr.
- *Frustulia* spp.
- *Gomphoneis herculeana* (Ehr.) Cl.
- *Gomphonema acuminatum* Ehr.
- *G. dichotomum* Kutz.
- *G. olivaceum* (Lyngb.) Kutz.
- *G. parvulum* (Kutz.)
- *G. subclavatum* (Grun.) Grun.
- *G. truncatum* Ehr.
- *Hantzschia* spp.
- *Melosira varians* Ag.
- *Navicula arvensis* Hust.
- *N. aurora* Sov.
- *N. bacillum* Ehr.
- *N. capitata* Ehr.
- *N. cocconeiformis* Greg. *ex* Grev.
- *N. cryptocephala* Kutz.
- *N. hambergii* Hust.
- *N. lanceolata* (Ag.) Kutz.
- *N. pupula* Kutz.
- *N. radiosa* Kutz.
- *N. rhynchocephala* Kutz.
- *N. salinarum* Grun.
- *N. seminulum* Grun.
- *N. tripunctata* (O.F. Mull.) Bory
- *Neidium* spp.
- *Nitzschia acicularis* W. Sm.
- *N. actinastroides* (Lemm) v. Goor
- *N. amphibia* Grun.
- *N. dissipata* (Kutz.) Grun.
- *N. frustulum* (Kutz.) Grun.
- *N. linearis* W. Sm.
- *N. palea* (Kutz.) W. Sm.
- *N. sigma* (Kutz.) W. Sm.
- *N. vitrea* Norman
- *Pinnularia nodosa* (Ehr.) W. Sm.
- *P. rupestris* Hantz.
- *Rhopalodia gibba* (Ehr.) O. Mull.
- *Stauroneis* spp.
- *Stephanodiscus* spp.
- *Surirella* spp.
- *Synedra acus* Kutz.
- *S. radians* Kutz.
- *S. rumpens* Kutz.
- *S. rumpens fragilaroides* Grun.
- *S. ulna* (Nitz.) Ehr.
- *S. ulna oxyrhynchus* Kutz.
- *S. ulna spathulifera* (Grun.) V.H.
- *Tabellaria fenestrata* (Lyngb.) Kutz.

RHODOPHYTA
- *Batrachospermum* spp.

Table 1 continued.

CYANOPHYTA	
	Amphithrix spp.
	Anabaena spp.
	Anabaenopsis spp.
	Aphanocapsa spp.
	Calothrix spp.
	Chamaesiphon incrustans (Grun.)
	Chroococcus spp.
	Coelosphaerium spp.
	Colosterium spp.
	Cylindrospermum spp.
	Dactylococcopsis spp.
	Dichothrix spp.
	Gloeotrichia spp.
	Hapalosiphon spp.
	Lyngbya spp.
	Merismopedia spp.
	Microcystis spp.
	Nodularia spp.
	Nostoc spp.
	Oscillatoria spp.
	Phormidium spp.
	Plectonema spp.
	Raphidiopsis spp.
	Rivularia spp.
	Schizothrix spp.
	Scytonema spp.
	Spirulina spp.
	Stigonema spp.
	Tolypothrix spp.

during the study. All of the most abundant taxa are diatoms, except for a few blue-greens that attain high abundance in late spring–summer. The composition of benthic algae in Sierra Nevada streams is poorly known. Hoffman (1978) provided a partial inventory (23 species) of diatoms in Martis Creek, a perennial stream in the Truckee River Basin. Twelve of the 23 species, all cosmopolitan in their distribution, are common in both Martis Creek and Convict Creek. Sanford (1972) listed the conspicuous benthic algae in streams draining Feeley Lake and Round Lake in Tahoe National Forest; the dominant taxa in these streams are not abundant in Convict Creek.

SEASONAL ABUNDANCES OF COMMON TAXA.—Mean population densities of 22 common benthic algae in Convict Creek from late spring through autumn are presented in Figure 2. An ordination method (detrended correspondence analysis [Hill 1979, Hill and Gauch 1980, Leland and Carter 1986]) was used to objectively order the taxa. The ordering emphasizes the seasonal progression from taxa most abundant in spring to taxa most abundant in autumn. The major exceptions were *Fragilaria crotonensis*, characteristically a planktonic species and perhaps an opportunist in the periphyton of Convict Creek (Convict Lake is 4 km upstream), and *Fragilaria construens*. Both taxa were highly variable spatially.

Late spring–summer: The principal species of *Gomphonema* (*parvulum*, *subclavatum*, and *truncatum*) in Convict Creek were apparently most abundant in winter and early spring. The dominant algae in late spring and summer were the diatom *Achnanthes minutissima* and the blue-green *Lyngbya* spp.; population densities of the two co-dominants declined markedly by early autumn. Densities of *A. minutissima* and *Lyngbya* spp. were 3 and 11 times higher, respectively, in late spring 1980 than in late spring 1979, which accounted for a higher standing stock (total number of individuals of all taxa) in 1980. Other diatoms that had population maxima in late spring-summer are *Synedra acus*, *S. rumpens*, and *S. ulna*. These species are early colonizers of denuded surfaces in Convict Creek (Leland and Carter 1984). The highly invasive blue-green *Chamaesiphon incrustans* was also most abundant in late spring-summer.

Late summer–early autumn: Stream discharge was substantially higher in late spring–summer 1980 than during the same period in 1979. By early August between-year differences in periphyton assemblages were apparent. The blue-green *Oscillatoria* spp. was very abundant in the summer of 1979 but not in 1980. The lower population density of *Oscillatoria* spp. in summer 1980 may have been related to the higher stream discharge. However, the rate of primary production was lower in 1980 (Leland and Carter 1985). Primary production (estimated from three-week accumulations of autotrophic biomass on artificial substrates) ranged from 0.22 to 0.58 mg C/m^2/hr in summer-autumn 1979, but it declined to 0.08 to 0.28 mg C/m^2/hr after peak discharge in summer 1980, apparently due to phosphorus-limited growth. *Oscillatoria* species are generally abundant only in areas of nutrient enrichment (VanLandingham 1982). The decrease in density of this taxon in summer 1980 may have been attributable to slower growth in a phosphorus-deficient environment.

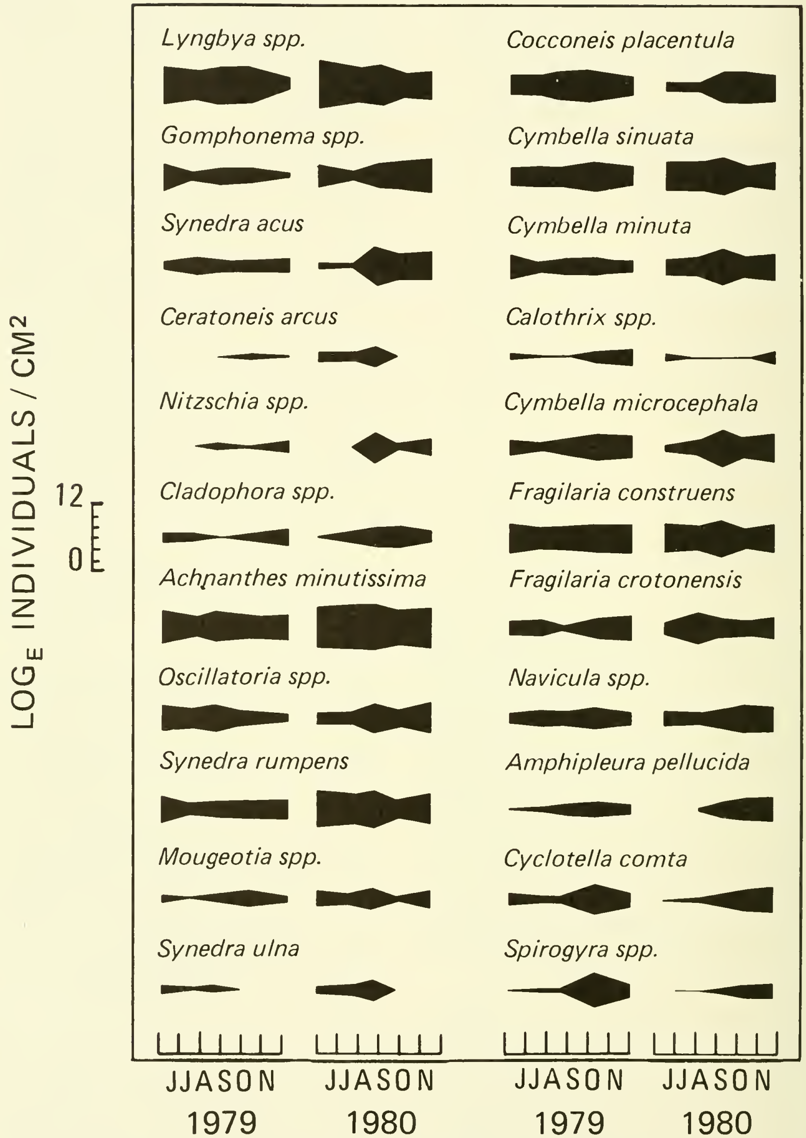

Fig. 2. Mean population densities (n = 6) of common benthic algae on streambed cobble of Convict Creek. Densities were normalized by natural logarithmic transformation prior to calculating means and standard errors. Seasonal population trends identified in the text are based on mean densities differing by at least the sum of the standard errors of the means.

TABLE 2. Benthic insects of Convict Creek.

EPHEMEROPTERA
Siphlonuridae
+ *Ameletus* sp.
Baetidae
Baetis devinctus Traver
Baetis tricaudatus Dodds
+ *Baetis* spp.
+ *Callibaetis pacificus* Seeman
Heptageniidae
Cinygmula sp.
+ *Epeorus dulciana* (McDunnough)
* *Epeorus longimanus* (Eaton)
Ironodes lepidus Traver
Rhithrogena sp.
Ephemerellidae
* *Caudatella heterocaudata* (McDunnough)
* *Caudatella hystrix* (Traver)
Drunella doddsi (Needham)
* *Drunella flavilinea* (McDunnough)
Drunella grandis (Eaton)
* *Drunella pelosa* (Mayo)
* *Ephemerella infrequens* McDunnough
Serratella tibialis (McDunnough)
Tricorythidae
Tricorythodes minutus Traver
Leptophlebiidae
* *Paraleptophlebia pallipes* (Hagen)

PLECOPTERA
Pteronarcidae
* *Pteronarcys princeps* Banks
* *Pteronarcella regularis* Hagen
Peltoperlidae
Yoraperla brevis (Banks)
Nemouridae
Malenka sp., probably *californica* (Claassen)
* *Zapada cinctipes* (Banks)
Perlidae
* *Calineuria californica* (Banks)
Doroneuria baumanni Stark & Gaufin
* *Hesperoperla pacifica* (Banks)
Chloroperlidae
* *Sweltsa* sp., probably *pacifica* (Banks)

HEMIPTERA
Belostomatidae
Belostoma bakeri Montd.
Corixidae
Corisella inscripta Uhler
Sigara washingtonensis Hungerford

MEGALOPTERA
Corydalidae
Orohermes crepusculus (Chandler)

TRICHOPTERA
Philopotamidae
* *Wormaldia* sp., probably *gabriella* Banks
Polycentropodidae
+ *Polycentropus* sp.
Hydropsychidae
* *Arctopsyche grandis* (Banks)

Table 2 continued.

* *Hydropsyche oslari* (Banks)
Rhyacophilidae
* *Rhyacophila acropedes* Banks
Rhyacophila angelita Banks
* *Rhyacophila vaccua* Milne
+ *Rhyacophila* sp.
Glossosomatidae
Agapetus taho Ross
* *Glossosoma califica* Denning
Hydroptilidae
+ *Agraylea saltesa* Ross
+ *Hydroptila* spp.
+ *Oxyethira* sp.
Brachycentridae
* *Brachycentrus americanus* (Banks)
+ *Micrasema* sp.
Lepidostomatidae
* *Lepidostoma cascadense* (Milne)
* *Lepidostoma rayneri* Ross
+ *Lepidostoma* sp.
Limnephilidae
+ *Dicosmoecus atripes* (Hagen)
+ *Neophylax* sp.
Leptoceridae
Triaenodes sp.

LEPIDOPTERA
Pyralidae
undetermined genus

COLEOPTERA
Dytiscidae
Agabus obsoletus (LeConte)
Bidessus sp.
Deronectes striatellus (LeConte)
Deronectes sp.
Hydroporus sp.
Laccophilus decipiens LeConte
Rhantus binotatus Harris
Hydrophilidae
Ametor scabrosus (Horn)
Berosus sp.
Laccobius ellipticus LeConte
undetermined genus
Hydraenidae
Hydraena vandykei d'Orchymont
Ochthebius interruptus LeConte
Elmidae
Cleptelmis addenda (Fall)
+ *Lara avara* LeConte
Narpus sp.
Optioservus divergens (LeConte)
Optioservus quadrimaculatus (Horn)
Zaitzevia parvula Horn

DIPTERA
Deuterophlebiidae
* *Deuterophlebia nielsoni* Kennedy
Blephariceridae
Agathon comstocki Kellogg
Tipulidae
* *Antocha monticola* Alexander

Table 2 continued.

	Cryptolabis sp.
+	*Dicranota* sp.
	Gonomyia sp.
+	*Hexatoma* sp.
	Pedicia sp.
	Tipula spp.
+	**Psychodidae**
	Pericoma sp.
	Maruina sp.
+	**Ceratopogonidae**
	Palpomyia or *Bezzia* spp.
	Simuliidae
*	*Simulium aureum* Fries
*	*Simulium arcticum* Malloch
+	*Simulium* spp.
	Prosimulium dicum Dyar & Shannon
	Chironomidae
	Tanypodinae
	Tanypus sp.
	Thienemannimyia group
	Diamesinae
+	*Diamesa* sp.
	Diamesa latitarsus (Goetghebuer)
	Pagastia sp.
	Prodiamesa sp.
	Orthocladiinae
	Chaetocladius spp.
	Corynoneura spp.
+	*Cricotopus* spp.
	Cricotopus bicinctus group
+	*Eukiefferiella* spp.
	Eukiefferiella bavarica group
	Eukiefferiella brevicalcar group
	Eukiefferiella potthasti group
	Krenosmittia sp.
	Nanocladius sp.
	Orthocladius spp.
	Orthocladius (*Euorthocladius*) sp.
	Pseudorthocladius sp.
	Thienemanniella sp. 1
	Thienemanniella spp.
	Chironominae
	Dicrotendipes sp.
	Polypedilum laetum (Meigen)
	Polypedilum (*Tripodura*) sp.
	Polypedilum spp.
	Pseudochironomus sp.
	Empididae
	Chelifera sp.
+	*Wiedemannia* sp.
	undetermined genus
	Muscidae
	Limnophora sp.

* Species reported by Kennedy (1967)
+ Genus or family reported by Kennedy (1967)

Common diatoms in Convict Creek with population maxima during late summer–early autumn were *Cocconeis placentula lineata*, *Cymbella microcephala*, *Cymbella sinuata*, *Nitzschia frustulum*, and *N. palea*. The green algae *Mougeotia* spp. and *Cladophora* spp. were also abundant at this time. *Cymbella microcephala* and *C. sinuata* were early colonizers in late summer, whereas the other taxa were later successional species.

Autumn: Common taxa with population maxima in autumn were the diatoms *Cyclotella comta*, *Navicula* spp. (principally *cryptocephala*, *rhynchocephala* and *arvensis*), and *Amphipleura pellucida*, the green alga *Spirogyra* spp. (principally *grantiana*), and the blue-green *Calothrix* spp. By mid-October 1979 *Spirogyra* spp. was a co-dominant but in 1980 it was never very abundant, whereas *Lyngbya* spp., *Achnanthes minutissima*, *Cocconeis placentula lineata*, *Cymbella microcephala*, *C. sinuata*, *Fragilaria construens*, *Navicula* spp. and *Synedra rumpens* were abundant both years. By mid-November *A. minutissima*, *F. construens*, and *F. crotonensis* were the most abundant diatoms. *Calothrix* spp. was abundant in late autumn 1979 but not in 1980. *Spirogyra* spp. was the principal green alga in late autumn 1979, whereas *Cladophora* spp. was more abundant in 1980.

Benthic Insects

COMMUNITY COMPOSITION.—Comprehensive lists of benthic insects exist for several streams of the eastern Sierra Nevada at approximately the same altitude as Convict Creek. Three streams in the Truckee River Basin, Sagehen Creek (Gard 1961, Siegfried and Knight 1975), Berry Creek (Siegfried and Knight 1975), and Prosser Creek (Needham and Usinger 1956), have faunal compositions (comparing genera) similar to that of Convict Creek (Convict Creek taxa are listed in Table 2). However, the Truckee River Basin streams have higher densities of the ephemeropterans *Cinygmula* and *Rhithrogena*, their species of Ephemerellidae are mostly different, and we did not collect the plecopteran families Leuctridae, Capniidae, and Perlodidae (but Kennedy [1967] did report Leuctridae and Capniidae in Convict Creek). Maciolek and Tunzi (1968) listed the fauna of Laurel Creek, which is near Convict Creek but at a higher elevation. Fewer taxa are present in Laurel Creek, but benthic insect compositions of the two streams are similar.

Kennedy (1967) listed the benthic insects of

Convict Creek during 1961–1963 but presented little information on population densities; most of the common taxa we observed in 1977–1980 were also found by Kennedy (Table 2). Some apparent differences in the stream fauna between the early 1960s and late 1970s are due to difficulties in identifying immature stages and differences in sampling method. Kennedy (1967) collected extensively only from riffles, whereas midriffle benthos and drift were sampled in the present study. Notable differences between our species list and that of Kennedy (1967) are (1) that *Optioservus divergens*, *Ironodes lepidus*, *Doroneuria baumanni*, and *Malenka* (*californica*?) are common taxa now but were not reported in 1961–1963 and (2) that Kennedy (1967) found three winter stoneflies (Leuctridae and Capniidae) not observed in 1977–1980. These stoneflies typically develop in winter-spring and may have been missed in our sampling program.

SEASONALITY AND LIFE HISTORIES OF COMMON TAXA.—Mean population densities of 28 common benthic insects in Convict Creek are given in Fig. 3. The taxa are ordered by their location on the primary axis in ordination space (detrended correspondence analysis—see Leland et al. 1986). Seasonality of taxa is emphasized in the ordering. Data on population densities (which emphasize early and middle instars) are supplemented with observations on the occurrences of late instars, pupae, and adults and on length-frequency data to determine life histories (Fig. 4).

Late spring (400 to 1,200 degree-days): Taxa most abundant during May and June are considered late-spring fauna. Species in this assemblage include ephemeropterans (*Epeorus longimanus*, *Drunella flavilinea*, and *Caudatella heterocaudata*), plecopterans (*Calineuria californica*, *Doroneuria baumanni*, and *Pteronarcys princeps*), and dipterans (*Cryptolabis* sp. and *Palpomyia* spp.). The three ephemeropterans occur as middle to late instars in late spring. Their major period of growth and development is early to late spring, and adults appear during late spring and summer (Fig. 4). Nymphs are not common in autumn, so most early instars must first appear during winter (as early as December for *D. flavilinea*) or early spring. *Caudatella heterocaudata* develops somewhat later than the other two species, and most individuals emerge later in the summer. Slow growth or a diapause in autumn and early winter for eggs and early instars, followed by a rapid development in spring, is suggested for all three species. This corresponds to the "fast seasonal" type of life history described by Hynes (1970). Similar life histories have been reported for *D. flavilinea* in Idaho (Andrews and Minshall 1979) and *E. longimanus* in Alberta (Hartland-Row 1964).

Early instars of the plecopterans *C. californica*, *D. baumanni*, and *P. princeps* are most abundant in late spring. These species typically have a two- or three-year life cycle, and egg development requires as long as 8 to 10 months (Siegfried and Knight 1977, Barton 1980). Hatching of *C. californica* and *D. baumanni* extends over several months since early instars are also present in autumn. Rates of development of all three species are probably highest during late spring and summer (Heiman and Knight 1975, Siegfried and Knight 1977).

Cryptolabis sp. is the most abundant tipulid in Convict Creek and is especially prevalent in late spring. Development occurs primarily between August and May and individuals overwinter as middle to late instars; pupation occurs in July. The relative scarcity of early instars indicates that at this stage *Cryptolabis* sp. may be hyporheic or inhabit regions of slower current. Two other common dipterans, *Deuterophlebia nielsoni* and *Palpomyia* spp., are most abundant during late spring, but their population densities are never high. *Deuterophlebia nielsoni* is multivoltine (Kennedy 1967); however, we did not observe larvae of this species after September.

Summer (1,200 to 2,200 degree-days): Population densities of many common taxa in Convict Creek are lowest in early summer. This is generally true for temperate streams (Hynes 1970) and is due at least in part to the lag between spring adult emergence and hatch of the next generation. Nighttime air temperatures generally remain above freezing during late spring and early summer, and emergence of most species occurs at this time (see Fig. 4). Scouring of the streambed during periods of high discharge in late spring–summer also appears to contribute to population declines. Other authors (Gaufin 1959, Canton and Ward 1978, Minshall 1981) have

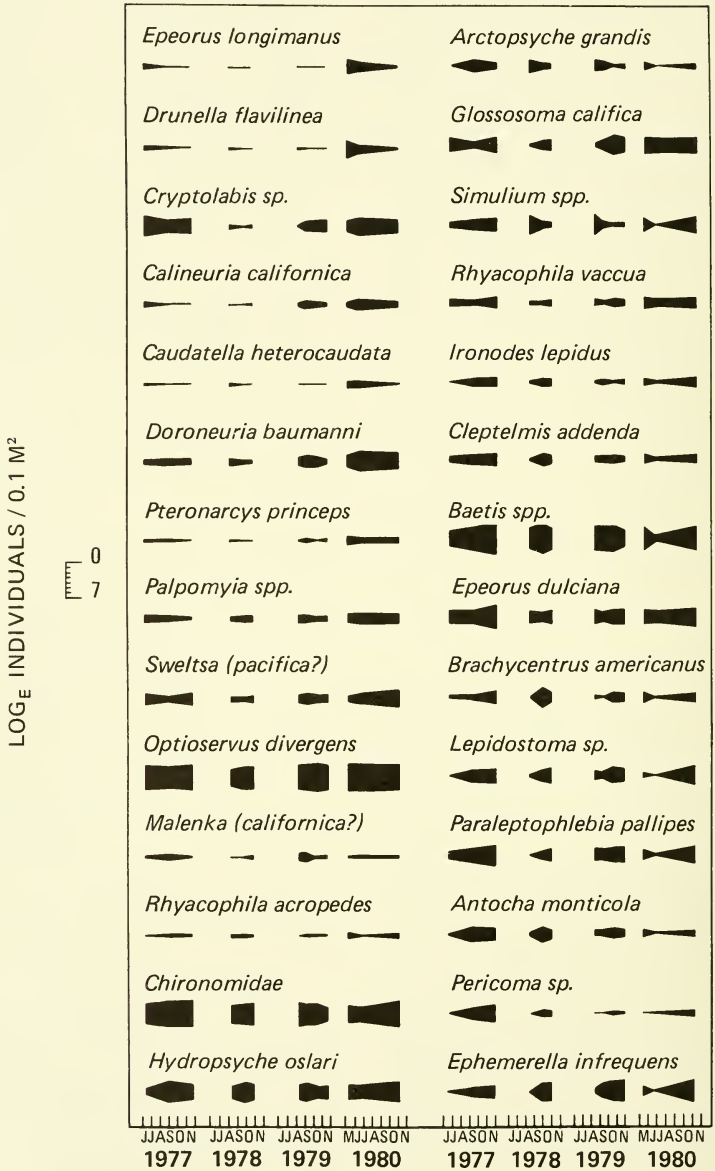

Fig. 3. Mean population densities (n = 3) of common benthic insects in riffle areas of Convict Creek. Densities were normalized by natural logarithmic transformation prior to calculating means and standard errors. Seasonal population trends identified in the text are based on mean densities differing by at least the sum of the standard errors of the means.

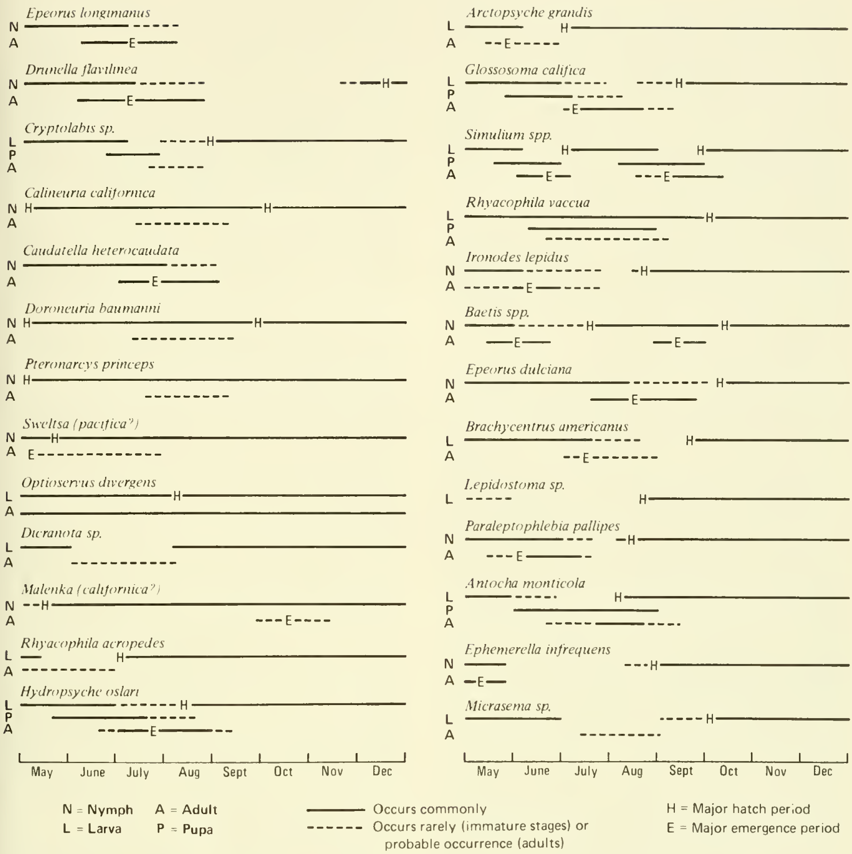

Fig. 4. Generalized life histories for common benthic insects of Convict Creek.

attributed low summer populations in streams of the western United States to the same factors.

The plecopteran *Malenka* (*californica*?) completes most of its development during summer and autumn. The main cohort emerges in October, but some individuals overwinter as late instars. The trichopteran *Arctopsyche grandis* is a common summer species; it is also the largest caddisfly in riffles and is thus an important component of the summer biomass. *Arctopsyche grandis* develops mostly between July and early September. A rapid summer development has also been reported in Idaho (Cuffney and Minshall 1981) and coastal California (Furnish 1979). The uniform size of individuals on each sampling date in Convict Creek suggests a univoltine life cycle; however, Smith (1968) found the species to be semivoltine in Idaho. *Hydropsyche oslari* is also most abundant (as early instars) in late summer, but most growth occurs after that of *A. grandis*. Growth of *H. oslari* begins about September and continues through autumn. *Rhyacophila acropedes* is another abundant summer trichopteran.

Several bivoltine and multivoltine taxa have summer cohorts. At least two species of the ephemeropteran genus *Baetis* develop between June and September. The dipterans

Simulium spp. and Chironomidae are usually most abundant from August through November. These taxa include a large number of species (see Table 2 for a list of the Chironomidae and Kennedy 1967 for a list of *Simulium* species.) Because of our inability to identify early instars, these taxa were enumerated by family; therefore, life histories cannot be described. The family Simuliidae was represented only by *Simulium* spp. in riffle samples, but a few adult *Prosimulium dicum* appeared in drift samples. A major emergence of *Simulium* spp. occurred in September 1980, but emergence was not as synchronous in other years.

Autumn (2,200 to 3,100 degree-days): Peak densities of many common taxa in Convict Creek occur in autumn. The community consists largely of early instars of "slow seasonal" species (Hynes 1970), insects that hatch quickly, develop partially during autumn, and emerge in spring (Fig. 4). Although some taxa are probably detritivores (for example, *Paraleptophlebia pallipes* and *Lepidostoma* spp.) and may have life histories timed to periods of leaf fall (Anderson and Cummins 1979), most are generalists and relative amounts of detritus and algae ingested vary seasonally (Chapman and Demory 1963, Gray and Ward 1979). Food quality probably influences life history patterns, but a more significant factor in Convict Creek may be that autumn is a period when the stream is typically at or near base flow. The moderate stream velocities may enhance survival of early instars by providing suitable substratum.

Ephemerella infrequens and *Epeorus dulciana* are common ephemeropterans in Convict Creek with autumn and early spring development. *Ephemerella infrequens* has a similar life history in Colorado (Ward and Berner 1980). *Ironodes lepidus* is less abundant in Convict Creek, but our limited data indicate a similar life history. *Paraleptophlebia pallipes* grows most rapidly in autumn, but hatching is apparently delayed in some individuals since recruitment continues through autumn. Low numbers of these taxa in June indicate a spring emergence.

Hydropsyche oslari is the dominant trichopteran by late autumn. Most individuals overwinter as third to fifth instars. This species overwinters at an earlier stage (first and second instars) in Montana (Hauer and Stanford 1982). Many other trichopterans also have peak abundances in autumn. Early instars of *Lepidostoma* spp. are common in riffles in autumn, but the taxon is rarely found there in spring. Larvae apparently move into areas of slower current in later developmental stages. *Glossosoma califica* and *Micrasema* sp. develop slowly during autumn, overwinter as early to middle instars, and pupate in late spring-summer. *Brachycentrus americanus* and *Neophylax* sp. develop to middle instars by December, but emergence does not occur until late spring or summer. *Rhyacophila vaccua* hatches during summer and autumn, overwinters primarily as middle instars, and emerges in early summer.

Chironomidae are abundant throughout autumn. Two other dipterans, *Antocha monticola* and *Pericoma* sp., also are at their maximum densities in autumn but neither is ever abundant. *Antocha monticola* completes most of its development in late summer and autumn. Although larvae were uncommon in riffles in summer, a large number of adults in August 1980 emergence samples indicates that emergence occurs throughout the summer.

Late winter/early spring (0 to 400 degree-days): Samples of benthic insects were not taken from January through April. This is apparently an active period for many species. Many late spring species must develop rapidly after overwintering as eggs or early instars. The autumn taxa are present primarily as later instars, and many of these emerge in the spring.

"Aseasonal" taxa: Some taxa are abundant throughout the snow-free months of the year, and population densities do not show strong seasonal trends. *Baetis* spp. (principally *B. devinctus* and *B. tricaudatus*) is the most abundant ephemeropteran taxon most of the year. Both species are bivoltine, with emergences in May-June and September. The autumn cohort is larger. Approximately 1,400 degree-days accumulate during development of a generation. The elmid *Optioservus divergens* appears to have a two-year life cycle (as was also described for *O. ampliatus* in eastern Canada by Le Sage and Harper 1976). Peak numbers of early instars occur between August and October, and most of this cohort reaches middle-instar stages by December.

Plecopterans in Convict Creek show less seasonal variation in abundance than do other

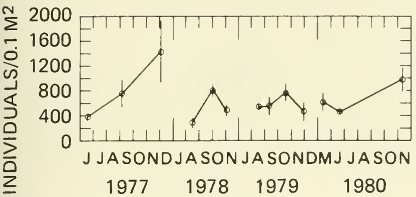

Fig. 5. Total densities (n = 3) of benthic insects in riffle areas of Convict Creek. Densities were normalized by natural logarithmic transformation prior to calculating means and standard errors.

orders of benthic insects. *Calineuria california*, *Doroneuria baumanni*, and *Pteronarcys princeps* all are semivoltine. However, the population density of *Sweltsa* sp., which is probably univoltine, did not vary much either. This may be due to the presence of more than one species.

YEARLY VARIATION IN RELATIVE ABUNDANCES OF TAXA.—Population densities of many common benthic insects in Convict Creek varied substantially among years. Because our sampling interval was wide and seasonal changes in population density were pronounced, only major among-year differences can be defined with certainty.

The total number of individuals of all benthic insect taxa was unusually high in late autumn 1977 (Fig. 5), a year of low discharge during all seasons and relatively high summer water temperatures (Fig. 1). Population densities of *Baetis* spp., *Paraleptophlebia pallipes*, *Epeorus dulciana*, and *Antocha monticola*, which hatch in autumn, were highest in late autumn 1977. Reproduction and survival of early instars of these taxa were apparently favored by the relatively mild hydrologic and climatic conditions. Except for *P. pallipes*, these taxa are all clinging, epilithic grazers (Merritt and Cummins 1984) and thus benefit from nondisruptive stream flows. *Pericoma* sp., which typically resides in fine sediments or algal mats (Usinger 1956, Merritt and Cummins 1984), was also common in riffles in autumn 1977. *Ephemerella infrequens*, another autumn-hatching ephemeropteran, was less abundant in 1977 than other years.

Sampling of benthic insects was not initiated until August in 1978, so any effects of the severe winter conditions on winter and spring fauna could not be observed. The high discharge accompanying Hurricane Norman in early autumn 1978 probably caused the low autumn densities of *Glossosoma califica*, *Paraleptophlebia pallipes*, *Epeorus dulciana*, *Optioservus divergens*, and some of the larger plecopterans. The severe winter conditions of early 1978 may have contributed to the population declines of the semivoltine *O. divergens*, *Pteronarcys princeps*, and *Doroneuria baumanni*. Severe winters appear to result in a high mortality of benthic insects. Reimers (1957) found that populations of ephemeropterans and elmid beetles in Convict Creek are reduced more by unusually cold winters than are populations of dipterans and trichopterans.

Winter air temperatures remained low longer (through March) in 1980 than in other years, but a heavy snow cover and unusually high winter baseflow prevented much anchor ice formation. The late spring-summer period of high discharge began late and continued through early August. Summer water temperatures were generally lower than in 1977 and 1979. Several taxa, including most plecopterans, were more abundant than in other years. These included *Doroneuria baumanni*, *Calineuria californica*, *Pteronarcys princeps*, *Rhyacophila vaccua*, and possibly *Micrasema* sp., *Palpomyia* spp., *Malenka* (*californica*?), and *Sweltsa pacifica*. The greater abundances of these taxa in autumn 1980 may be the result of a more effective sorting of streambed sediments due to the unusually high discharge in late spring-summer (DeMarch 1976). The absence of anchor ice in winter may have contributed to the increased survival rate of the 1979 cohorts of *D. baumanni*, *C. californica*, and *P. princeps*.

Benthic Insect Production

The total annual production of herbivorous and detritivorous benthic insects in Convict Creek riffle areas was an estimated 3.9 g/m^2 (dry weight) (Table 3). Not included in this estimate is the contribution of oligochaetes and molluscs, which is approximately 10%–20% of the mean annual standing stock. The total annual production of benthic insect predators was an estimated 1.7 g/m^2. These annual production estimates compare favorably with the values of Krueger and Waters (1983) for the Caribou River and Blackhoof River, streams in Minnesota with similar sub-

TABLE 3. Annual production, mean annual standing stock, and cohort production interval (CPI) for the more abundant benthic insects in 1979–80.

	Annual production (g/m^2 dry wt.)		Mean annual standing stock (g/m^2 dry wt.)	Estimated CPI (days)
	Estimate	95% C.I.		
PLECOPTERA				
Calineuria californica	.021	.001– .041	.006	780
Doroneuria baumanni	.233	.073– .394	.075	780
Sweltsa (*pacifica?*)	.012	.003– .020	.002	300
EPHEMEROPTERA				
Drunella flavilinea	.104	.070– .139	.014	210
Ephemerella infrequens	.117	.082– .152	.018	270
Paraleptophlebia pallipes	.041	.020– .062	.007	300
Baetis spp.	.937	.721–1.152	.079	150
Epeorus dulciana	.115	.061– .168	.014	300
Epeorus longimanus	.158	.079– .237	.009	150
TRICHOPTERA				
Hydropsyche oslari	.556	.320– .792	.057	300
Arctopsyche grandis	1.417	.903–1.932	.150	300
Rhyacophila vaccua	.261	.128– .393	.034	300
Glossosoma califica	.087	.025– .149	.014	300
Brachycentrus americanus	.056	.020– .092	.008	300
COLEOPTERA				
Optioservus divergens	.128	.098– .158	.069	660
Cleptelmis addenda	.003	.001– .005	.002	660
DIPTERA				
Simulium spp.	.099	.049– .149	.007	120
Chironomidae	.12	—	.012	—

strate but higher discharge and nutrient concentrations. Annual production of herbivores/detritivores in the two streams was 4.6 g/m^2 and 6.3 g/m^2 (corrected to dry weight), respectively, and the annual production of predators was 0.94 g/m^2 and 1.1 g/m^2.

There are several potential sources of error in the production estimates. Some large insects, such as *Pteronarcys princeps* and certain tipulids, may have contributed substantially to production in Convict Creek, but these individuals were not abundant enough to estimate production with confidence. Multiple-species populations (*Baetis* spp., *Simulium* spp.) and sexual dimorphism may have yielded overestimations because the size frequency method assumes that all individuals can reach the largest size class. Although nonlinear growth has been shown not to affect production estimates severely (Hamilton 1969, Cushman et al. 1978), taxa such as *Arctopsyche grandis* are less accurately estimated. Emigration from the sampled area (riffles) during some portion of the life cycle, such as with *Paraleptophlebia pallipes* (Anderson and Lehmkuhl 1968), also would give an inaccurate estimate. Finally, the production estimates may be biased due to unequal sampling intervals.

Stream conditions during the study period (mid-August 1979 to mid-June 1980) were not extreme. There was little anchor ice during winter, and the annual high discharge in late spring–summer was delayed. Consequently, insect mortalities were probably not unusually high. With most taxa hatching during summer and autumn, the period of highest mortality (early instars) was well sampled. Exceptions were *Epeorus longimanus* and *Drunella flavilinea*, which hatch in late autumn–winter.

Phenology

This investigation was not designed as a watershed phenological study, but rather a discussion of major recurring climatic and hydrologic events that influence life history patterns in Convict Creek. Winter is a harsh season lasting approximately four months (December through mid-March), when the stream is at or near baseflow, nighttime water temperatures are near freezing, and anchor ice forms occasionally. The dominant winter periphyton are diatoms (*Achnanthes*, *Fragi-*

laria, and *Gomphonema*) and primary production is low. It is a period of activity for many benthic insects, with taxa that reproduce in autumn present primarily as later instars. Unusually cold winters cause a high but selective mortality of benthic insects (Reimers 1957). Despite low water temperatures, brown trout (*Salmo trutta* L.) feed throughout the season (Jenkins 1969).

The water temperature begins to rise about mid-March and increases through June or July. Snowmelt in higher areas of Convict Creek Basin causes a substantial increase in discharge, beginning in May or June, which lasts for one to two months. In early summer a dense riparian canopy dominated by willows and quaking aspen develops in some stream reaches. The high discharge in late spring–summer is accompanied by declines in standing crops of periphyton and benthic insects.

Succession in the periphyton community is interrupted by scouring of the streambed in late spring and early summer. Relative abundances of periphyton taxa in late summer and autumn appear to reflect the magnitude of discharge in late spring–summer and the availability of nutrients (see also Leland and Carter 1985). When stream discharge in late spring was exceptionally high and primary productivity relatively low, the community was dominated by early-colonizing diatoms during summer; diatoms and filamentous green and blue-green algae were all abundant in autumn. When stream discharge in late spring was only moderately high and the rate of production relatively high, blue-green algae dominated in summer and remained abundant in autumn.

There is a total emergence (hence reproductive) period of at least seven months (April–October) for benthic insects, but most species emerge in late spring and early summer. Low population densities during late spring and early summer are thus due at least in part to the lag between emergence and hatch of the next generation. Scouring of the streambed also appears to contribute to the population declines.

Summer is the only season when nighttime air temperatures consistently remain above freezing; stream discharge declines progressively during this period. Later successional species of periphyton are relatively more abundant in summer than in late spring, and primary productivity is at its annual maximum. Some bivoltine and multivoltine benthic insects have summer cohorts and grow more rapidly than do individuals of the autumn cohorts.

Autumn is a season of declining water temperature and stream discharge, and baseflow is reached in October. Leaf-fall occurs from mid-September through October, with leaf litter in the stream most abundant in October. Between-year differences in periphyton composition were large, apparently due to environmental factors influencing the relative abundances of taxa at earlier successional stages (see also Leland and Carter 1986). Most slow-seasonal and multivoltine insects hatch during autumn, so this is a period of high abundance of early instars. Some of these are detritivorous (for example *Paraleptophlebia pallipes* and *Lepidostoma* spp.) and may have life histories timed to the autumn abundance of leaf litter.

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