

SECONDARY PRODUCTION ESTIMATES OF BENTHIC INSECTS IN THREE COLD DESERT STREAMS

W. L. Gaines^{1,2}, C. E. Cushing³, and S. D. Smith¹

ABSTRACT.—We studied aquatic insect production in three cold desert streams in southeastern Washington. The Size-Frequency (SF) and P/B methods were used to assess production, which is expressed by taxon, functional group, and trophic level.

Dipterans (midges and black flies) were the most productive taxa, accounting for 40–70% of the total insect production. Production by collectors and detritivores was the greatest of all functional groups and trophic levels, respectively, in all study streams.

Insects with rapid development times and multiple cohorts are very important in cold desert streams; they were major contributors to the total insect production. Total insect production rates in our study streams (14–23 g DW·m⁻²·yr⁻¹) were greater than those found in Deep Creek, Idaho (1.2 g DW·m⁻²·yr⁻¹), the only other cold desert stream for which production data are available. Our values also were generally greater than published data for most cold/mesic (3–27 g DW·m⁻²·yr⁻¹) and humid/mesic (3–25 g DW·m⁻²·yr⁻¹) streams, but lower than in Sonoran Desert Streams (>120 g DW·m⁻²·yr⁻¹) or New Zealand streams (~40 g DW·m⁻²·yr⁻¹).

Our data support the contention of others that production, rather than density or biomass, is the most accurate and meaningful way to assess the role of these organisms in lotic ecosystems.

Key words: productivity, benthos, spring-streams, cold desert, functional groups, trophic levels, Diptera, Trichoptera, Coleoptera, Ephemeroptera, Odonata, Plecoptera.

Community-level production of insects has been assessed in relatively few stream types, and of all macroinvertebrates in even fewer. Particularly, little is known about secondary production in arid region streams. The only studies of secondary production in arid region streams that we are aware of are those of Minshall et al. (1973) in Deep Creek, Idaho, in the cold desert province, and Fisher and Gray (1983) and Jackson and Fisher (1986) in Sycamore Creek, Arizona, in the hot desert region.

Secondary production is the rate of animal tissue elaboration over time regardless of the fate (e.g., carnivory, emergence) of that production (Benke and Wallace 1980). Estimating secondary production in a stream provides one assessment of the role of animals in the ecosystem (Benke and Wallace 1980) as well as insight into ecosystem dynamics. Estimating only density and biomass, regardless of time, may not accurately describe the role of organisms in the stream. For instance, the role of gathering-collector invertebrates was underestimated by bio-

mass analysis and overestimated by numerical analysis in a southeastern stream (Benke et al. 1984). Waters (1977) states that production is important to understanding ecosystem dynamics because it is the means by which energy is made available to higher trophic levels.

While most secondary production studies have focused on one or a few species in a stream (Benke and Wallace 1980, Waters and Hokenstrom 1980, O'Hop et al. 1984), more recent studies have estimated secondary production of the entire macrobenthic fauna (Krueger and Waters 1983, Benke et al. 1984, Smock et al. 1985, Huryn and Wallace 1987). Yet to be integrated into community-level analyses are the hyporheic fauna, protozoa, and other microinvertebrates. The community-level approach provides a more integrated insight into the ecology of stream ecosystems.

The purpose of this study was to measure the secondary production of insects in three streams located in the cold desert physiographic province of southeastern Washington. We emphasize

¹ Department of Biological Sciences, Central Washington University, Ellensburg, Washington 98926.

² Present address: U.S. Forest Service, Leavenworth Ranger District, Leavenworth, Washington 98826.

³ Environmental Sciences Department, Pacific Northwest Laboratory, Richland, Washington 99352.

TABLE 1. Physical and chemical characteristics of study reaches in Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Stream	Average width (m)	Average depth (m)	Average discharge (m ³ /s)	Dissolved O ₂ (mg/L)
Douglas Creek	4.0	0.31	0.6	9.6–14
Snively Springs	1.3	0.10	0.04	8.6–12
Rattlesnake Springs	1.7	0.05	0.05	8.2–10

TABLE 2. Percent substratum types in study reaches of Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Stream	Substratum type				
	Boulder (>256 mm)	Cobble (64–225 mm)	Pebble (16–64 mm)	Gravel (2–16 mm)	Sand/silt (<2 mm)
Douglas Creek	21	29	24	16	10
Snively Springs	7	20	25	11	37
Rattlesnake Springs	0	1	7	11	81

that the estimates published here are, in several cases, based on assumptions that we have explained (see Methods). Given the choices to which we could devote the available resources, we chose to produce an estimate of total insect production in these spring-streams rather than detailed data on a few taxa. We hope future studies will provide data on growth, CPIs, etc., for all taxa in these spring-streams which we can then use to refine the initial estimates presented here.

STUDY SITES

This shrub-steppe region is characterized by a climax community consisting of big sage (*Artemisia tridentata*) and bluebunch wheatgrass (*Agropyron spicatum*). Mean annual precipitation in the area is about 14 cm. The study streams were Douglas Creek (DC), Snively Springs (SS), and Rattlesnake Springs (RS) (Fig. 1). The average width, depth, discharge, and dissolved oxygen concentration for each study reach are shown in Table 1, and the substratum composition is given in Table 2. Figure 2 shows the daily and seasonal temperature ranges.

Douglas Creek

DC is a spring-fed stream located in Douglas County, Washington. It is the largest of the three streams studied, the stream itself draining an area of 530 km². Our study sites were located in

the upper reaches where flow is permanent and not affected by irrigation withdrawal. Riparian vegetation is dominated by water birch (*Betula occidentalis*) and peachleaf willow (*Salix amygdaloides*).

Snively Springs

SS is a small spring-stream located on the U.S. Department of Energy's Hanford Site, Washington. It drains an area of approximately 40 km². The lower reaches of the spring-stream dry up during the summer, leaving about 3.6 km of perennial flow (Cushing 1988). Riparian vegetation is dominated by cattails (*Typha latifolia*) along the upper and lower reaches, and willow (*Salix* sp.) and wild rose (*Rosa* sp.) along the mid-reaches, where it flows through a canyon. Watercress (*Nasturtium officinale* = *Rorippa nasturtium-aquaticum*) grows extensively within the spring-stream.

Rattlesnake Springs

RS is a small spring-stream also located on the Hanford Site. It drains an area of 350 km² (Cushing et al. 1980). Portions of the lower reaches dry up during the summer, leaving about 2.5 km of perennial flow. Mean annual total alkalinity (as CaCO₃) is 127 ppm, and the spring-stream is subject to periodic severe spates in winter (Cushing and Wolf 1982, Cushing and Gaines 1989). Riparian vegetation is dominated by peachleaf willow and cattails.

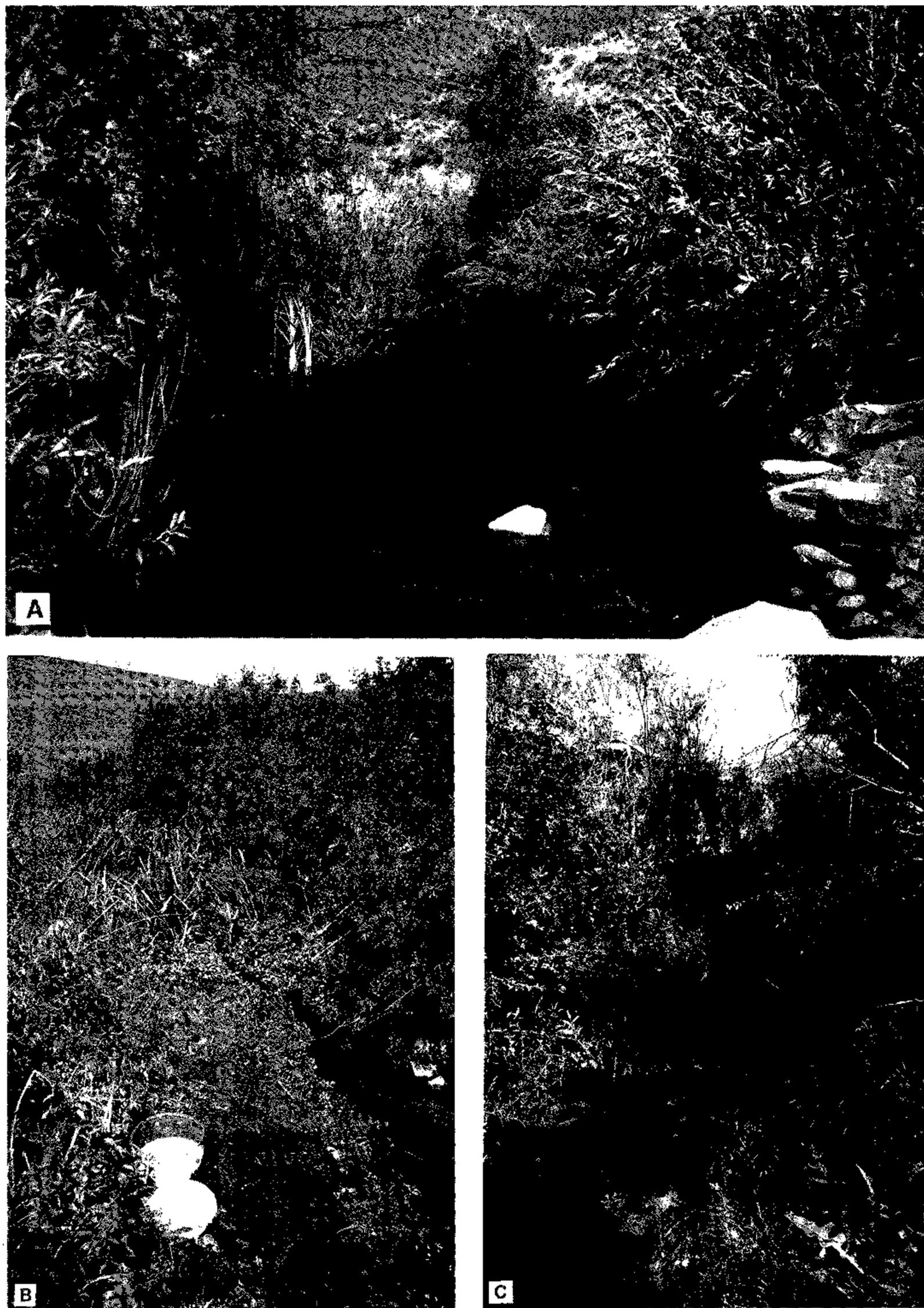


Fig. 1. Study reaches: A, Douglas Creek; B, Snively Springs; C, Rattlesnake Springs.

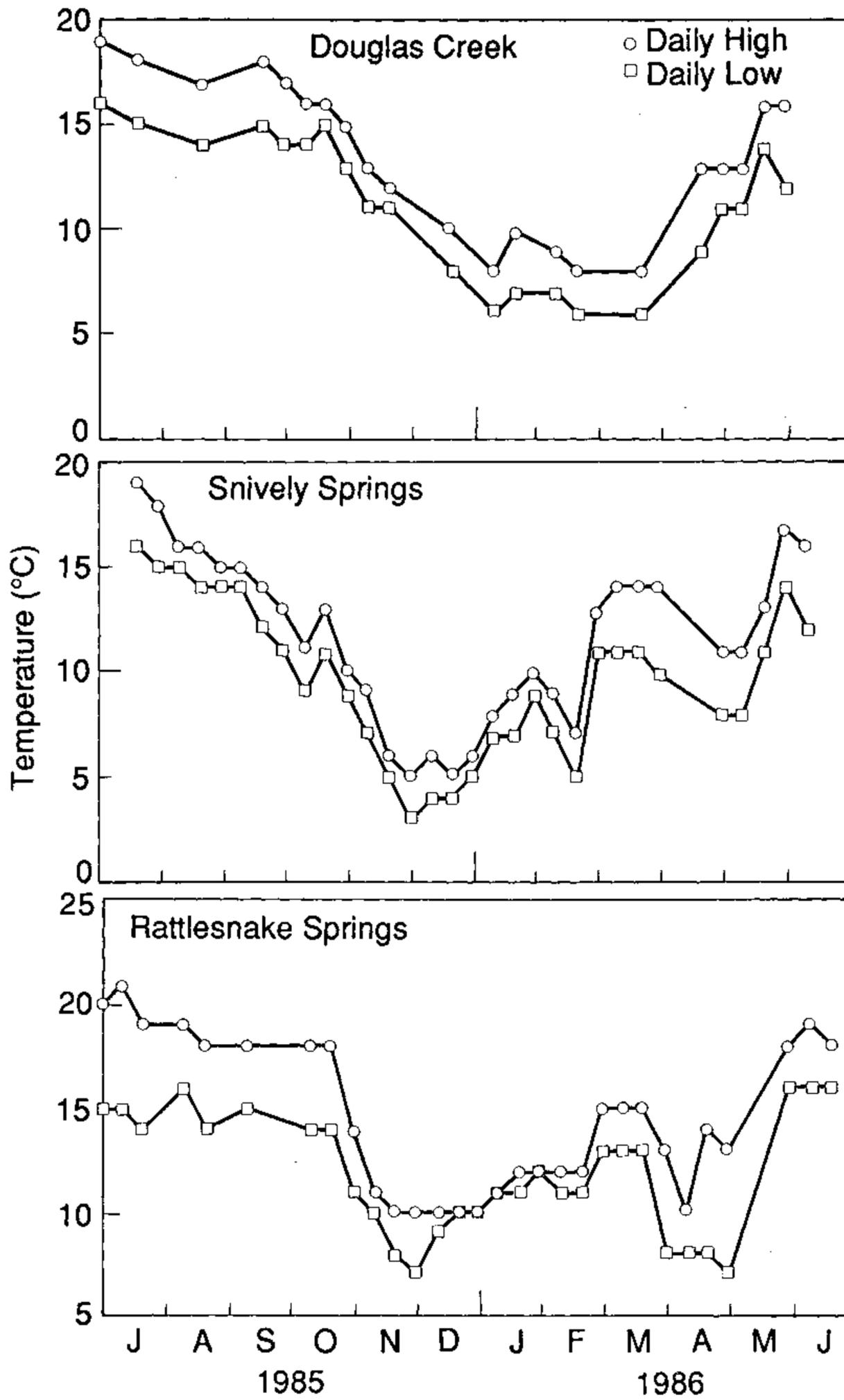


Fig. 2. Annual water temperature regimes: Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Watercress is presently the dominant in-stream autotroph, although periphyton primary production exceeded that of watercress in 1969-70 (Cushing and Wolf 1984).

METHODS

We sampled segments of each stream representing the various habitats that were present.

One study reach was sampled in SS and one in RS, and three reaches were sampled in the larger DC. Samples were taken to calculate an average standing stock for each stream to be used to calculate production estimates. The sampling scheme was not designed to allow intrastream comparisons of production estimates between different habitats, but rather to provide representative production estimates of the entire stream.

Samples were collected monthly from July 1985 through June 1986. We collected three samples during each visit. A Portable Invertebrate Box Sampler (PIBS) (0.1 m^2 , mesh size $350 \mu\text{m}$) was used in DC. A Surber sampler (0.09 m^2 , mesh size $350 \mu\text{m}$) was used in SS and RS because these spring-streams are too shallow for a PIBS. Samples were taken to a depth of 10 cm and preserved in 70% ethyl alcohol.

Insects were separated from organic debris by sugar flotation (Anderson 1959) and sorted by taxa. Insects were identified to the lowest taxonomic level possible and counted, and body length was measured to the nearest 1 mm using a microscope and ocular micrometer. The trophic status of each taxon was determined by examining gut contents (Gaines et al. 1989) or by reference to Merritt and Cummins (1984). Biomass was determined as dry weight (DW) for all size classes after drying at 60 C for 24 h and weighing to the nearest 0.1 mg.

The Size-Frequency (SF) method (Hynes and Coleman 1968, Hamilton 1969, Hynes 1980, Waters and Hokenstrom 1980) was used to estimate secondary production of the most common taxa. An average SF distribution was determined from monthly sample sets; these represented the survivorship curve of an "average cohort" (Hamilton 1969, Benke and Waide 1977); "zero" values were included when calculating densities. Production was estimated by calculating the loss between successive size classes and then multiplying the loss by the number of size classes using the equation given by Hamilton (1969). Production estimates were refined by multiplying by 365/CPI (Cohort Production Interval; Benke 1979).

We found that conducting growth studies for all taxa present within each of the streams was not practicable. To establish reasonable estimates of larval development times and CPIs, we followed the example of Benke et al. (1984), who used available life-history data and field data to estimate CPIs. We used three major

sources of information to estimate CPIs for each taxon in our study streams. First, we surveyed the available life-history data gathered from literature reviews and extrapolated the results to apply to our situations. Second, we made field observations to determine presence/absence of taxa and collected size-frequency information for each taxon to estimate larval development times and CPIs. Lastly, we conducted in situ growth studies for *Baetis* sp., *Cheumatopsyche* sp., and *Simulium* sp. to allow further refinement of our CPI estimates. These growth studies involved placing insects within growth chambers in RS. Chambers were constructed with mesh netting on each end to allow water and food material to pass through. Measurements were taken and development times recorded to estimate CPIs. Using the combination of all these data sources, we feel confident that our CPI estimates are reasonable approximations.

Production/Biomass (P/B) ratios (Waters 1977) were used to estimate secondary production for less-abundant taxa. These P/B ratios were either taxon-specific values derived from the study streams or an assumed cohort P/B value of 5 (Waters 1977, Benke et al. 1984). These taxa were not present in sufficient numbers to provide an accurate SF distribution curve that is necessary to compute SF production estimates.

RESULTS

Production calculations for DC, SS, and RS are given in Tables 3, 4, and 5, respectively. The following text describes some of the assumptions we used in our calculations, data supporting these assumptions, and other information relevant to the production calculations. All production estimates, unless noted otherwise, are given in units of $\text{mg DW}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$.

Douglas Creek

EPHEMEROPTERA.—Mayflies typically exhibit widely varied larval development times (Clifford 1982). Clifford (1982) examined life-cycle data of 85 species of Heptageniidae and found that >90% had at least one univoltine cycle. Field data for *Baetis* sp. in DC provided little clarification of the CPI. Based upon field data of *Baetis* sp. from RS and SS, and a growth study in RS, we estimated a CPI of 60 d. Similar temperature regimes in DC and RS support this

TABLE 3. Annual production of insects in Douglas Creek, July 1985 to June 1986.

	Calculation		N/m ²	SE	CV	B		CV	Annual production (mg DW/m ²)	Annual P/B
	365/CPI ^a	method				(mg DW/m ²)	SE			
Ephemeroptera										
<i>Baetis</i> sp. (gc, D) ^b	6°	SF ^c	2416	0.41	92.4	263.7	0.41	91.9	8320	31.5
<i>Paraleptophlebia</i> sp. (gc, D)	1°	SF	225	0.35	78.5	48.1	0.38	85.4	249	5.2
<i>Leucrocuta</i> sp. (g, H)	1 ^{+∞}	SF	160	0.47	104.0	51.4	0.51	104.0	238	4.6
<i>Tricorythodes</i> sp. (gc, D)	9°	PB ^d	6	0.80	159.2	1.7	0.67	151.0	77	45.0 ^e
TOTAL			2807			364.9			884	
Odonata										
<i>Argia tibialis</i> (p, C)	1 ⁺	PB	30	0.46	103.9	8.9	0.49	110.3	44	5.0 ^e
Plecoptera										
<i>Isoperla</i> sp. (p, C)	1 ⁻	SF	77	0.58	129.4	42.8	0.58	113.9	183	4.3
Trichoptera										
<i>Hydropsyche</i> sp. (fc, D)	1 ^{+∞}	SF	445	0.57	127.1	413.5	0.65	145.8	1700	4.1
<i>Cheumatopsyche</i> sp. (fc, D)	2 ^{+,∞}	SF	156	0.53	118.3	84.1	0.60	135.0	818	9.7
<i>Leucotrichia pictipes</i> (g, H)	1 ^{+,∞}	SF	95	0.63	139.7	7.7	0.68	153.2	32	4.2
TOTAL			696			505.3			2550	
Coleoptera										
<i>Optioservus</i> sp. (g, H)	1 ⁺	SF	4322	0.37	83.5	606.7	0.36	80.0	2160	3.6
Diptera										
<i>Chironomus</i> sp. (gc, D)	15°	PB	753	0.71	152.3	60.7	0.69	153.8	4920	81.1 ^f
<i>Simulium</i> sp. (fc, D)	12°	PB	41	0.75	168.6	31.2	0.72	136.1	1680	54.0 ^f
<i>Parametriocnemus</i> sp. (gc, D)	15°	SF	196	0.44	98.0	10.4	0.46	101.9	875	84.1
<i>Chaetocladius</i> sp. (gc, D)	15°	SF	115	0.57	127.8	3.5	0.66	129.4	426	121.7
<i>Heleniella</i> sp. (gc, D)	15°	SF	141	0.52	116.4	4.5	0.54	116.5	423	94.0
Tipulidae (s, D)	1°	PB	37	0.37	82.5	82.1	0.48	103.1	411	5.0 ^e
<i>Phaenospectra</i> sp. (g, H)	9°	PB	60	0.07	15.5	4.9	0.07	15.0	221	45.0 ^e
<i>Polypedilum</i> sp. (s, H)	18°	SF	33	0.69	154.5	2.2	0.78	129.1	161	73.1
Tabanidae (p, C)	1°	PB	51	0.48	106.6	27.8	0.48	107.5	130	5.0 ^e
<i>Thienemannimyia</i> sp. (p, C)	15°	PB	11	0.81	180.5	0.9	0.83	185.4	75	83.6 ^f
<i>Brillia flavifrons</i> (s, D)	15°	PB	12	0.25	55.0	0.9	0.26	57.4	68	75.0 ^e
Empididae (p, C)	15°	PB	1	0.22	50.0	0.1	0.18	40.0	8	75.0 ^e
TOTAL			1451			229.2			9358	
GRAND TOTAL			9383			1757.8			23219	

^aSource of CPI used: ° = derived from growth studies; + = field data and SF distributions; ∞ = literature; - = based upon CPI for similar cited insects (used when other sources were not available).

^bs = shredder, gc = gathering-collector, fc = filtering-collector, g = grazer/scrapper, p = predator, H = herbivore, D = detritivore, C = carnivore.

^cSF = production calculated by the Size-Frequency method.

^dPB = production calculated by an assumed P/B ratio.

^eAssumed cohort P/B of 5.

^fAssumed annual P/B is the same as derived by SF for this taxon in one of the other study streams.

estimate. *Paraleptophlebia* sp. is generally univoltine, having either summer or winter cycles (Clifford 1982). In DC, however, seasonal cycles could not be distinguished. *Paraleptophlebia* were present in DC throughout the study year, and we assumed a CPI of 1 yr. Because of low numbers of *Tricorythodes* sp., field data provided little indication of their CPI. McCullough et al. (1979) reported a 34-d larval development time for *T. minutus* grown in the field at 18 C; therefore, we estimated a CPI of 40 d for *Tricorythodes* sp. because of lower stream temperatures in DC.

ODONATA.—The damselfly *Argia tibialis* is univoltine.

PLECOPTERA.—A CPI estimate for *Isoperla* sp.

could not be made from field data. Several studies (Mackay 1969, Harper 1973, Barton 1980) of *Isoperla* sp. showed seasonal variation in growth rate, but generally their development time was about 1 yr. Therefore, we assumed a CPI of 1 yr.

TRICHOPTERA.—*Leucotrichia pictipes* was univoltine, and as SF distributions and field data indicated, the larvae overwintered as late instars and emerged in spring. This observation is supported by studies on *L. pictipes* in Owl Creek, Montana (McAuliffe 1982).

COLEOPTERA.—An accurate CPI estimate for the riffle beetle *Optioservus* sp. was difficult to estimate because few data are available concerning their development times. We thus assumed a CPI of 1 yr.

TABLE 4. Annual production of insects from Snively Springs, July 1985 to June 1986.

	365/CPI ^a	Calculation method	N/m ²			B (mg DW/m ²)			Annual production (mg DW/m ²)	Annual P/B
			N/m ²	SE	CV	(mg DW/m ²)	SE	CV		
Ephemeroptera										
<i>Baetis</i> sp. (gc, D) ^b	6 ^{+o}	SF ^c	1388	0.62	104.7	185.4	0.55	96.3	7010	37.8
<i>Paraleptophlebia</i> sp. (gc, D)	1 ⁺	SF	54	0.27	47.5	15.5	0.28	48.2	67	4.3
TOTAL			1442			200.9			7077	
Odonata										
<i>Argia tibialis</i> (p, C)	1 ⁺	PB ^d	22	0.61	106.6	27.8	0.68	118.6	139	5.0 ^e
Trichoptera										
<i>Cheumatopsyche</i> sp. (fc, D)	2 ^{+o}	SF	433	0.41	83.0	200.9	0.51	86.9	1300	6.5
Diptera										
<i>Simulium</i> sp. (fc, D)	12 ^{+o}	SF	276	0.70	121.3	34.3	0.82	142.6	1880	54.8
<i>Chironomus</i> sp. (gc, D)	15 ^o	SF	412	0.54	93.2	17.1	0.58	99.8	1390	81.1
Tipulidae (s, D)	1 ^o	PB	25	0.60	103.8	219.2	0.50	87.4	1100	5.0 ^e
<i>Heleniella</i> sp. (gc, D)	15 ^o	SF	381	0.40	69.2	9.2	0.37	64.7	550	60.3
<i>Polypedilum</i> sp. (s, H)	18 ^o	SF	123	0.56	96.2	3.2	0.52	89.1	220	68.6
<i>Chaetocladius</i> sp. (gc, D)	15 ^o	SF	92	0.63	108.3	2.7	0.69	120.2	210	77.8
Dixidae (gc, D)	15 ^o	PB	21	0.55	95.9	1.3	0.65	111.5	98	75.0 ^e
<i>Thienemannimyia</i> sp. (p, C)	15 ^o	PB	18	0.42	72.3	1.1	0.33	57.3	92	83.6 ^f
Tabanidae (p, C)	1 ^o	PB	52	0.47	81.5	10.5	0.50	86.4	53	5.0 ^e
Empididae (p, C)	15 ^o	PB	4	0.15	26.6	0.6	0.12	32.1	45	75.0 ^e
TOTAL			1404			299.2			5638	
GRAND TOTAL			3301			728.8			14,154	

^aSource of CPI used: ° = derived from growth studies; + = field data and SF distributions; o = literature; - = based upon CPI for similar cited insects (used when other sources were not available).

^bs = shredder; gc = gathering-collector; fc = filtering-collector; g = grazer/scrapper; H = herbivore; D = detritivore; C = carnivore.

^cSF = production calculated by the Size-Frequency method.

^dPB = production calculated by an assumed P/B ratio.

^eAssumed cohort P/B of 5.

^fAssumed annual P/B is the same as derived by SF for this taxon in one of the other study streams.

DIPTERA.—*Simulium* sp. were not present in sufficient numbers in DC to calculate an SF production estimate. The P/B ratio was calculated by averaging the P/B ratios obtained for *Simulium* sp. in SS and RS by the SF method. Accurate CPI estimates for Chironomidae could not be obtained from field observations or SF distribution. Therefore, we derived CPI estimates, as did Benke et al. (1984), and used growth data from Mackey (1977). Mackey (1977) reported larval development times of 21 d for *Chironomus* sp., 13 d for *Polypedilum convictum*, and 36 d for *Phaenospectra flavipes* at 15 C. CPIs were compensated for slightly lower average temperatures in DC (13 C) and environmental stress (e.g., food availability, competition, etc.). These P/B ratios seem high but are comparable to other data where short CPIs were used to estimate P/B ratios (Benke et al. 1984, Jackson and Fisher 1986). Tabanidae and Tipulidae were assumed to be univoltine with a development time of 1 yr (Krueger and Cook 1984). This is consistent with the estimate of a 1-yr development time for *Tabanus dorsifer* in Sycamore Creek, Arizona (Gray 1981).

Empididae grew to a maximum size similar to many of the midges; therefore, a CPI of 25 d was used.

Snively Springs

EPHEMEROPTERA.—Gray (1981) reported a larval development time of 20 d for *Baetis quilleri* in Sycamore Creek, Arizona. Because of lower stream temperatures, however, *Baetis* sp. developed more slowly in all streams in this study. We assumed a CPI of 60 d. *Paraleptophlebia* sp. was present only during the summer; thus, we used only summer data to calculate production because annual P was essentially equal to summer P.

ODONATA.—*Argia tibialis* was not present in sufficient numbers to make an SF production estimate.

TRICHOPTERA.—Field data and SF data indicated a bivoltine life cycle and a CPI of 6 mo for *Cheumatopsyche* sp., the only caddisfly in SS.

DIPTERA.—Becker (1973) reported a larval development time of 13 d for *S. vittatum* grown in the laboratory at 17 C. A 30-d CPI was estimated considering lower stream temperatures

TABLE 5. Annual production of insects from Rattlesnake Springs, July 1985 to June 1986.

	Calculation		N/m ²	SE	CV	B			Annual production (mg DW/m ²)	Annual P/B
	365/CPI ^a	method				(mg DW/m ²)	SE	CV		
Ephemeroptera										
<i>Baetis</i> sp. (gc, D) ^b	6 ^{++o}	SF ^c	1336	0.61	107.2	47.3	0.58	104.0	2540	53.8
<i>Tricorythodes</i> sp. (gc, D)	9 ^o	PB ^d	1	0.05	8.3	0.3	0.07	12.2	14	45.0 ^e
TOTAL			1337			47.6			2554	
Odonata										
<i>Argia tibialis</i> (p, C)	1 ⁺	PB	67	0.72	124.1	74.3	0.78	134.9	372	5.0 ^e
Trichoptera										
<i>Cheumatopsyche</i> sp. (fc, D)	2 ^{++o}	SF	140	0.69	118.9	48.6	0.78	134.5	486	10.0
<i>Parapsyche</i> sp. (fc, D)	1 ⁻	PB	10	0.24	41.7	26.8	0.25	43.4	134	5.0 ^e
<i>Limnephilus</i> sp. (s, D)	1 ⁻	PB	52	0.45	76.9	22.0	0.38	66.3	115	5.0 ^e
TOTAL			202			97.4			735	
Coleoptera										
<i>Hydraticus</i> sp. (p, C)	1 ⁻	PB	4	0.50	87.4	1.2	0.35	60.1	6	5.0 ^e
Hydrophilidae (p, C)	1 ⁻	PB	1	0.27	47.6	0.3	0.25	43.1	2	5.0 ^e
TOTAL			5						8	
Diptera										
<i>Simulium</i> sp. (fc, D)	12 ^{++o}	SF	1777	0.73	125.8	212.3	0.73	127.5	11,180	52.6
<i>Chironomus</i> sp. (gc, D)	15 ^o	SF	192	0.50	87.3	7.0	0.58	100.8	489	69.9
<i>Heleniella</i> sp. (gc, D)	15 ^o	SF	352	0.51	89.0	5.4	0.51	88.4	480	88.9
<i>Thienemannimyia</i> sp. (p, C)	15 ^o	SF	114	0.55	94.9	3.3	0.55	95.2	279	83.6
Tabanidae (p, C)	1 ^o	PB	34	0.51	85.6	15.9	0.64	111.0	80	5.0 ^e
Misc. Chironomidae (gc, D)	15 ^o	PB	18	0.29	50.1	0.8	0.38	66.3	60	75.0 ^e
<i>Polypedilum</i> sp. (s, H)	18 ^o	PB	13	0.62	108.2	0.6	0.46	78.9	41	68.6 ^f
<i>Chaetocladius</i> sp. (gc, D)	15 ^o	SF	59	0.73	126.4	0.4	0.56	97.7	30	75.0
Empididae (p, C)	15 ⁻	PB	8	0.39	68.3	0.4	0.23	39.8	30	75.0 ^e
Tipulidae (s, D)	1 ^o	PB	3	0.21	35.9	2.0	0.26	44.3	10	5.0 ^e
Dixidae (gc, D)	15 ⁻	PB	2	0.28	64.7	0.1	0.29	50.0	8	75.0 ^e
TOTAL			2572			248.2			12,687	
GRAND TOTAL			4183			469.0			16,356	

^aSource of CPI used: ° = derived from growth studies; + = field data and SF distributions; o = literature; - = based upon CPI for similar cited insects (used when other sources were not available).

^bs = shredder; gc = gathering-collector; fc = filtering-collector; g = grazer/scrapper; p = predator; H = herbivore; D = detritivore; C = carnivore.

^cSF = production calculated by the Size-Frequency method.

^dPB = production calculated by an assumed P/B ratio.

^eAssumed cohort P/B of 5.

^fAssumed annual P/B is the same as derived by SF for this taxon in one of the other study streams.

and environmental stress. CPIs of Chironomidae in SS were estimated as they were in DC. We used Gray's (1981) estimate of a 1-yr CPI and univoltinism for Tabanidae and Tipulidae. Dixidae and Empididae reached maximum sizes similar to many of the midges, and a CPI of 25 d was assumed.

Rattlesnake Springs

EPHEMEROPTERA.—We isolated several *Baetis* sp. larvae in growth chambers in RS to estimate larval development time. These data and field data indicated a CPI of 60 d. *Tricorythodes* sp. were not present in sufficient numbers for an SF production estimate.

ODONATA.—Field data for *Argia tibialis* indicated a CPI of 1 yr.

TRICHOPTERA.—We isolated several *Cheumatopsyche* sp. larvae in growth chambers in RS to estimate larval development time. These data indicated a bivoltine life cycle and a CPI of 6 mo. Because of low densities, field data gave no indication of the CPIs of *Limnephilus* sp. or *Parapsyche* sp.

COLEOPTERA.—Field data provided little indication of the CPIs of beetles because of low numbers.

DIPTERA.—Several *Simulium* sp. larvae were isolated in growth chambers in RS to estimate larval development time. As in SS, we used Gray's (1981) estimate of a 1-yr CPI and univoltinism for Tabanidae and Tipulidae. Dixidae and Empididae grew to maximum sizes similar to many of the midges, and CPIs of 25 d were assumed.

TABLE 6. Annual production (P, mg DW·m⁻²·yr⁻¹) and percent production of insect functional groups in Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Functional group	Douglas Creek		Snively Springs		Rattlesnake Springs	
	P	%	P	%	P	%
Grazer/scrapper	2651	11.4	0	0.0	0	0.0
Collector						
Gatherer	15,282	65.8	9332	65.9	3621	22.2
Filterer	4198	18.1	3177	22.5	11,800	72.1
(Total)	(19,480)	(83.9)	(12,509)	(88.4)	(15,421)	(94.3)
Shredder	639	2.8	1316	9.3	166	1.0
Predator	449	1.9	329	2.3	769	4.7
GRAND TOTAL	23,219	100.0	14,154	100.0	16,356	100.0

TABLE 7. Annual production (P, mg DW·m⁻²·yr⁻¹) and percent production of insect trophic levels in Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Trophic level	Douglas Creek		Snively Springs		Rattlesnake Springs	
	P	%	P	%	P	%
Herbivore	2812	12.1	220	1.6	41	0.3
Detritivore	19,967	86.0	13,605	96.1	15,546	95.0
Carnivore	440	1.9	329	2.3	769	4.7
TOTAL	23,219	100.0	14,154	100.0	16,356	100.0

Functional Group Production

Production by collectors was greatest of all functional groups in all study streams. Collector production was highest in DC, 19.5 g·m⁻²·yr⁻¹, accounting for 83.9% of the total annual production of insects. In SS and RS, collector production was 12.5 g and 15.4 g, representing 88.4 and 94.3% of the total annual production, respectively. The annual production of all functional groups in each study stream is shown in Table 6.

Trophic Level Production

Herbivores and detritivores are both secondary producers at the same trophic level; carnivores are tertiary producers. For this discussion, we address them separately. Detritivore production was greatest of all trophic levels in each study stream. In DC, detritivore production was about 20.0 g·m⁻²·yr⁻¹, accounting for 86.0% of the total annual insect production. In SS and RS, detritivore production was 13.6 g and 15.5 g, representing 96.1 and 95.0% of the total annual insect production. Herbivores contributed 12.1% of the productivity in DC, but no other trophic level in any of the three streams was an important contributor to secondary production. The annual production of all trophic levels in each stream is given in Table 7.

DISCUSSION

Interstream Comparisons

DC was clearly the most productive of the three streams studied (Table 6), and this is probably related to the variety of substratum (Table 2) and resulting increase in microhabitat diversity. Minshall (1984) thoroughly reviewed the importance of substratum heterogeneity and its influence on insect abundance and distribution. SS and RS were similar in size and had similar total productivity estimates (Table 6), although important differences existed among the biotic components.

In terms of functional group productivity, collectors dominated in each of the streams. Gatherers were more important in DC and SS, and filterers in RS. The greater filterer/gatherer ratio in RS is probably related to the shifting nature of the sandy substratum (Table 2) and resulting absence of areas for detritus to collect and be harvested. The filtering simuliids occurred on the abundant watercress plants. The scarcity of solid substratum for periphyton development in RS also explains the absence of grazers in this stream. However, substratum composition does not explain a lack of grazers in SS, where solid substratum is present (Table 2).

In SS, the dense riparian canopy almost completely shaded and obscured the stream. This probably prevented the development of a substantial periphytic food base for grazers. In DC, which had both solid substratum and unshaded stream bottom, a significant grazer community was present (Table 6).

Comparing the productivity of taxa common to all three streams shows some differences that are difficult to explain (Table 8). For example, *Simulium* sp. production was similar in DC and SS, but was an order of magnitude greater in RS. This may indicate a richer source of suspended food in RS; however, comparative measurements of this resource were not made. Cushing and Wolf (1982) report a value of 1513 Kcal·m⁻²·yr⁻¹ of suspended POM in RS, but comparable data are not available for DC and SS. This value is much less than that reported by Minshall (1978) for Deep Creek, a small, cold desert stream in southeastern Idaho. Since *Simulium* sp. production far exceeded that of any other insect in RS (Table 5), competitive exclusion (Hemphill and Cooper 1983) may make it more successful in competing for the limited attachment sites. *Cheumatopsyche* sp. and *Parapsyche* sp., two filtering Trichoptera in RS, had a combined production of 620 mg as compared with *Simulium* sp. production of >11,000 mg. This is a 20-fold difference for organisms of the same functional group. Except for *Simulium* sp., dipteran production was highest in DC for *Chironomus* sp. and Tabanidae, while in SS, production of *Polypedilum* sp. and Tipulidae was highest. Tipulidae production increased by an order of magnitude from RS to DC to SS. This may be related to the relatively high amounts of particulate organic matter (POM) found in the study section of SS (Cushing 1988). Production of *Baetis* sp. is three to four times lower in RS than in the other two streams (Table 8).

A likely explanation for some of the differences shown in Table 8 is the winter spates that occur in RS, but not in SS or DC. These spates, described by Cushing and Gaines (1989), scour the entire streambed, flushing out accumulated POM and much of the fauna. They occur about every three years and act as a "reset" mechanism. Because they occur in winter when there are no ovipositing adults, and because they scour and eliminate sources for both upstream migration and downstream drift, they must

TABLE 8. Comparative annual production (mg DW·m⁻²·yr⁻¹) of taxa common to Douglas Creek, Snively Springs, and Rattlesnake Springs, July 1985 to June 1986.

Taxon	Douglas Creek	Snively Springs	Rattlesnake Springs
Ephemeroptera			
<i>Baetis</i> sp.	8317	7012	2542
Odonata			
<i>Argia tibialis</i>	44	139	372
Trichoptera			
<i>Cheumatopsyche</i> sp.	818	1298	486
Diptera			
<i>Simulium</i> sp.	1680	1879	11,175
<i>Chironomus</i> sp.	4920	1386	489
<i>Polypedilum</i> sp.	161	220	41
Tabanidae	130	53	80
Tipulidae	411	1096	10

severely limit the potential productivity of RS. It is notable that the dominant secondary producers in RS are the black flies, organisms that are found in abundance soon after discharge diminishes (Cushing and Gaines 1989).

Intrastream Comparisons

DOUGLAS CREEK.—Secondary production in DC was spread over a wider variety of functional groups (Table 6) and trophic levels (Table 7), even though it was dominated by detritus-feeding collector-gatherers. *Chironomus* sp. and *Baetis* sp. were the dominant secondary producers in the stream.

SNIVELY SPRINGS.—In SS, about 50% of the secondary production was due to *Baetis* sp., a detritus-feeding collector-gatherer; and, as mentioned above, the grazing component was absent. Total dipteran production was of the same order of magnitude as that for *Baetis* sp. but was spread out among several organisms, notably *Simulium* sp., *Chironomus* sp., and Tipulidae (Table 4).

RATTLESNAKE SPRINGS.—Secondary production in RS was less diverse than in the other study streams, with over 68% of the production due to the filtering detritivore *Simulium* sp. The second highest producer was *Baetis* sp., but production was far lower than the black flies (Table 5). The high production of simuliids in RS can be attributed to the presence of multiple cohorts with short development times. Gray (1981) suggested that rapid development may be advantageous in streams subject to spates.

TABLE 9. Comparative whole stream secondary production of insects (P , $g\ DW\cdot m^{-2}\cdot yr^{-1}$), except as indicated, in five geoclimatic regions. Streams grouped by geographical region, not by temperature regimes.

Stream	P	S ^a	Fc	Gc	Gr/sc	Pred	Source
Cold/mesic							
Unnamed, Quebec	5.8 ^b						Harper 1978
Factory Br., Maine	12.2						Neves 1979
Sand R., Alberta	0.8 ^c						Soluk 1985
Caribou R., Minnesota	3.54	0.83	0.62	1.36	0.14	0.59	Krueger and Waters 1983
Blackhoof R., Minnesota	7.13	1.00	3.53	1.15	0.37	1.08	Krueger and Waters 1983
No. Branch Cr., Minnesota	13.23	0.73	5.33	9.43	1.00	2.07	Krueger and Waters 1983
Fort R., Massachusetts	3.3						Fisher 1977
Bear Br., Massachusetts	4.8						Fisher and Likens 1973
L'Ance du Nord, France	12.5	(Total detritivore P = P - Pred.)				2.0	Maslin and Pattee 1981
Bisballe baek, Denmark	26.7					1.3	Mortensen and Simonsen 1983
Humid/mesic							
Satilla R. Georgia ^d	25.2		2.9	18.0		4.3	Benke et al. 1984
Snag substrate ^e	64.8		49.3	8.1		7.5	
Sandy substrate ^e	21.0		0	17.9		3.1	
Mud substrate ^e	17.9		0.2	8.6		9.2	
Cedar R., So. Carolina	3.0	0.1	1.0	1.3	0.02	0.6	Smock et al. 1985
Lower Shope Fk., No. Carolina					1.4		Georgian and Wallace 1983
Upper Ball Cr., No. Carolina							Hurn and Wallace 1987
Bedrock-outcrop	6.1	0.6	2.1	2.1	0.6	0.7	
Riffle	5.6	1.4	0.3	1.8	1.0	1.1	
Pool	7.6	2.4	0.03	3.0	0.3	1.9	
Hot desert							
Sycamore Cr., Arizona	120.9						Jackson and Fisher 1986
New Zealand							
Hinai R.	38.2						Hopkins 1976
Horokiwi R.	41.5						Hopkins 1976
Cold desert							
Deep Cr., Sta. 1, Idaho	1.2						Minshall et al. 1973
Douglas Cr., Washington	23.2	0.6	4.2	15.3	2.7	0.4	This study
Snively Spr., Washington	14.2	1.3	3.2	9.3	0	0.3	This study
Rattlesnake Spr., Washington	16.4	0.2	3.6	11.8	0	0.8	This study

^aS = shredder; Fc = filtering-collector; Gc = gathering-collector; Gr/sc = grazer/scrapper; Pred = predators.

^bEmergers only.

^cOnly two species of chironomids.

^dExpressed per unit area of total stream bottom.

^eExpressed per unit area of habitat.

Comparisons with Other Streams

Annual P/B ratios ranged from 3.6 to 121.7 for insects from the study streams. The high annual P/B ratios are attributed to insects with rapid development and multiple cohorts (e.g., many Chironomidae). The annual P/B ratios found in these cold desert spring-streams are generally lower than those reported by Jackson and Fisher (1986) for Sonoran Desert stream insects and by Benke et al. (1984) for southeastern blackwater stream insects. The Sonoran and blackwater streams are warmer and insect development is faster, resulting in a greater number of cohorts. Our annual P/B ratios were generally higher than reported for northern temperate streams (Krueger and Waters 1983), where cooler streams result in insect development at slower rates with fewer cohorts.

Total insect production rates in this study ranged from 14 to 23 $g\ DW\cdot m^{-2}\cdot yr^{-1}$ and are compared with values for other streams grouped by geographical region (Table 9). Production rates in cold desert streams are well below the higher values found in New Zealand streams, the richer areas (snags) of humid/mesic streams in the southeastern United States, and Sonoran hot desert streams. However, production rates in cold desert streams are higher than those in streams in cold/mesic areas of the United States. These rankings relate to the interaction among stream water temperature, insect development, cohort production intervals, and other factors. However, it should be kept in mind that other factors, e.g., geochemistry, may be influential in governing production as well as temperature. Production values in

Rattlesnake Springs, which has a sandy substratum, are comparable to the sandy areas of the Satilla River in Georgia (16.4 vs 13.1 g DW·m⁻²·yr⁻¹, respectively); production of collector-gatherers was identical.

Benke et al. (1984) stated that measurement of secondary productivity of benthic organisms provides a truer indication of their importance in lotic ecosystems than does measurement of either density or biomass. This is intuitively reasonable since measurement of P, a rate, includes consideration of both biomass and density. Our results support the validity of Benke et al.'s (1984) contention. Clearly, our data reveal that collectors are the dominant functional group, and detritivores the dominant trophic level in terms of the secondary productivity of insects in these three streams (Tables 6 and 7). If only biomass or density data are evaluated from these streams (Tables 3, 4, and 5; Gaines et al. 1989), anomalies become evident. Density data in DC reveal that herbivores are equally as numerous as detritivores, but biomass data reveal that detritivores are about two times greater than herbivores. Conversely, when the insects are separated into functional groups, the biomass of grazer/scrapers (herbivores) exceeds that of collectors in DC by a factor of two. Further, collector-filterers in DC represent 18% of the production and 30% of the biomass, but only 7% of the density. In SS, trophic level comparisons reveal that detritivores dominate production, biomass, and density, but if functional groups are compared, biomass data would overemphasize the importance of shredders (30%), which form only 5% of the density and 9% of total production. In RS, the largest anomaly appears when comparing functional groups. Although collector-filterers represent 72% of the total production and 61% of the biomass, their density is similar to the collector-gatherers.

In conclusion, we have found that taxa with short development times and multiple cohorts, such as midges and black flies, are important to cold desert spring-stream production. Previous studies have addressed the difficulties in obtaining accurate field estimates of Simuliidae (black fly) and Chironomidae (midge) larvae CPIs, and thus production estimates (Benke et al. 1984, Behmer and Hawkins 1986, Stites and Benke 1989). Their small size, rapid turnover rate, high density, and diversity make accurate species-specific CPI estimates difficult. These same characteristics, however, make midges and black flies very important

to stream communities in terms of production. In many streams, they contribute a large percentage of the total community production because of their rapid development and high turnover rates. We found high P/B ratios for simuliids and chironomids, but other investigators have reported similar results (Fisher and Gray 1983, Benke et al. 1984, Stites and Benke 1989). This life-history strategy is particularly advantageous for insects inhabiting the streams that are subjected to severe spates.

Detritus is the major food resource in these small streams; collector-gatherers predominate where there is more substratum diversity (DC and SS), and filterers in systems more prone to the effects of spates (RS). Grazer/scrapers are present whenever suitable substratum and sufficient sunlight are available for development of a periphyton crop. Shredders, surprisingly, are not well represented in these small headwater streams. This may be related to the flushing of the systems by the spates and/or the low amounts of allochthonous detritus reaching the streams (Cushing 1988). Secondary productivity of these cold desert spring-streams was less than that of streams in hot deserts, but generally higher than that in most cold/mesic and humid/mesic streams. Finally, our results underscore the contentions of Benke et al. (1984) that measuring the secondary production of insects in streams provides a better assessment of their role than density or biomass, but the anomalies described above argue for care in applying this generalization to all streams.

ACKNOWLEDGMENTS

This paper represents a portion of the thesis submitted by WLG to Central Washington University for the M.S. degree. The research was performed at Pacific Northwest Laboratory during a Northwest College and University Association for Science (NORCUS) Fellowship (University of Washington) to WLG. It was funded under Contract DE-AM06-76-RLO2225 and was supported by the U.S. Department of Energy (DOE) under Contract DE-AC06-76RLO 1830 between DOE and Battelle Memorial Institute.

We would like to thank Dr. William Coffman for identifying the chironomids, and Dr. Pat Scheffer for identifying the caddisflies. The manuscript was improved by comments from three anonymous reviewers; our thanks to them.

LITERATURE CITED

- ANDERSON, R. O. 1959. A modified flotation technique for sorting bottom fauna samples. *Limnology and Oceanography* 4: 223-225.
- BARTON, D. R. 1980. Observations on the life histories and biology of Ephemeroptera and Plecoptera in north-eastern Alberta. *Aquatic Insects* 2: 97-111.
- BECKER, C. D. 1973. Development of *Simulium vittatum* Zett. (Diptera: Simuliidae) from larvae to adults at thermal increments from 17.0 to 27.0 C. *American Midland Naturalist* 89: 246-251.
- BEHMER, D. J., and C. P. HAWKINS. 1986. Effects of overhead canopy on macroinvertebrate production in a Utah stream. *Freshwater Biology* 16: 287-300.
- BENKE, A. C. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnology and Oceanography* 24: 168-171.
- BENKE, A. C., and J. B. WAIDE. 1977. In defense of average cohorts. *Freshwater Biology* 7: 61-63.
- BENKE, A. C., and J. B. WALLACE. 1980. Trophic basis production among net-spinning caddisflies in a southern Appalachian stream. *Ecology* 61: 108-118.
- BENKE, A. C., T. C. VAN ARSDALI, and D. M. GILLESPIE. 1984. Invertebrate productivity in a subtropical black-water river: importance of habitat and life history. *Ecological Monographs* 54: 25-63.
- CLIFFORD, H. F. 1982. Life cycles of mayflies (Ephemeroptera), with special reference to voltinism. *Quaestiones Entomologicae* 18: 15-90.
- CUSHING, C. E. 1988. Allochthonous detritus input to a small, cold desert spring-stream. *Verhandlungen der Internationalen Vereinigung für Limnologie* 23: 1107-1113.
- CUSHING, C. E., and W. L. GAINES. 1989. Thoughts on recolonization of endorheic cold desert spring-streams. *Journal of the North American Benthological Society* 8: 277-287.
- CUSHING, C. E., and E. G. WOLF. 1982. Organic energy budget of Rattlesnake Springs, Washington. *American Midland Naturalist* 107: 404-407.
- _____. 1984. Primary production in Rattlesnake Springs, a cold-desert spring-stream. *Hydrobiologia* 114: 229-236.
- CUSHING, C. E., C. D. MCINTIRE, J. R. SEDELL, K. W. CUMMINS, G. W. MINSHALL, R. C. PETERSEN, and R. L. VANNOTE. 1980. Comparative study of physical-chemical variables of streams using multivariate analysis. *Archiv für Hydrobiologie* 89: 343-352.
- FISHER, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. *Internationale Revue gesamten Hydrobiologie* 62: 701-727.
- FISHER, S. G., and L. G. GRAY. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. *Ecology* 64: 1217-1224.
- FISHER, S. G., and G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecological Monographs* 43: 421-439.
- GAINES, W. L., C. E. CUSHING, and S. D. SMITH. 1989. Trophic relations and functional group composition of benthic insects in three cold desert streams. *Southwestern Naturalist* 34: 478-482.
- GEORGIAN, T., and J. B. WALLACE. 1983. Seasonal production dynamics in a guild of periphyton-grazing insects in a southern Appalachian stream. *Ecology* 64: 1236-1248.
- GRAY, L. J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran desert stream. *American Midland Naturalist* 106: 229-242.
- HAMILTON, A. L. 1969. On estimating annual production. *Limnology and Oceanography* 14: 771-782.
- HARPER, P. P. 1973. Emergence, reproduction, and growth of setipalpi Plecoptera in southern Ontario. *Oikos* 24: 94-107.
- _____. 1978. Variations in the production of emerging insects from a Quebec stream. *Verhandlungen der Internationalen Vereinigung für Limnologie* 20: 1317-1323.
- HEMPHILL, N., and S. D. COOPER. 1983. The effect of physical disturbance on the relative abundances of two filter-feeding insects in a small stream. *Oecologia* 58: 378-382.
- HOPKINS, C. L. 1976. Estimate of biological production in some stream invertebrates. *New Zealand Journal of Marine and Freshwater Research* 10: 629-640.
- HURYN, A. D., and J. B. WALLACE. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. *Ecology* 68: 1932-1942.
- HYNES, H. B. N. 1980. A name change in the secondary production business. *Limnology and Oceanography* 25: 778.
- HYNES, H. B. N., and M. J. COLEMAN. 1968. A simple method of assessing the annual production of stream benthos. *Limnology and Oceanography* 13: 569-573.
- JACKSON, J. K., and S. G. FISHER. 1986. Secondary production, emergence, and export of aquatic insects of a Sonoran desert stream. *Ecology* 67: 629-638.
- KRUEGER, C. C., and E. F. COOK. 1984. Life cycles, standing stocks, and drift of some Megaloptera, Ephemeroptera, and Diptera from streams in Minnesota, U.S.A. *Aquatic Insects* 6: 101-108.
- KRUEGER, C. C., and T. F. WATERS. 1983. Annual production of macroinvertebrates in three streams of different water quality. *Ecology* 64: 840-850.
- MACKAY, R. J. 1969. Aquatic insect communities of a small stream on Mont St. Hilaire, Quebec. *Journal of the Fisheries Research Board of Canada* 26: 1157-1183.
- MACKEY, A. P. 1977. Growth and development of larval Chironomidae. *Oikos* 28: 270-275.
- MASLIN, J.-L., and E. PATTEE. 1981. La production du peuplement benthique d'une petite rivière: son évaluation par la méthode de Hynes, Coleman et Hamilton. *Archiv für Hydrobiologie* 92: 321-345.
- MCAULIFFE, J. R. 1982. Behavior and life history of *Leucotrichia pictipes* (Banks) (Trichoptera: Hydroptilidae) with special emphasis on case reoccupancy. *Canadian Journal of Zoology* 60: 1557-1561.
- MCCULLOUGH, D. A., G. W. MINSHALL, and C. E. CUSHING. 1979. Bioenergetics of a stream "collector" organism, *Tricorythodes minutus* (Insecta: Ephemeroptera). *Limnology and Oceanography* 24: 45-58.
- MERRITT, R. W., and K. W. CUMMINS, EDS. 1984. An introduction to the aquatic insects of North America. 2nd ed. Kendall/Hunt Publishing Company, Dubuque, Iowa.
- MINSHALL, G. W. 1978. Autotrophy in stream ecosystems. *BioScience* 28: 767-771.

- _____. 1984. Aquatic insect-substratum relationships. Pages 358-400 in V. H. Resh and D. M. Rosenberg, eds., *The ecology of aquatic insects*. Praeger Publishers, New York.
- MINSHALL, G. W., D. A. ANDREWS, F. L. ROSE, D. W. SHAW, and R. L. NEWELL. 1973. Validation studies at Deep Creek, Curlew Valley. Idaho State University Research Memorandum No. 73-48.
- MORTENSEN, E., and J. L. SIMONSEN. 1983. Production estimates of the benthic invertebrate community in a small Danish stream. *Hydrobiologia* 102: 155-162.
- NEVES, R. J. 1979. Secondary production of epilithic fauna in a woodland stream. *American Midland Naturalist* 102: 209-224.
- O'HOP, J., J. B. WALLACE, and J. D. HAEFNER. 1984. Production of a stream shredder, *Peltoperla maria* (Plecoptera: Peltoperlidae) in disturbed and undisturbed hardwood catchments. *Freshwater Biology* 14: 13-21.
- SMOCK, L. A., E. GILINSKY, and D. L. STONEBURNER. 1985. Macroinvertebrate production in a southeastern United States blackwater stream. *Ecology* 66: 1491-1503.
- SOLUK, D. A. 1985. Macroinvertebrate abundance and production of psammophilous Chironomidae in shifting sand areas of a lowland river. *Canadian Journal of Fisheries and Aquatic Sciences* 42: 1296-1302.
- STITES, D. L., and A. C. BENKE. 1989. Rapid growth rates of chironomids in three habitats of a subtropical blackwater river and their implications for P:B ratios. *Limnology and Oceanography* 34: 1278-1289.
- WATERS, T. F. 1977. Secondary production in inland waters. *Advances in Ecological Research* 10: 91-164.
- WATERS, T. F., and J. C. HOKENSTROM. 1980. Annual production and drift of the stream amphipod *Gammarus pseudolimnaeus* in Valley Creek, Minnesota. *Limnology and Oceanography* 25: 700-710.

Received 1 June 1991

Revised 1 December 1991

Accepted 10 January 1992