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Secondary Production of Benthic Insects in Three Cold-Desert Streams

W. L. Gaines

July 1987

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Pacific Northwest Laboratory
Richland, Washington 99352

SUMMARY

I studied aquatic insect production in three cold-desert streams in eastern Washington (Douglas Creek, Snively Springs, and Rattlesnake Springs). The size-frequency method was applied to individual taxa to estimate total insect production. Production was also assessed for functional groups and trophic levels in each stream.

Optioservus sp. (riffle beetles) and *Baetis* sp. (mayflies) accounted for 72% of the total insect numbers and 50% of the total biomass in Douglas Creek. *Baetis* sp. accounted for 42% of the total insect numbers and 25% of the total biomass in Snively Springs. *Simulium* sp. (blackflies) and *Baetis* sp. comprised 74% of the total insect numbers and 55% of the total biomass in Rattlesnake Springs.

Grazer-scrapers (49%) and collectors (48%) were the most abundant functional groups in Douglas Creek. Collectors were the most abundant functional group in Snively Springs and Rattlesnake Springs. Herbivores and detritivores were the most abundant trophic level in Snively Springs and Rattlesnake Springs.

Dipterans (midges and blackflies) were the most productive taxa within the study streams, accounting for 40% to 70% of the total community production. Production by collectors and detritivores was the highest of all functional groups and trophic levels in all study streams.

Insects with rapid development times and multiple cohorts were very important in cold-desert streams, contributing significantly to the total community production. Total community production rates were generally higher than in northern temperate streams, lower than in southeastern blackwater streams, and much lower than in Sonoran Desert streams. Much of the production in cold-desert streams can be attributed to insects feeding upon detritus, and detritus was obtained by collecting (filtering and gathering). I suggest that production, not

density or biomass, is the most accurate and meaningful way to assess the roles of organisms in aquatic ecosystems, and that the procedure given by Benke *et al.* (1984) should be followed to calculate production.

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INTRODUCTION

Secondary production is defined as the rate of animal tissue elaboration over time regardless of the fate (carnivory, emergence, etc.) of that production (Benke and Wallace 1980). Estimating secondary production within a stream provides an assessment of the roles of animals within the ecosystem (Benke and Wallace 1980) while gaining insight into ecosystem dynamics.

Studies dealing only with density and biomass values may not accurately describe the roles of aquatic organisms within the stream. Benke et al. (1984) provide an example where the importance of gathering-collector invertebrates is underestimated by biomass analysis and overestimated by numerical analysis. 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 within 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 benthic fauna (Krueger and Waters 1983, Benke et al. 1984, Smock et al. 1985). This community-level approach provides the greatest insight into the ecology of stream ecosystems.

Community-level production studies, however, have been performed on very few kinds of streams. In particular, very little is known about the secondary production of the benthic invertebrate community in desert streams. The only publications on the subject to date are those of Fisher and Gray (1983) and Jackson and Fisher (1986) on Sycamore Creek, Arizona.

I estimated the production of aquatic insects in three cold-desert streams in Washington State: Rattlesnake Springs, Snively Springs, and Douglas Creek. Ecosystem dynamics in cold-desert streams will be more fully understood by estimating the secondary production of each species, functional group, trophic level, and community.

LITERATURE REVIEW

In his textbook on limnology, Welch (1935) defined his discipline as that branch of science that deals with the biological productivity of inland waters. Subsequently, scientists attempted to measure production rates of all trophic levels within an ecosystem in attempts to quantify ecosystem dynamics. Production is an important pathway of energy flow in ecosystems and is thus of great interest (Waters 1977).

Until recently, estimates of secondary production lagged behind those made of primary production. Reasons for the lag are: 1) the organisms are very diverse and some have complex life histories; 2) large numbers of samples are needed to reduce sample variation caused by a great variation in the distribution of organisms; and 3) separating, sorting, and analyzing samples are tedious and time-consuming, thus costly, tasks. Hynes (1970) reviewed the literature through 1966 and found only four attempts at directly estimating benthic invertebrate production in streams.

Several methods have been developed to estimate secondary production in streams. The Removal-Summation, Increment-Summation, Instantaneous Growth Rate, Allen Curve, and Hynes method have all been used. The Hynes method and its modifications have stood the test of time and is the most popular secondary production estimator in use today.

Originally proposed by Hynes and Coleman (1968), the Hynes method was designed as a shortcut approach to estimate production of entire benthic faunas. The method was unique in that it was not necessary to identify individual cohorts, thus making it easier to apply (Benke 1979). Hamilton (1969) modified the method by introducing the term "average cohort" when describing the size-frequency distribution that is necessary to make Hynes production estimates. Hamilton (1969) also pointed out three assumptions of the Hynes method that are difficult to justify: 1) all species in the samples are univoltine, 2) all species can potentially grow to maximum length used in the size-frequency distribution, and 3) all species require the same amount of time to grow

through each length class. These assumptions are difficult to meet when the Hynes method is applied to species with very different life histories. Benke and Waide (1977), however, showed that many of these assumptions can be met when the method is applied to single or similar species. Another problem that plagued the Hynes method was how to accurately estimate production of semivoltine or multivoltine populations. Benke (1979) addressed this problem by introducing the Cohort Production Interval (CPI). He suggested that the Hynes production value be multiplied by 365/CPI, where CPI is the time in days from hatching to attainment of the largest aquatic size class. A final modification was proposed by Waters (1977) and confirmed by Hynes (1980) to change the name to the size-frequency (SF) method. This method is now commonly used by secondary production biologists and is the method I used in this study.

Recently the SF method has been used to assess secondary production of entire benthic communities (Benke et al. 1984, Jackson and Fisher 1986). Community production estimates are calculated by summing the species estimates and, in this way, accounting for variations in life histories (Benke et al. 1984). As life history data on greater numbers of species are obtained, the SF method will be more widely used and will become more accurate.

STUDY AREA

I studied three streams in the cold-desert Physiographic Province of Eastern Washington. This shrub-steppe region is characterized by the climatic climax community of big sage (*Artemesia tridentata*)-bluebunch wheatgrass (*Agropyron spicatum*). Mean annual precipitation is approximately 14 cm.

DOUGLAS CREEK

Douglas Creek is a spring-fed stream located in Douglas County, Washington, near the small community of Palisades, Washington. The stream drains an area of 530 km^2. The lower reaches of Douglas Creek, which are used extensively for irrigation, cease to flow during dry summers. For this reason, I located all study sites in the upper reaches where flow is permanent. Riparian vegetation is dominated by water birch (*Betula occidentalis*) and peachleaf willow (*Salix amygdaloides*). Populations of crayfish (*Pacifasticus leniscullus*) and rainbow trout (*Salmo gairdneri*) inhabit this stream.

Douglas Creek is the largest of the three streams studied. The average width was 4.0 m and average depth was 31 cm during base flow. The average discharge during the study period was 0.6 m^3/s, and ranged from 0.5 m^3/s in late summer to 0.9 m^3/s in the early spring. Dissolved oxygen concentrations measured at midday ranged from a low of 9.6 mg/l in late summer to a high of 14.0 mg/l in midwinter. The temperature regime for Douglas Creek during the study period is shown in Figure 1. Table 1 shows the substrate composition of each study site.

SNIVELY SPRINGS

Snively Springs is a small spring-stream located on the U.S. Department of Energy's Hanford Site. It drains an area of approximately 40 km^2. During the summer portions of the spring-stream dry up, leaving about 3.6 km of perennial flow. Riparian vegetation is dominated by

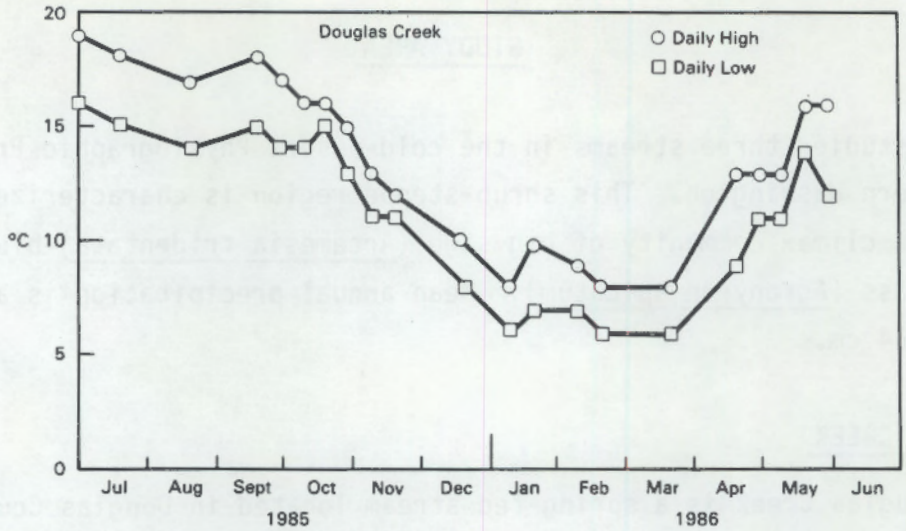

FIGURE 1. Temperature Regime for Douglas Creek

TABLE 1. Substrate Composition of Douglas Creek, Snively Springs, and Rattlesnake Springs

Stream	Substrate Size (%)				
	Boulder (>255 mm)	Cobble (64-256 mm)	Pebble (2-16 mm)	Gravel (2-16 mm)	Sand/Silt (<2 mm)
Rattlesnake	0	0.9	7.3	10.8	81.0
Snively	7.4	20.4	25.3	10.5	36.4
Douglas (Site 1)	24.0	26.0	20.0	22.0	4.0
Douglas (Site 2)	26.0	44.0	16.0	12.0	2.0
Douglas (Site 3)	14.0	18.0	38.0	16.0	24.0

dominated by cattails (Typha latifolia) along the upper and lower reaches, and willow (Salix sp.) and wild rose (Rosa sp.) along the midreaches where it flows through a canyon. Watercress (Rorippa nasturtium-aquatica) grows extensively within the spring-stream. A small population of crayfish [(Pacifasticus lenisculus (trowbridgii)] inhabits Snively Springs.

The average width and depth of Snively Springs during base flow was 1.3 m and 10 cm, respectively. Average discharge during the study period was 0.04 m^3/s, and ranged from 0.02 m^3/s in the late spring to 0.05 m^3/s in the winter. Dissolved oxygen concentrations measured at

midday ranged from 8.6 mg/l during the summer to 12.3 mg/l during the winter. The temperature regime for Snively Springs during the study period is shown in Figure 2, and the substrate composition is shown in Table 1.

RATTLESNAKE SPRINGS

Rattlesnake Springs is a small spring-stream also located on the U.S. Department of Energy's Hanford Site. It drains an area of 350 sq km (Cushing *et al.* 1980). Portions of the lower reaches of the spring-stream dry up during the summer, leaving about 2.5 km of perennial flow. This spring-stream is subject to severe flash flooding during the late winter about every four years (Cushing and Wolf 1982). Riparian vegetation is dominated by peachleaf willow (*Salix amygdaloides*). Watercress (*Rorippa nasturtium-aquatica*) is the dominant in-stream autotroph, although periphyton productivity exceeded that of watercress in 1969 and 1970 (Cushing and Wolf 1984).

The average width and depth of Rattlesnake Springs during base flow was 1.7 m and 5 cm, respectively. Average discharge during the study period was 0.05 m^3/s, and ranged from 0.03 m^3/s in the spring to

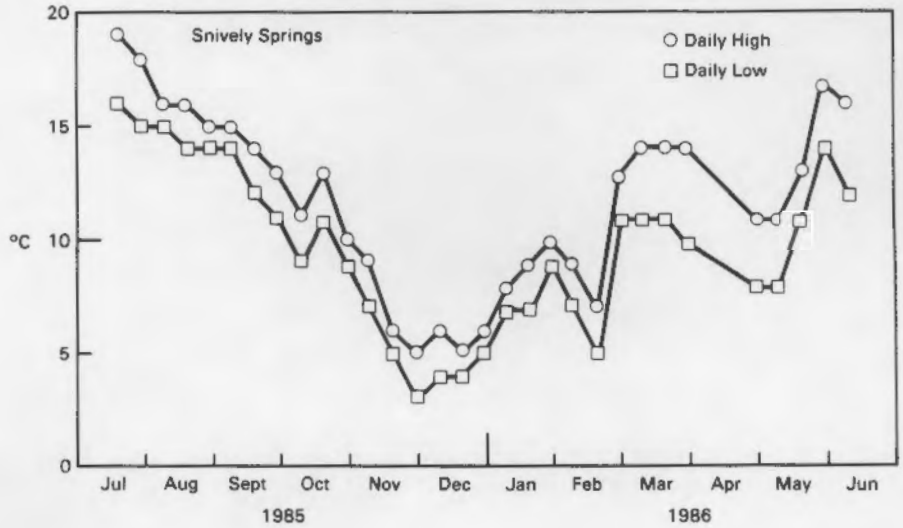

FIGURE 2. Temperature Regime for Snively Springs

0.07 m^3/s during the winter. Midday dissolved oxygen concentrations ranged from 8.2 mg/l during the summer to 10.1 mg/l in midwinter. The temperature regime for Rattlesnake Springs during the study period is shown in Figure 3, and stream substrate composition is shown in Table 1.

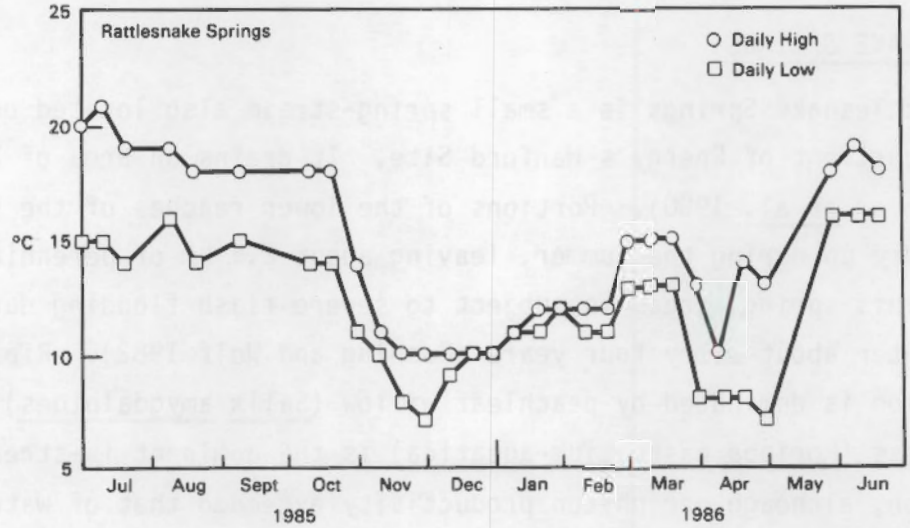

FIGURE 3. Temperature Regime for Rattlesnake Springs

METHODS

I used a stratified random sampling regime (as recommended by Cummins 1962) in each stream to assure that all habitats were sampled. One study site was established in each of Snively Springs and Rattlesnake Springs, with each study site being large enough to include all habitat types. Three study sites were established in Douglas Creek: a shallow riffle (Site 1), a midsize pool and riffle (Site 2), and a large slow pool (Site 3).

Samples were taken at monthly intervals from July 1985 through June 1986. I collected three Surber samples (0.093 m^2/sample) from Snively Springs and Rattlesnake Springs on each sampling date. A Surber sampler was used because these spring-streams are very shallow. A Portable Invertebrate Box Sampler (0.1 m^2/sample) was used at Douglas Creek to collect one sample from Site 1, two samples from Site 2, and two samples from Site 3 on each sampling date. Fewer samples were collected from Site 1 because it was located in the upper reaches where streamflow was reduced. Douglas Creek is larger than the other study streams so the more efficient Portable Invertebrate Box Sampler was used. All samples were taken to a minimum depth of 10 cm and preserved in 70% ETOH for later lab analysis.

I separated insects from organic debris by sugar flotation (Anderson 1959) and sorted them into taxa. Insects were identified to the species level when possible, counted, and body length measured to the nearest 1 mm using a microscope equipped with an ocular micrometer. The trophic status of each species was determined by reference to Merritt and Cummins (1984) and examination of gut contents. Biomass [dry wt (DW)] was determined for all size classes after insects were dried at 60°C for 24 hours and weighed to the nearest 0.1 mg. I calculated the mean coefficient of variation (CV) and the mean standard error (SE) for all density and biomass estimates.

The SF method (Hynes and Coleman 1968, Hamilton 1969, Hynes 1980, Waters and Hokenstrom 1980) was used to estimate secondary production of

the most common benthic insect species. An average size-frequency distribution was determined from monthly sample sets that represented the survivorship curve of an "average cohort" (Hamilton 1969, Benke and Waide 1977). Production was estimated by calculating the difference in biomass between successive size classes and then multiplying this difference by the number of size classes (Hynes and Coleman 1968, Hamilton 1969). Production estimates were refined by multiplying by 365/CPI (Cohort Production Interval) (Benke 1979). The CPI (Benke et al. 1984) was estimated from life history data, field observations, and in situ growth studies.

Production/biomass (P/B) ratios were used to estimate secondary production for less abundant taxa. These P/B ratios were either species-specific values derived from one of the other two 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 size-frequency distribution curve that is necessary to compute size-frequency production estimates.

RESULTS

INSECT DENSITY AND BIOMASS

Douglas Creek

Optioservus sp. (riffle beetles) and Baetis sp. (mayflies) were by far the most abundant insects found in Douglas Creek. These taxa accounted for 72% of the total insect numbers and 50% of the total biomass. Annual mean density and biomass of Optioservus sp. were $4322/m^2$ and 606.7 mg DW/m^2, respectively. Annual mean density and biomass of Baetis sp. were $2416/m^2$ and 263.7 mg DW/m^2, respectively (Table 2).

Snively Springs

Baetis sp. (mayflies) were the most numerous insects in Snively Springs, accounting for 42% of the total insect numbers and 25% of the total biomass. Annual mean density was $1388/m^2$ and the annual mean biomass was 185.4 mg DW/m^2 (Table 3).

Rattlesnake Springs

The most abundant insects in Rattlesnake Springs were Simulium sp. (blackflies) and Baetis sp. (mayflies). These taxa accounted for 74% of the total insect numbers and 55% of the total biomass. Annual mean density and biomass of Simulium sp. were $1777/m^2$ and 212.3 mg DW/m^2, respectively. Annual mean density and biomass of Baetis sp. were $1336/m^2$ and 47.3 mg DW/m^2, respectively (Table 4).

FUNCTIONAL GROUP DENSITY AND BIOMASS

Results of gut content analysis and subsequent functional group classification for insects from Douglas Creek, Snively Springs, and Rattlesnake Springs are shown in Tables 5, 6, and 7, respectively.

Douglas Creek

The most abundant functional groups in Douglas Creek were grazer-scrapers (49%) and collectors (48%). These groups accounted for 97% of

TABLE 2. Annual Mean Density and Biomass of Insects from Douglas Creek (SE = standard error, CV = coefficient of variation)

Taxa	Density (no./m^2)	SE/$\bar{X}$	CV	Biomass (mg/m^2)	SE/$\bar{X}$	CV
Diptera						
Simulium sp.	41	0.75	168.6	31.2	0.72	136.1
Brilla flavifrons	12	0.25	55.0	0.9	0.26	57.4
Chironomus sp.	753	0.71	152.3	60.7	0.69	153.8
Parametriocnemus sp.	196	0.44	98.0	10.4	0.46	101.9
Thienemannimyia sp.	11	0.81	180.5	0.9	0.83	185.4
Chaetocladius sp.	115	0.57	127.8	3.5	0.66	129.4
Polypedilum sp.	33	0.69	154.5	2.2	0.78	129.1
Heleniella sp.	141	0.52	116.4	4.5	0.54	116.5
Phaenospectra sp.	60	0.07	15.5	4.9	0.07	15.0
Tabanidae	51	0.48	106.6	27.8	0.48	107.5
Tipulidae	37	0.37	82.5	82.1	0.48	103.1
Empididae	1	0.22	50.0	0.1	0.18	40.0
(TOTAL)	(1451)			(229.2)		
Trichoptera						
Leucotrichia pictipes	95	0.63	139.7	7.7	0.68	153.2
Hydropsyche sp.	445	0.57	127.1	413.5	0.65	145.8
Cheumatopsyche sp.	156	0.53	118.3	84.1	0.60	135.0
(TOTAL)	(696)			(505.3)		
Coleoptera						
Optioservus sp.	4322	0.37	83.5	606.7	0.36	80.0
Ephemeroptera						
Leucrocuta sp.	160	0.47	104.0	51.4	0.51	104.0
Baetis sp.	2416	0.41	92.4	263.7	0.41	91.9
Paraleptophlebia sp.	225	0.35	78.5	48.1	0.38	85.4
Tricorythodes sp.	6	0.80	159.2	1.7	0.67	151.0
(TOTAL)	(2807)			(364.9)		
Odonata						
Argia tibialis	30	0.46	103.9	8.9	0.49	110.3
Plecoptera						
Isoperla sp.	77	0.58	129.4	42.8	0.58	113.9
(GRAND TOTAL)	(9383)			(1757.8)		

TABLE 3. Annual Mean Density and Biomass of Insects from Snively Springs (SE = standard error, CV = coefficient of variation)

Taxa	Density (no./m^2)	SE/$\bar{X}$	CV	Biomass (mg/m^2)	SE/$\bar{X}$	CV
Diptera						
Simulium sp.	276	0.70	121.3	34.3	0.82	142.6
Chaetocladius sp.	92	0.63	108.3	2.7	0.69	120.2
Chironomus sp.	412	0.54	93.2	17.1	0.58	99.8
Heleniella sp.	381	0.40	69.2	9.2	0.37	64.7
Polypedilum sp.	123	0.56	96.2	3.2	0.52	89.1
Thienemannimyia sp.	18	0.42	72.3	1.1	0.33	57.3
Dixidae	21	0.55	95.9	1.3	0.65	111.5
Tabanidae	52	0.47	81.5	10.5	0.50	86.4
Tipulidae	25	0.60	103.8	219.2	0.50	87.4
Empididae	4	0.15	26.6	0.6	0.12	32.1
(TOTAL)	(1404)			(299.2)		
Trichoptera						
Cheumatopsyche sp.	433	0.41	83.0	200.9	0.51	86.9
Ephemeroptera						
Baetis sp.	1388	0.62	104.7	185.4	0.55	96.3
Paraleptophlebia sp.	54	0.27	47.5	15.5	0.28	48.2
(TOTAL)	(1442)			(200.9)		
Odonata						
Argia tibialis	22	0.61	106.6	27.8	0.68	118.6
(GRANO TOTAL)	(3301)			(728.8)		

the total insect numbers and 90% of the total biomass. Annual mean density and biomass of grazer-scrapers was 4637/m^2 and 670.7 mg DW/m^2, respectively. Annual mean density and biomass of collectors was 4494/m^2 and 917.9 mg DW/m^2, respectively (Table 8).

Snively Springs

Collectors were by far the most abundant functional group in Snively Springs, accounting for 93% of the total insect numbers and

TABLE 4. Annual Mean Density and Biomass of Insects from Rattlesnake Springs (SE = standard error, CV = coefficient of variation)

Taxa	Density (no./m^2)	SE/$\bar{X}$	CV	Biomass (mg/m^2)	SE/$\bar{X}$	CV
Diptera						
Simulium sp.	1777	0.73	125.8	212.3	0.73	127.5
Chironomus sp.	192	0.50	87.3	7.0	0.58	100.8
Thienemannimyia sp.	114	0.55	94.9	3.3	0.55	95.2
Chaetocladius sp.		0.73	126.4	0.4	0.56	97.7
Heleniella sp.	352	0.51	89.0	5.4	0.51	88.4
Polypedilum sp.	13	0.62	108.2	0.6	0.46	78.9
Misc. Chironomidae	18	0.29	50.1	0.8	0.38	66.3
Dixidae	2	0.28	64.7	0.1	0.29	50.0
Tabanidae	34	0.51	85.6	15.9	0.64	111.0
Tipulidae	3	0.21	35.9	2.0	0.26	44.3
Empididae	8	0.39	68.3	0.4	0.23	39.8
(TOTAL)	(2572)			(248.2)		
Trichoptera						
Cheumatopsyche sp.	140	0.69	118.9	48.6	0.78	134.5
Limnephilus sp.	52	0.45	76.9	22.0	0.38	66.3
Parapsyche sp.	10	0.24	41.7	26.8	0.25	43.4
(TOTAL)	(202)			(98.3)		
Coleoptera						
Hydaticus sp.	4	0.50	87.4	1.2	0.35	60.1
Hydrophilidae	1	0.27	47.6	0.3	0.25	43.1
(TOTAL)	(5)			(1.5)		
Ephemeroptera						
Baetis sp.	1336	0.61	107.2	47.3	0.58	104.0
Tricorythodes sp.	1	0.05	8.3	0.3	0.07	12.2
(TOTAL)	(1337)			(47.6)		
Odonata						
Argia tibialis	67	0.72	124.1	74.3	0.78	134.9
(GRAND TOTAL)	(4183)			(469.9)		

TABLE 5. Results of Qualitative Gut Content Analysis and Subsequent Functional Group and Trophic Level Classification for Insects from Douglas Creek (N = number of guts examined)

Taxa	N	Gut Content	Functional Group	Trophic Level
Diptera				
Simulium sp.	14	detritus	coll-gath	detritivore
Brilla flavifrons[a]			shredder	detritivore
Chiromonus sp.	21	detritus/ some algae	coll-gath	detritivore
Parametriocnemus sp.	14	detritus/ some algae	coll-gath	detritivore
Thienemannimyia sp.[a]			predator	carnivore
Chaetocladius sp.	10	detritus	coll-gath	detritivore
Polypedilum sp.[a]			shredder	herbivore
Heleniella sp.	10	detritus	coll-gath	detritivore
Phaenospectra sp.[a]			scraper	herbivore
Tabanidae[a]			predator	carnivore
Tipulidae[a]			shredder	detritivore
Empididae[a]			predator	carnivore
Trichoptera				
Leucotrichia pictipes	17	algae/some detritus	scraper	herbivore
Hydropsyche sp.	45	detritus	coll-filt	detritivore
Cheumatopsyche sp.	16	detritus	coll-filt	detritivore
Coleoptera				
Optioservus sp.	50	algae/some detritus	scraper	herbivore
Ephemeroptera				
Leucrocuta sp.	44	algae/some detritus	scraper	herbivore
Baetis sp.	51	detritus/ some algae	coll-gath	detritivore
Paraleptophlebia sp.	44	detritus/ some algae	coll-gath	detritivore
Tricorythodes sp.	7	detritus/ some algae	coll-gath	detritivore
Odonata				
Argia tibialis[a]			predator	carnivore
Plecoptera				
Isoperla sp.	26	animal-tissue	predator	carnivore

(a) Classifications based upon literature only (Merritt and Cummins 1984).

TABLE 6. Results of Qualitative Gut Content Analysis and Subsequent Functional Group and Trophic Level Classification of Insects from Snively Springs (N = number of guts analyzed)

Taxa	N	Gut Content	Functional Group	Trophic Level
Diptera				
Simulium sp.	43	detritus	coll-filt	detritivore
Chaetocladius sp.[a]			coll-gath	detritivore
Chironomus sp.	14	detritus/ some algae	coll-gath	detritivore
Heleniella sp.	14	detritus/ some algae	coll-gath	detritivore
Polypedilum sp.[a]			shredder	herbivore
Thienemannimyia sp.[a]			predator	carnivore
Dixidae[a]			coll-gath	detritivore
Tabanidae[a]			predator	carnivore
Tipulidae[a]			shredder	detritivore
Empididae[a]			predator	carnivore
Trichoptera				
Cheumatopsyche sp.	41	detritus	coll-filt	detritivore
Ephemeroptera				
Baetis sp.	36	detritus	coll-gath	detritivore
Paraleptophlebia sp.	10	detritus	coll-gath	detritivore
Odonata				
Argia tibialis	11	animal-tissue	predator	carnivore

(a) Classifications based upon literature only (Merritt and Cummins 1984).

64% of the total biomass. Annual mean density was 3057/m^2 and the annual mean biomass was 466.4 mg DW/m^2. No grazer-scrapers were found in Snively Springs (Table 9).

Rattlesnake Springs

As in Snively Springs, collectors were the most abundant functional group in Rattlesnake Springs, accounting for 93% of the total insect

TABLE 7. Results of Qualitative Gut Content Analysis and Subsequent Functional Group and Trophic Level Classification of Insects from Rattlesnake Springs (N = number of guts analyzed)

Taxa	N	Gut Content	Functional Group	Trophic Level
Diptera				
Simulium sp.	47	detritus	coll-filt	detritivore
Chironomus sp.	14	detritus	coll-gath	detritivore
Thienemannimyia sp.[a]			predator	carnivore
Chaetocladius sp.	7	detritus/ some algae	coll-gath	detritivore
Heleniella sp.	13	detritus/ some algae	coll-gath	detritivore
Polypedilum sp.[a]			shredder	herbivore
Misc. Chironomidae[a]			coll-gath	detritivore
Dixidae[a]			coll-gath	detritivore
Tabanidae[a]			predator	carnivore
Tipulidae[a]			shredder	detritivore
Empididae[a]			predator	carnivore
Trichoptera	37	algae/some detritus	coll-filt	detritivore
Cheumatopsyche sp.				
Limnephilus sp.	8	detritus	shredder	detritivore
Parapsyche sp.	7	detritus/ animal-tissue	coll-filt	detritivore
Coleoptera				
Hydaticus sp.[a]		predator	carnivore	
Hydrophilidae[a]			predator	carnivore
Ephemeroptera	36	detritus	coll-gath	detritivore
Baetis sp.				
Tricorythodes sp.[a]			coll-gath	detritivore
Odonata	42	animal-tissue	predator	carnivore
Argia tibialis				

(a) Classifications based upon literature only (Merritt and Cummins 1984).

TABLE 8. Annual Mean Density and Biomass of Insect Functional Groups in Douglas Creek

Functional Group	Density (no./m^2)	Composition (%)	Biomass (mg/m^2)	Composition (%)
Grazer-scraper	4637	49.4	670.7	38.2
Collector (TOTAL)	(4494)	(47.9)	(917.9)	(52.2)
Gatherer	3852	41.1	389.1	22.1
Filterer	642	6.8	528.8	30.1
Shredder	82	0.9	86.1	4.9
Predator	170	1.8	83.1	4.7
(GRAND TOTAL)	(9383)	(100.0)	(1757.8)	(100.0)

TABLE 9. Annual Mean Density and Biomass of Insect Functional Groups in Snively Springs

Functional Group	Density (no./m^2)	Composition (%)	Biomass (mg/m^2)	Composition (%)
Collector (TOTAL)	(3057)	(92.6)	(466.4)	(64.0)
Gatherer	2348	71.1	231.2	31.7
Filterer	709	21.5	235.2	32.3
Shredder	148	4.5	222.4	30.5
Predator	96	2.9	40.0	5.5
(GRAND TOTAL)	(3301)	(100.0)	(728.8)	(100.0)

numbers and 74% of the total biomass. Annual mean density and biomass of collectors was 3887/m^2 and 349.0 mg DW/m^2, respectively. Grazer-scrapers were absent from Rattlesnake Springs (Table 10).

TROPHIC LEVEL DENSITY AND BIOMASS

Trophic level classifications for insects from Douglas Creek, Snively Springs, and Rattlesnake Springs are shown in Tables 5, 6, and 7, respectively.

Douglas Creek

Herbivores (50%) and detritivores (48%) were the most abundant trophic levels in Douglas Creek. These trophic levels accounted for

TABLE 10. Annual Mean Density and Biomass of Insect Functional Groups in Rattlesnake Springs

Functional Group	Density (no./m^2)	Composition (%)	Biomass (mg/m^2)	Composition (%)
Collector (TOTAL)	(3887)	(92.9)	(349.0)	(74.3)
Gatherer	1960	46.9	61.3	13.1
Filterer	1927	46.1	287.7	61.2
Shredder	68	1.6	25.5	5.4
Predator	228	5.5	95.4	20.3
(GRAND TOTAL)	(4183)	(100.0)	(469.9)	(100.0)

98% of the total insect numbers and 95% of the total biomass. Annual mean density and biomass of herbivores was 4670/m^2 and 672.9 mg DW/m^2, respectively. The annual mean density and biomass of detritivores was 4543/m^2 and 1004.4 mg DW/m^2, respectively (Table 11).

Snively Springs

Detritivores were by far the most abundant trophic level in Snively Springs, accounting for 93% of the total insect numbers and 94% of the total biomass. Annual mean density was 3082/m^2 and the annual mean biomass was 685.6 mg DW/m^2 (Table 12).

Rattlesnake Springs

Detritivores were the most abundant trophic level in Rattlesnake Springs. Detritivores comprised 94% of the total insect numbers and 80% of the total biomass. Annual mean density was 3942/m^2 and the annual mean biomass was 373.9 mg DW/m^2 (Table 13).

TABLE 11. Annual Mean Density and Biomass of Insect Trophic Levels in Douglas Creek

Trophic Level	Density (no./m^2)	Composition (%)	Biomass (mg/m^2)	Composition (%)
Herbivore	4670	49.8	672.9	38.3
Detritivore	4543	48.4	1004.4	57.1
Carnivore	170	1.8	80.5	4.6
(GRAND TOTAL)	(9383)	(100.0)	(1757.8)	(100.0)

TABLE 12. Annual Mean Density and Biomass of Insect Trophic Levels in Snively Springs

Trophic Level	Density (no./m^2)	Composition (%)	Biomass (mg/m^2)	Composition (%)
Herbivore	123	3.7	3.2	0.4
Detritivore	3082	93.4	685.6	94.1
Carnivore	96	2.9	40.0	5.5
(GRAND TOTAL)	(3301)	(100.0)	(728.8)	(100.0)

TABLE 13. Annual Mean Density and Biomass of Insect Trophic Levels in Rattlesnake Springs

Trophic Level	Density (no./m^2)	Composition (%)	Biomass (mg/m^2)	Composition (%)
Herbivore	13	0.3	0.6	0.1
Detritivore	3942	94.2	373.9	79.6
Carnivore	228	5.5	95.4	20.3
(GRAND TOTAL)	(4183)	(100.0)	(469.9)	(100.0)

INSECT PRODUCTION

Douglas Creek

Diptera--Previous studies have addressed the difficulties in obtaining accurate field estimates of blackfly larvae (Simuliidae) and midge larvae (Chironomidae) CPIs, and thus production estimates (Benke *et al*. 1984, Behmer and Hawkins 1986). Their small size, rapid turnover rate, high density, and diversity make accurate species-specific CPI estimates difficult. These same characteristics, however, make midges and blackflies very important to a stream community. In many streams these insects contribute a large percentage of the total community production because of their rapid development and high turnover rates.

Simulium sp. (blackflies) from Douglas Creek were not present in sufficient numbers to calculate a size-frequency (SF) production estimate. A P/B ratio of 54.0 was used to estimate production. This P/B ratio was calculated by using the SF method to average the P/B

ratios obtained for Simulium sp. in Snively Springs and Rattlesnake Springs. Blackfly production in Douglas Creek was 1638.2 mg DW/m^2/yr (Table 14).

Accurate CPI estimates for Chironomidae (midges) could not be obtained from field observations or SF distributions. Benke et al. (1984) provide an extensive review of literature concerning midge development times. Using these data and Mackey's (1977) laboratory growth studies, I feel that reasonable CPI estimates were derived.

Mackey (1977) reported larval development times of 21 days for Chironomus sp., 13 days for Polypedilum convictim, and 36 days for Phaenospectra flavipes at 15°C. To compensate for slightly lower average temperatures (13°C) in Douglas Creek, and environmental stress, I estimated CPIs of 25 days for Chironomus, 20 days for Polypedilum, and 40 days for Phaenospectra. For the remaining midge species I assumed a CPI of 25 days. Production estimates ranged from 67.5 mg DW/m^2/yr by Brilla flavifrons to 4922.8 mg DW/m^2/yr by Chironomus. Annual P/B ratios ranged from 45.0 by Phaenospectra to 121.7 by Chaetocladius. These P/B ratios seem high but are comparable to those reported in other studies when short CPIs were utilized (Benke et al. 1984, Jackson and Fisher 1986).

Tabanidae and Tipulidae were assumed to be univoltine with a development time of 1 year. This is consistent with Gray's (1981) estimate of a 1-year development time for Tabanus dorsifer (Tabanidae) in Sycamore Creek, Arizona. Empididae grew to a maximum size that was similar to many of the midges, therefore a CPI of 25 days was assumed. Table 14 shows production data for all dipterans in Douglas Creek.

Trichoptera--Leucotrichia pictipes (microcaddisfly) was univoltine, and as SF distributions and field observations indicated the larvae overwintered as a late instar and emerged as adults in the spring. This observation is supported by McAuliffe's (1982) studies on L. pictipes in Owl Creek, Montana. Production and the annual P/B ratio of Leucotrichia sp. in Douglas Creek were 32.0 mg DW/m^2/yr and 4.2, respectively.

TABLE 14. Annual Production of Insects from Douglas Creek, July 1985 to June 1986

Taxa	365/CPI	Calculation Method[a,b]	Production ($mg/m^2/yr$)	Annual P/B
Diptera				
Simulium sp.	12	PB	1638.2	54.0[c]
Brilla flavifrons	15	PB	67.5	75.0[d]
Chironomus sp.	15	PB	4922.8	81.1[c]
Parametriocnemus sp.	15	SF	874.5	84.1
Thienemannimyia sp.	15	PB	75.2	83.6[c]
Chaetocladius sp.	15	SF	426.0	121.7
Polypedilum sp.	18	SF	160.9	73.1
Heleniella sp.	15	SF	423.0	94.0
Phaenospectra sp.	9	PB	220.5	45.0[c]
Tabanidae	1	PB	130.0	5.0[c]
Tipulidae	1	PB	410.5	5.0[c]
Empididae	15	PB	7.5	75.0[c]
(TOTAL)			(9365.6)	
Trichoptera				
Leucotrichia pictipes	1	SF	32.0	4.2
Hydropsyche sp.	1	SF	1700.0	4.1
Cheumatopsyche sp.	2	SF	817.5	9.7
(TOTAL)			(2549.5)	
Coleoptera				
Optioservus sp.	1	SF	2162.7	3.6
Ephemeroptera				
Leucrocuta sp.	1	SF	237.8	4.6
Baetis sp.	6	SF	8316.5	31.5
Paraleptophlebia sp.	1	SF	249.4	5.2
Tricorythodes sp.	9	PB	76.5	45.0[c]
(TOTAL)			(8880.2)	
Odonata				
Argia tibialis	1	PB	44.3	5.0[c]
Plecoptera				
Isoperla sp.	1	SF	182.8	4.3
(GRAND TOTAL)			(23185.1)	

(a) PB = production calculated by an assumed P/B ratio.
(b) SF = production calculated by the size-frequency method.
(c) Assumed cohort P/B of 5.
(d) Assumed annual P/B is the same as derived by SF for this species in one of the other study streams.

Field observations and SF distributions of Hydropsyche sp. and Cheumatopsyche sp. indicated CPIs of 1 year and 6 months, respectively. Production and the annual P/B ratio of Hydropsyche sp. were 1700.0 mg DW/m^2/yr and 4.1, respectively. Production of Cheumatopsyche sp. was 817.5 mg OW/m^2/yr and the annual P/B ratio was 9.7. Total caddisfly production was 2549.5 mg DW/m^2/yr (Table 14).

Coleoptera-An accurate CPI estimate for Optioservus sp. (riffle beetles) was difficult to make because few data are available concerning their development times. Field data, though not clearcut, indicated a CPI of 1 year. Using this CPI estimate, production of riffle beetles was 2162.7 mg DW/m^2/yr and the annual P/B ratio was 3.6 (Table 14).

Ephemeroptera--Mayflies typically exhibit widely varied larval development times (Clifford 1982). I assumed Leucrocuta sp. (Heptageniidae) to be univoltine with a CPI of 1 year. Clifford (1982) examined life-cycle data of 85 species of Heptageniidae and found >90% had at least one univoltine life cycle. Production of Leucrocuta sp. was 237.8 mg DW/m^2/yr and the annual P/B ratio was 4.6.

Field data for Baetis sp. from Douglas Creek provided little clarification of their CPI. Based upon field observations of Baetis sp. from the other study streams, and a growth study in Rattlesnake Springs (Gaines, unpublished data), I estimated a CPI of 60 days. Temperature regimes were similar between study streams, making this estimation reasonable. Production of Baetis sp., 8316.5 mg DW/m^2/yr, was the highest of all insects from Douglas Creek. The annual P/B ratio was 31.5 (Table 14).

Paraleptophlebia sp. are generally univoltine, having either a summer or winter cycle (Clifford 1982). In Douglas Creek, however, seasonal cycles could not be distinguished. Since all Paraleptophlebia species have at least one univoltine cycle (Clifford 1982) and were present in Douglas Creek throughout the study year, I assumed a CPI of 1 year. Production was 249.4 mg DW/m^2/yr and the annual P/B ratio was 5.2 (Table 14).

Because of low numbers of Tricorythodes sp., field data provided little indication of their CPI. McCullough et al. (1979) reported a 34-day larval development time for Tricorythodes minutus grown in the field at 18°C. I estimated a CPI of 40 days for Tricorythodes sp. because of lower stream temperatures in Douglas Creek. A cohort P/B ratio of 5 was assumed to estimate production of 76.5 mg DW/m^2/yr (Table 14).

Odonata--Argia tibialis (damselflies) were univoltine and field data indicated a CPI of 1 year. I assumed a cohort P/8 ratio of 5.0 to estimate production of 44.3 mg DW/m^2/yr (Table 14).

Plecoptera--A CPI estimate for Isoperla sp. (stoneflies) could not be made from field data. I assumed a CPI of 1 year because stoneflies grew to a maximum size that was similar to damselflies. Production was 182.8 mg DW/m^2/yr and the annual P/B ratio was 4.3 (Table 14).

Snively Springs

Diptera--Field data and observations indicated a larval development time (CPI) of 30 days for Simulium sp. (blackflies) in Snively Springs. Becker (1973) reported a larval development time of 13 days for S. vittatum grown in the laboratory at 17°C. A 30-day CPI was a reasonable estimate when lower stream temperatures and environmental stress are considered. On this basis, production was 1878.7 mg DW/m^2/yr and the annual P/B ratio was 54.8 (Table 15).

The larval development times (CPIs) of Chironomidae (midges) in Snively Springs were estimated as they were in Douglas Creek. I assumed CPIs of 20 days for Polypedilum sp. and 25 days for all other midges. Production estimates ranged from 92.0 mg DW/m^2/yr by Thienemannimyia sp. to 1386.0 mg DW/m^2/yr by Chironomus sp. The P/B ratios ranged from 60.3 by Heleniella sp. to 83.6 by Thienemannimyia sp.

I assumed Tabanidae and Tipulidae to be univoltine with a CPI of 1 year (Gray 1981). Dixidae and Empididae reached maximum sizes that were very similar to many of the midges, and I assumed a CPI of 25 days. Table 15 shows the production data of all dipterans in Snively Springs.

TABLE 15. Annual Production of Insects from Snively Springs, July 1985 to June 1986

Taxa	365/CPI	Calculation Method[a,b]	Production ($mg/m^2/yr$)	Annual P/B
Diptera				
Simulium sp.	12	SF	1878.7	54.8
Chaetocladius sp.	15	SF	210.0	77.8
Chironomus sp.	15	SF	1386.0	81.1
Heleniella sp.	15	SF	550.0	60.3
Polypedilum sp.	18	SF	219.6	68.6
Thienemannimyia sp.	15	PB	92.0	83.6[c]
Dixidae	15	PB	97.5	75.0[d]
Tabanidae	1	PB	52.5	5.0[d]
Tipulidae	1	PB	1096.0	5.0[d]
Empididae	15	PB	45.0	75.0[d]
(TOTAL)			(5627.3)	
Trichoptera				
Cheumatopsyche sp.	2	SF	1297.9	6.5
Ephemeroptera				
Baetis sp.	6	SF	7011.6	37.8
Paraleptophlebia sp.	1	SF	67.0	4.3
(TOTAL)			(7078.6)	
Odonata				
Argia tibialis	1	PB	139.1	5.0[d]
(GRAND TOTAL)			(14142.9)	

(a) PB = production calculated by an assumed P/B ratio.
(b) SF = production calculated by the size-frequency method.
(c) Assumed cohort P/B of 5.
(d) Assumed annual P/B is the same as derived by SF for this species in one of the other study streams.

Trichoptera--Field observations and SF data indicated a bivoltine life cycle and a CPI of 6 months for *Cheumatopsyche* sp., the only caddisfly in Snively Springs. Production was 1297.9 mg $DW/m^2/yr$ and the annual P/B ratio was 6.5 (Table 15).

Ephemeroptera--Field observations and SF data indicated a CPI of 60 days for Baetis sp. in Snively Springs. Gray (1981) reported a larval development time of 20 days for Baetis quilleri in Sycamore Creek, Arizona. Due to lower stream temperatures, however, Baetis sp. developed more slowly in all of the streams in this study. Production by Baetis sp. was 7011.6 mg DW/m^2/yr and the annual P/B ratio was 37.8 (Table 15).

In Snively Springs, Paraleptophlebia sp. were present only during the summer. Thus, I used only data collected during the summer to calculate production. Production of Paraleptophlebia sp. was 67.0 mg DW/m^2/yr and the annual P/B ratio was 4.3 (Table 15).

Odonata--Argia tibialis were not present in sufficient numbers to make an SF production estimate. I assumed a cohort P/B ratio of 5 and a CPI of 1 year to estimate production of 139.1 mg DW/m^2/yr (Table 15).

Rattlesnake Springs

Diptera--Several Simulium sp. larvae were isolated in growth chambers in Rattlesnake Springs to estimate larval development time. These data and field observations indicated a CPI of 30 days. Production by blackflies, 11174.8 mg DW/m^2/yr, was the highest of all species in Rattlesnake Springs, and the annual P/B ratio was 52.6.

I estimated larval development times (CPIs) of Rattlesnake Springs Chironomidae as I did in the other study streams. CPIs of 20 days for Polypedilum sp. and 25 days for all other midges were assumed. Production estimates ranged from 30.0 mg DW/m^2/yr by Chaetocladius sp. to 489.0 mg DW/m^2/yr by Chironomus sp. Annual P/B ratios ranged from 68.6 by Polypedilum sp. to 83.6 by Thienemannimyia sp.

Tabanidae and Tipulidae were assumed to be univoltine with CPIs of 1 year (Gray 1981). Dixidae and Empididae grew to maximum sizes similar to many of the midges and CPIs of 25 days were assumed. Table 16 shows the production data of all dipterans from Rattlesnake Springs.

Trichoptera--I isolated several Cheumatopsyche sp. larvae in growth chambers in Rattlesnake Springs to estimate larval development time. These data indicated a bivoltine life cycle and a CPI of 6 months. Production by caddisflies in Rattlesnake Springs was 486.0 mg DW/m^2/yr and the annual P/B ratio was 10.0 (Table 16).

Because of low densities, field data gave no indication of the CPIs of Limnephilus sp. or Parapsyche sp. To estimate their production, I assumed a CPI of 1 year and a cohort P/B ratio of 5. Production was 114.6 mg DW/m^2/yr by Limnephilus sp. and 133.8 mg DW/m^2/yr by Parapsyche sp. (Table 16).

Coleoptera--Field data provided little indication of the CPIs of beetles (coleopterns) because of low numbers. To estimate production, I assumed a CPI of 1 year and a cohort P/B ratio of 5. Production by Hydaticus sp. was 6.0 mg DW/m^2/hr (Table 16). Production by Hydrophilidae was 1.5 mg DW/m^2/yr (Table 16).

Ephemeroptera--I isolated several Baetis sp. larvae in growth chambers in Rattlesnake Springs to estimate larval development time. These data and field observations indicated a CPI of 60 days. Production by Baetis sp. was 2542.3 mg DW/m^2/yr and the annual P/B ratio was 53.8 (Table 16).

Tricorythodes sp. were not present in sufficient numbers for an SF production estimate. I assumed a cohort P/B ratio of 5 and a CPI of 40 days (McCullough et al. 1979) to calculate production of 13.5 mg DW/m^2/yr (Table 16).

Odonata--Field observations of Argia tibialis indicated a CPI of 1 year, and I assumed a cohort P/B ratio of 5 to calculate production. Production by damselflies in Rattlesnake Springs was 371.6 mg DW/m^2/yr (Table 16).

FUNCTIONAL GROUP PRODUCTION

Production by collectors was the highest of all functional groups in all study streams. Collector production was highest in Douglas Creek

TABLE 16. Annual Production of Insects from Rattlesnake Springs, July 1985 to June 1986

Taxa	365/CPI	Calculation Method[a,b]	Production ($mg/m^2/yr$)	Annual P/B
Diptera				
Simulium sp.	12	SF	11174.8	52.6
Chironomus sp.	15	SF	489.0	69.9
Thienemannimyia sp.	15	SF	279.0	83.6
Chaetocladius sp.	15	SF	30.0	75.0[c]
Heleniella sp.	15	SF	480.0	88.9
Polypedilum sp.	18	PB	41.2	68.6[d]
Miscellaneous Chironomidae	15	PB	60.0	75.0[c]
Dixidae	15	PB	7.5	75.0[c]
Tabanidae	1	PB	79.5	5.0[c]
Tipulidae	1	PB	10.0	5.0[c]
Empididae	15	PB	30.0	75.0[c]
(TOTAL)			(12681.0)	
Trichoptera				
Cheumatopsyche sp.	2	SF	486.0	10.0
Limnephilus sp.	1	PB	114.6	5.0[c]
Parapsyche sp.	1	PB	133.8	5.0[c]
(TOTAL)			(734.4)	
Coleoptera				
Hydaticus sp.	1	PB	6.0	5.0[c]
Hydrophilidae	1	PB	1.5	5.0[c]
(TOTAL)			(7.5)	
Ephemeroptera				
Baetis sp.	6	SF	2542.3	53.8
Tricorythodes sp.	9	PB	13.5	45.0[c]
(TOTAL)			(2555.8)	
Odonata				
Argia tibialis	1	PB	371.6	5.0[c]
(GRAND TOTAL)			(16350.3)	

(a) PB = production calculated by an assumed P/B ratio.
(b) SF = production calculated by the size-frequency method.
(c) Assumed cohort P/B of 5.
(d) Assumed annual P/B is the same as derived by SF for this species in one of the other study streams.

at 19444.4 mg DW/m^2/yr, accounting for 84% of the total annual production. In Snively Springs, collector production was 12498.7 mg DW/m^2/yr, comprising 88% of the total annual production. Production of collectors in Rattlesnake Springs was 15416.9 mg DW/m^2/yr, accounting for 94% of the total annual production. Table 17 shows the annual production by functional groups in each study stream.

TROPHIC LEVEL PRODUCTION

Detritivore production was the highest of all trophic levels in each study stream. In Douglas Creek, detritivore production was 19922.4 mg DW/m^2/yr, accounting for 86% of the total annual production. In Snively Springs detritivore production was 13594.7 mg DW/m^2/yr, accounting for 96% of the total annual production. Detritivore production in Rattlesnake Springs was 15541.5 mg DW/m^2/yr, accounting for 95% of the total annual production. Table 18 shows the annual production by trophic levels in each study stream.

TABLE 17. Annual Production of Insect Functional Groups in Douglas Creek, Snively Springs, and Rattlesnake Springs

Functional Group	Douglas Creek (mg/m^2/yr)	(%)	Snively Springs (mg/m^2/yr)	(%)	Rattlesnake Springs (mg/m^2/yr)	(%)
Grazer-Scraper	2653.0	11.4	0.0	0.0	0.0	0.0
Collector						
(TOTAL)	(19444.4)	(83.9)	(12498.7)	(88.4)	(15416.9)	(94.3)
Gatherer	15288.7	66.0	9322.1	65.9	3622.3	22.2
Filterer	4155.7	17.9	3176.6	22.5	11794.6	72.1
Shredder	638.9	2.8	1315.6	9.3	165.8	1.0
Predator	448.8	1.9	328.6	2.3	767.6	4.7
(GRAND TOTAL)	(23185.1)	(100.0)	(14142.9)	(100.0)	(16350.3)	(100.0)

TABLE 18. Annual Production of Insect Trophic Levels in Douglas Creek, Snively Springs, and Rattlesnake Springs

Trophic Level	Douglas Creek ($mg/m^2/yr$)	(%)	Snively Springs ($mg/m^2/yr$)	(%)	Rattlesnake Springs ($mg/m^2/yr$)	(%)
Herbivore	2813.9	12.2	219.6	1.6	41.2	0.3
Detritivore	19922.4	85.9	13594.7	96.1	15541.5	95.0
Carnivore	448.8	1.9	328.6	2.3	767.6	4.7
(GRAND TOTAL)	(23185.1)	(100.0)	(14142.9)	(100.0)	(16350.3)	(100.0)

DISCUSSION

ESTIMATING SECONDARY PRODUCTION

Benke *et al.* (1984) attempted to describe a methodological framework for other investigators to follow when estimating secondary production. They stressed the importance and difficulty of accurately estimating the CPI of each taxon within a benthic community. They suggested using laboratory growth data and life history data when direct field data were not available. I followed their framework when estimating secondary production. Many of my CPI estimates are based upon a review of the literature because of a lack of direct field data. These estimates may be refined as the body of information grows concerning larval development times of aquatic invertebrates. I have stated all assumptions clearly to aid investigators in this process.

Benke *et al.* (1984) also stressed the importance and value of estimating secondary production. They stated that production analysis, more than density or biomass, is the most meaningful way to analyze functional feeding groups in natural ecosystems. They then provided an example where the importance of gathering-collector invertebrates was underestimated by biomass analysis and overestimated by density analysis (e.g. in Douglas Creek, grazer-scraper importance was overestimated and collector importance was underestimated). My work provides another example of the importance of estimating secondary production to accurately describe the roles of organisms in streams and to understand ecosystem dynamics.

COMPARISON BETWEEN STUDY STREAMS

Insect Faunas

Similarities occurred between the aquatic insect faunas in Douglas Creek, Snively Springs, and Rattlesnake Springs. Dipterans, midges, and blackflies were very important in all study streams and accounted for 40% to 70% of the total annual community production. Also, several insect taxa had short development times and multiple cohorts in each of

the study streams. Gray (1981) suggested that rapid development may be advantageous in streams subject to flash floods. Flash floods occur in all of the study streams [approximately every four years in Rattlesnake Springs (Cushing and Wolfe 1982)].

Functional Groups and Trophic Levels

The River Continuum Concept (RCC) provides a template to which various physical factors of a stream can be compared for predicting biotic responses (Vannote et al. 1980). An important factor affecting the stream biota is the amount of sunlight reaching the substrate for primary production. The amount of light is influenced by shading from riparian vegetation and instream autotrophs. The biota in Snively Springs and Rattlesnake Springs are greatly influenced by this interaction, as riparian vegetation and watercress shade much of the substrate. The substrate of Snively Springs and Rattlesnake Springs is mainly sand/silt (see Table 1), limiting the area available for algae to attach and grow. Based upon RCC assumptions, a lack of grazer-scrapers that rely on algae and periphyton as a food source would be expected. This occurred in Snively Springs and Rattlesnake Springs where grazer-scrapers were completely absent.

Douglas Creek, however, is larger and shading from riparian vegetation affected a smaller portion of the stream cross section. Watercress is limited to the stream banks, leaving more water open to receive sunlight. The substrate is rocky (see Table 1), which provides habitat for algae. As suggested by the RCC, grazer-scrapers are an important functional group.

The RCC predicts a significant proportion of shredders to be present when the riparian vegetation covers the stream and contributes large amounts of allochthonous detritus. However, shredders were of little importance in any of the streams I studied. The reasons for this are unclear and require further investigation. Cushing (in press) found the amount of allochthonous detritus entering these streams to be low, indicating a lack of food for shredders. Fisher and Gray (1983) found

that shredders were virtually absent from the Sonoran Desert stream, Sycamore Creek, as was their food source of large particulate organic matter.

Detritivores were dominant in all study streams, indicating a large dependence upon detritus as a food source. Collecting (filtering and gathering) was the major feeding strategy used to obtain detritus, and collectors generally consume Fine Particulate Organic Matter (FPOM) (Merritt and Cummins 1984). The conclusion can then be inferred that detritus in the form of FPOM was the major food source of the insects in these study streams. This conclusion is supported by the results of my analyses of gut contents and the results of Cushing and Rader (1982).

COMPARISON WITH OTHER STREAMS

Annual P/B ratios ranged from 3.6 to 121.7 for insects from the three 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 that I calculated for cold-desert 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. Their study streams are warmer and insect development occurs faster, resulting in a greater number of cohorts. The annual P/B ratios in my study were generally higher, however, than those reported by Krueger and Waters (1983) for northern temperate streams. Northern temperate streams are generally cooler and insect development occurs at a slower rate with fewer cohorts.

Community production rates ranged from 14 to 23 g $DW/m^2/yr$ in my three study streams. These rates are lower than the 50 to 70 g $DW/m^2/yr$ in southeastern blackwater streams (Nelson and Scott 1962, Benke *et al.* 1984), and much lower than in the Sonoran Desert stream, Sycamore Creek, where community production exceeded 120 g $DW/m^2/yr$ (Fisher and Gray 1983, Jackson and Fisher 1986). However, the rates reported here are

generally higher than the 5 to 15 g $DW/m^2/yr$ reported for northern temperate streams (Fisher and Likens 1973, Neves 1979, Krueger and Waters 1983).

CONCLUSIONS

In conclusion, I want to stress the most important findings of my investigation.

1) Taxa with short development times and multiple cohorts, such as midges and blackflies, are very important to cold-desert streams in terms of total production. This life history strategy may be advantageous in streams such as the ones I studied, where flash floods occur.

2) Insects in cold-desert streams depend largely on detritus as a food source and obtain it mainly by collecting (filtering and gathering).

3) Community production rates in cold-desert streams are generally higher than in northern temperate streams, lower than in southeastern blackwater streams, and much lower than in Sonoran Desert streams. Stream temperature is an important factor (maybe the most important) in controlling production rates and causing rates to differ across physiographic regions.

4) Investigators should calculate secondary production, not density or biomass, to accurately assess the roles of organisms in aquatic ecosystems. In Douglas Creek, for example, collector and grazer-scraper importance was misrepresented by density and biomass analysis.

5) The framework given by Benke *et al.* (1984) to estimate secondary production provides a workable process, and if followed in other studies, will make comparisons between streams more meaningful.

More research needs to be conducted on cold-desert streams before their ecology is fully understood. This study provides a significant piece to the complex puzzle of these unique ecosystems.

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APPENDIX

INSECTS FOUND IN DOUGLAS CREEK, SNIVELY SPRINGS, AND RATTLESNAKE SPRINGS

APPENDIX

INSECTS FOUND IN DOUGLAS CREEK, SNIVELY SPRINGS, AND RATTLESNAKE SPRINGS

DOUGLAS CREEK

- Diptera
  - Chironomidae
    - *Brilla flavifrons* sp.
    - *Chaetocladius* sp.
    - *Chironomus* sp.
    - *Heleniella* sp.
    - *Parametriocnemus* sp.
    - *Phaenospectra* sp.
    - *Polypedilum* sp.
    - *Thienemannimyia* sp.
  - Empididae
  - Simuliidae
    - *Simulium* sp.
  - Tabanidae
  - Tipulidae
- Trichoptera
  - Hydroptilidae
    - *Leucotrichia pictipes*
  - Hydropsychidae
    - *Cheumatopsyche* sp.
    - *Hydropsyche* sp.
- Coleoptera
  - Elmidae
    - *Optioservus* sp.

Ephemeroptera

Baetidae

Baetis sp.

Leptophlebiidae

Paraleptophlebia sp.

Heptageniidae

Leucrocuta sp.

Tricorythidae

Tricorythodes sp.

Odonata

Coenagrionidae

Argia tibialis

Plecoptera

Perlodidae

Isoperla sp.

SNIVELY SPRINGS

Diptera

Chironomidae

Chaetocladius sp.

Chironomus sp.

Heleniella sp.

Polypedilum sp.

Thienemannimyia sp.

Dixidae

Empididae

Simuliidae

Simulium sp.

Tabanidae

Tipulidae

Trichoptera
- Hydropsychidae
  - *Cheumatopsyche* sp.

Ephemeroptera
- Baetidae
  - *Baetis* sp.
- Leptophlebiidae
  - *Paraleptophlebia* sp.

Odonata
- Coenagrionidae
  - *Argia tibialis*

RATTLESNAKE SPRINGS

Diptera
- Chironomidae
  - *Chaetocladius* sp.
  - *Chironomus* sp.
  - *Heleniella* sp.
  - *Polypedilum* sp.
  - *Thienemannimyia* sp.
- Dixidae
- Empididae
- Simuliidae
  - *Simulium* sp.
- Tabanidae
- Tipulidae

Trichoptera
- Hydropsychidae
  - *Cheumatopsyche* sp.
  - *Parapsyche* sp.
- Limnephilidae
  - *Limnephilus* sp.

Coleoptera

- Dytiscidae
  - *Hydaticus* sp.
- Hydrophilidae

Ephemeroptera

- Baetidae
  - *Baetis* sp.
- Tricorythidae
  - *Tricorythodes* sp.

Odonata

- Coenagrionidae
  - *Argia tibialis*

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