SECONDARY PRODUCTION, EMERGENCE, AND EXPORT OF AQUATIC INSECTS OF A SONORAN DESERT STREAM[1]

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Abstract. Aquatic insect secondary production, emergence, and export of adults to the adjacent terrestrial ecosystem were assessed in Sycamore Creek, Arizona, by means of benthic sampling, emergence traps, and catch-nets that passively sampled adults falling into the stream. Annual secondary production was 120.9 ± 18.0 $g \cdot m^{-2} \cdot yr^{-1}$ and emergence was 23.1 $g \cdot m^{-2} \cdot yr^{-1}$ (in dry mass units). The ratio of annual emergence to annual production (E/P) varied among taxa and ranged from 2 to 29%. Chironomids comprised 48.2% of production and 59.7% of emergence and mayflies accounted for 45.9 and 19.2%, respectively. Approximately 3% of emergent insect biomass returned to the stream; thus 22.4 $g \cdot m^{-2} \cdot yr^{-1}$ was transferred to the adjacent terrestrial ecosystem. The transfer of a significant portion of aquatic insect biomass to the terrestrial habitat reduced insects available to stream insectivores while providing prey for insectivores in neighboring terrestrial ecosystems.

Key words: aquatic insects; desert; emergence; export; secondary production; stream.

INTRODUCTION

Terrestrial and aquatic ecosystems exchange nutrients and energy in the form of particulate and dissolved substances (Likens and Bormann 1974, Hynes 1975). Import of materials to streams (e.g., leaf litter) has been studied extensively, but less is known about export, for example as emigration of adult aquatic insects and amphibians. This export may be only a small fraction of total energy and nutrient budgets (Vallentyne 1952, Webster and Patton 1979) but can be critical to terrestrial predators that consume fish and larval (Davies 1976, Custer and Pitelka 1978) and adult aquatic insects (Orians 1966, Sjöberg and Danell 1982). Riparian communities often have higher animal diversity and density than adjoining terrestrial communities. This is a result of proximity of surface water, abundant and diverse food, and the heterogenous vegetative habitat of riparian zones (MacArthur 1964, Brinson et al. 1981). In southwestern United States, riparian faunas are not only extremely abundant and diverse (Carothers et al. 1974, Stamp 1978, Clark 1984), but extended availability of food and mild air temperature allow autumn and winter residents to remain active (O'Farrell et al. 1967, O'Farrell and Bradley 1970, Stamp and Ohmart 1979). Aquatic ecosystems contribute to the distinctiveness of the southwestern riparian zones by providing water and food to riparian inhabitants throughout the year.

Many aquatic insects emerge from the aquatic system after their metamorphosis into adults. Adults that fail to return to the aquatic system represent a loss of potential food to aquatic insectivores. At the same time, these emerging adults represent potential food for terrestrial insectivores of the stream corridor. The magnitude of aquatic–terrestrial interaction via adult aquatic insects is thus inherently related to insect secondary production and emergence. We examined this interaction by estimating benthic macroinvertebrate secondary production, emergence, and net transfer of aquatic insect biomass from a desert stream to the adjacent riparian habitat.

MATERIALS AND METHODS

Study site

The study site is located at 640 m elevation on Sycamore Creek, an intermittent Sonoran Desert stream 32 km northeast of Phoenix, Arizona, USA. The 505-km² watershed is dominated by rugged, mountainous terrain. Like most intermittent desert streams, Sycamore Creek has predominately coarse sand and gravel substrates, warm water, and low summer discharge. In warm months surface flow is often restricted to areas where impervious bedrock forces water to the surface, where it flows for distances of a few metres to several kilometres before seeping into the sand. These isolated surface reaches are connected by long stretches of hyporheic flow. Winter discharge is usually higher and surface flow is continuous. Isolated storms in late summer and early autumn produce an average of two but up to nine flash floods annually. These floods scour the stream bed and remove biota in proportion to flood magnitude. Between floods, Sycamore Creek is typically 5–10 cm deep, 3–4 m wide, and has a mean current velocity of 0.15 m/s. Mean discharge fluctuates around 0.05 m³/s and water temperature ranges from 18° to 25°C in summer and 9° to 15° in winter.

Measurement of secondary production, emergence, and adult return

Secondary production and emergence were estimated for seven groups of aquatic insects (Chironomidae [14 species], *Baetis quilleri* Dodds [Baetidae], *Lepto-*

hyphes packeri Allen [Tricorythidae], *Tricorythodes dimorphus* Allen [Tricorythidae], *Helicopsyche mexicana* Banks [Helicopsychidae], *Cheumatopsyche arizonensis* [Ling] [Hydropsychidae], *Cryptolabis* sp. [Tipulidae]). Most are collector-detritivores, but *Helicopsyche mexicana* is a scraper-grazer and a few chironomids are predaceous. Species studied comprise 20 of the 99 insect species found in Sycamore Creek (Gray 1981) and represent 85% of biomass and numbers (Fisher et al. 1982) and an even greater proportion of species that exhibit emergence of adults.

Thirteen to fifteen benthic samples were taken biweekly to a depth of 10 cm with an 80-cm² coring device during periods of low flow (204 d of the study year). During the other 161 d, samples were taken at irregular intervals. Samples were taken in a random or stratified random pattern from a 150-m reach of Sycamore Creek. Immature insects were elutriated from the substrate through a 0.25-mm mesh, fixed in Kahle's fluid (Wiggins 1977), and later transferred to 70% aqueous ethanol. Immatures were sorted and counted, and their lengths measured to the nearest 1.0 mm. Individual masses for size classes and species were obtained from L. J. Gray (*personal communication*) and Smock (1980). Cohort length (development time from egg to adult) was 12 d except for *Cryptolabis* sp. (22 d), *Helicopsyche mexicana* (50 d), and *Cheumatopsyche arizonensis* (50 d). Secondary production (daily and annual) of immature insects was calculated using the size-frequency method (Hynes and Coleman 1968, Hamilton 1969, Benke 1979). Confidence intervals (95%) were computed for annual production estimates (Krueger and Martin 1980). Ratios of production to average standing biomass (cohort and annual P/B) were also calculated.

Emergence was sampled weekly with 452-cm² emergence traps constructed from plastic buckets with net tops (0.3-mm mesh). Sixteen traps placed in a random or stratified random pattern into the stream substrate remained in place for 24 h. Screens (0.3-mm mesh) on the sides of the traps allowed water to flow through the sampler, maintaining ambient oxygen level, temperature, and current. Ratios of emergence to production (cohort and annual E/P) were calculated. Secondary production, emergence, P/B, and E/P are reported by period and as annual rates with all mass values reported as dry mass unless otherwise indicated. This allows analysis of seasonal trends and variations in abundance not available from annual estimates alone.

Elutriation of benthic samples underestimated immature densities of the stone-cased caddisfly *Helicopsyche mexicana*. These density underestimates do not affect estimates of emergence or cohort and annual P/B, because P and B are underestimated by equal proportions (Waters 1977), but render production and E/P meaningless for this taxon; thus, *H. mexicana* data are excluded from E/P discussions.

Adult return was estimated with two 1.0-m² catch-nets placed randomly in the stream near emergence traps. Catch-nets of 0.3-mm mesh netting on a wooden frame permitted current to flow through the net, prevented insect loss, and minimized possible sampling errors from insect avoidance. Catch-nets passively sampled adults falling into the stream, in a manner similar to litterfall traps. After 24 h, captured insects were collected and preserved in 70% ETOH.

RESULTS

Characteristics of sampling periods

Based on an analysis of stream discharge and insect abundance, the sampling year was divided into four unequal periods (Fig. 1, Table 1). Rapid development and continuous reproduction resulted in multiple cohorts (1–8 cohorts per period) and continuously changing insect densities (Fig. 1). Period I started on 1 September 1982 and was a period of recolonization from flash floods occurring in late August and during period I. A flash flood ended period I and initiated period II. Unusually heavy precipitation during period II resulted in high and fluctuating discharge in Sycamore Creek. Unstable, shifting substrates associated with high discharge slowed or halted benthic recolonization and permitted only qualitative observations of the abundance of adult and immature insects (Jackson 1984). For calculations, densities of adults and immatures were assumed to be zero during this period, although low densities were in fact present. Period III began when winter flooding stopped and discharge dropped to a level permitting recolonization; we then resumed quantitative sampling of stream benthos. Dramatic, unexplained decreases in abundances of insects, the alga *Cladophora glomerata* (Chlorophyta), and FPOM were first recognized on 18 July 1983 and marked the end of period III. Recovery from the drastic alteration in benthos that initiated period IV was slowed by three minor flash floods that changed stream substrates substantially and reduced insect abundances. Period IV ended 365 d after period I began.

Abundances of aquatic insects

Aquatic insect community structure (species richness and evenness) varied among periods. Chironomids were present throughout the year and were especially abundant during periods I and III (Fig. 1). Greatest immature chironomid density was in period III (68 817 individuals/m²) while chironomid emergence was greatest in period I (2690 individuals·m⁻²·d⁻¹). The tipulid *Cryptolabis* sp. was numerous in late summer and autumn, especially after flash floods, but rare at other times (Fig. 1).

Three mayfly taxa were abundant in periods III and IV, but temporal overlap for these populations was limited. *Baetis quilleri* immatures were common in period III, although emergence was erratic (Fig. 1). Abundance of *Tricorythodes dimorphus* peaked at the
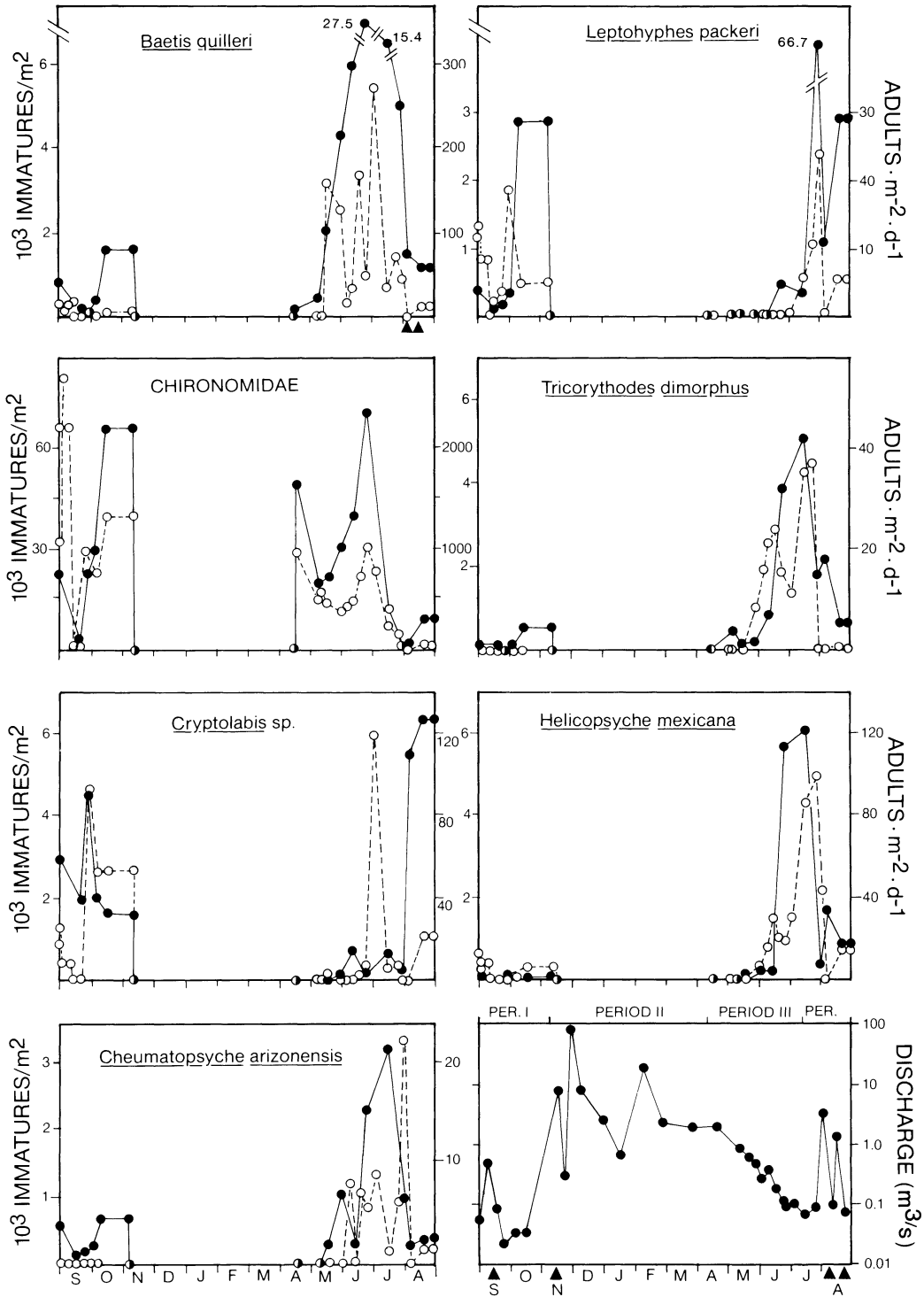
FIG. 1. Immature standing stock (●, left ordinate of each graph) and adult emergence (○, right ordinate of each graph) for each of seven taxa in Sycamore Creek, September 1982–August 1983. Stream discharge for the same interval is shown in lower right figure; flash floods are indicated by ▲ on this abscissa scale. Coefficient of variation (CV = 100%·standard deviation/mean) of immature density ranged from 13.9 to 386.5% and averaged ≈107%. For adult emergence CV's ranged from 39.8 to 399.5%, averaging 170.0%. For both parameters, CV's were generally lowest for chironomids.

TABLE 1.   Selected physical parameters for periods I–IV (1 September 1982–1 September 1983) in Sycamore Creek.

Period	Dates	Water temperature (°C)	Low flow discharge (m³/s)	Low flow stream width (m)	Flash flood discharge (m³/s)
I	1 Sep–9 Nov 1982	20–25	0.02–0.45	1.9–3.0	20
II	10 Nov 1982–18 Apr 1983	9–15	1.0–3.0	5.0–10.0	50–100
III	19 Apr–18 Jul 1983	15–25	0.06–0.53	3.5–8.0	none
IV	19 Jul–1 Sep 1983	19–24	0.07–0.09	2.8–3.2	1.3–2.6

end of period III and decreased through period IV (Fig. 1). *Leptohyphes packeri* was found in the stream during periods I and IV (Fig. 1). A large population of *L. packeri* (66 688 immatures/m²) was devastated by floods in period IV, but reestablishment was rapid. Two other mayfly species (*Baetis insignificans* [McDunnough] and *Callibaetis montanus* [Eaton]) appeared briefly and in low densities during period III.

Two caddisfly species, *Helicopsyche mexicana* and *Cheumatopsyche arizonensis*, were found in the stream during all periods but became abundant only in June and July (Fig. 1). Flash floods in periods I and IV reduced densities of these two populations.

Daily production and emergence

Numbers of immatures and adults were converted into average production and emergence (daily and cohort) for each period and were used to calculate indices describing population dynamics and metabolism (cohort P/B and E/P) for each taxon. Both total daily production and total daily emergence were similar among the periods when quantitative data were gathered (periods I, III, and IV), but contributions of the various taxa to these rates varied among those periods. Chironomids were abundant and productive in periods I, III, and IV, while mayflies made important contributions to total production only in periods III and IV (Table 2). Chironomids dominated emergence in periods I and III and were important in period IV (Table 2). *Helicopsyche mexicana* and mayflies made significant contributions to emergence in periods III and IV. High secondary production was not always followed by high emergence. This resulted in variation among taxa in the ratio of emergence to production (see Table 3). Therefore the aquatic insect community as indicated by numbers of immatures or production of immatures differed from the aquatic insect community reflected in emergence of adults.

Cohort P/B varied little among and within species (range = 3.1 to 4.8) with three exceptions. Flash floods changed the shapes of survivorship curves for *Leptohyphes packeri* and *Tricorythodes dimorphus* in period I and *L. packeri* in period IV, which elevated cohort P/B to ≈ 8 (Table 3). Cohort E/P, unlike cohort P/B, varied greatly depending on period and species (Table 3). Differences in E/P among periods may have been a function of the physical and biotic conditions associated with each period. For example, flash floods in August removed insect biomass prior to emergence and lowered E/P.

Annual production and emergence

During the sampling year (1 September 1982–1 September 1983), Sycamore Creek received above-average precipitation, experienced five flash floods between April and November, and sustained high discharge for 161 d. Still, annual secondary production (dry mass) was very high, 121 g·m⁻²·yr⁻¹ (Table 4). Chironomids were dominant, comprising 48.2% of production, while three mayflies accounted for an additional 45.4%. Total emergence was 23.1 g·m⁻²·yr⁻¹, of which 59.7% was chironomids and 19.2% mayflies, largely *Baetis quilleri*. *Helicopsyche mexicana* accounted for 13.7% of emergence.

Average standing stock biomass used for calculation of annual P/B includes an assumed winter benthic density of 0.0. Inclusion of zero densities reduced mean standing biomass and increased annual P/B, but is the conventional procedure according to Waters (1969, 1977, 1979). Annual P/B's reported here are often >100

TABLE 2.   Average daily production and emergence of Sycamore Creek aquatic insects (dry mass) during periods (see Table 1 for dates) I, III, and IV.

Taxon	Production (mg·m⁻²·d⁻¹)			Emergence (mg·m⁻²·d⁻¹)		
	I	III	IV	I	III	IV
Baetis quilleri	19.1	162.2	77.2	1.4	27.3	8.5
Leptohyphes packeri	34.4	7.3	348.0	2.4	0.2	3.1
Tricorythodes dimorphus	26.6	109.6	115.5	0.0	8.2	8.4
Chironomidae	309.2	364.7	75.8	93.4	73.7	13.1
Other taxa*	28.4	19.3	79.5	14.6	21.0	39.9
Total	417.7	663.1	696.0	111.8	130.4	73.0

* Includes *Helicopsyche mexicana*.

TABLE 3. Ratios of average cohort production to average standing biomass (P/B), and average cohort emergence to production (E/P), for selected Sycamore Creek aquatic insects. Cohort length (development time from egg to adult) was ≈ 12 d in all taxa.

Taxon	Cohort P/B			Cohort E/P (%)		
	I	III	IV	I	III	IV
Baetis quilleri	4.5	3.7	4.7	7.3	16.8	11.0
Leptohyphes packeri	7.8	3.9	8.4	7.0	2.4	0.9
Tricorythodes dimorphus	8.1	3.5	4.8	0.0	7.5	7.3
Chironomidae	4.7	3.7	3.1	30.4	20.2	17.3

(Table 4) and differ from those of Fisher and Gray (1983) because of our inclusion of zero densities in winter.

The relationship between emergence and annual secondary production (E/P) varied among taxa (Table 4). Dipterans and *Cheumatopsyche arizonensis* displayed relatively high values, $\approx 25\%$, while *Baetis quilleri* was lower (15%) and tricorythids lower yet (2–7%).

Return of adult biomass

Only $3.1 \pm 0.7\%$ (95% CI) of total adult insect biomass emerging from the stream fell back into the water (Table 4). *Tricorythodes dimorphus* had the highest return percentage (20.5%), partially due to its adult life history traits (Jackson 1984). Winged forms of this species live for a brief period (<12 h) mostly at night and close to the stream, thus reducing chances of adult mortality by predators. *Cryptolabis* sp. lived longest as adults (>2 d) and experienced extended exposure to predators, yet it had the second highest return rate. Overall, 96.9% of the biomass that emerged was lost from the aquatic ecosystem, a net transfer of 22.4 $g \cdot m^{-2} \cdot yr^{-1}$ to the terrestrial ecosystem (Table 4).

DISCUSSION

Secondary production

Secondary production measurements (as dry mass) are available for many aquatic insect species and more

recently for entire benthic communities (Waters 1977). Community rates range from 5 to 15 $g \cdot m^{-2} \cdot yr^{-1}$ for north temperate streams (Fisher and Likens 1973, Neves 1979, Krueger and Waters 1983) to 50–70 $g \cdot m^{-2} \cdot yr^{-1}$ in southeastern blackwater streams (Nelson and Scott 1962, Benke et al. 1984). Waters (1977) predicted a maximum annual secondary production of 50 $g \cdot m^{-2} \cdot yr^{-1}$, yet noted that exceptions might occur where hyporheic zones are extensive (e.g., Hynes and Coleman 1968, recalculated by Waters 1977) or when multiple cohorts with rapid development characterize the fauna (e.g., Fisher and Gray 1983, Benke et al. 1984).

Macroinvertebrate secondary dry mass production in Sycamore Creek exceeded 120 $g \cdot m^{-2} \cdot yr^{-1}$ in this study and in the study by Fisher and Gray (1983). Characteristics intrinsic to desert streams (high temperatures, adequate food quantity, short invertebrate development times) were responsible for this unusually high rate. Animal standing biomasses in Sycamore Creek and temperate streams were similar, but turnover was much higher in Sycamore Creek. Immature aquatic insects grow to adulthood in fewer degree days and at a smaller size than related temperate species (Gray 1980, 1981). Rapid development may be advantageous in streams subject to flash floods and periodic drying (Gray 1981). Macroinvertebrate numbers and biomass reach 50% of preflood levels 2–3 wk after disturbance (Fisher et al. 1982). Furthermore, contin-

TABLE 4. Annual secondary production, average standing stock biomass, emergence, net transfer of insect biomass out of stream, production : standing stock (P/B), and emergence : production (E/P) for Sycamore Creek macroinvertebrates (1 September 1982–1 September 1983). All mass units are dry mass.

Taxon	Production ($g \cdot m^{-2} \cdot yr^{-1}$, $\bar{X} \pm 2$ SE)	Standing stock (g/m^2)	Emergence ($g \cdot m^{-2} \cdot yr^{-1}$)	Net transfer ($g \cdot m^{-2} \cdot yr^{-1}$)	P/B	E/P (%)
Baetis quilleri	19.5 ± 5.0	0.165	$3.00*$	$2.96*$	117.9	$15.0*$
Baetis insignificans	0.6 ± 0.1	0.006			94.5	
Leptohyphes packeri	18.5 ± 3.4	0.077	0.32	0.31	239.9	1.7
Tricorythodes dimorphus	16.9 ± 3.6	0.136	1.12	0.89	123.7	6.7
Chironomidae	58.3 ± 4.3	0.480	13.79	13.60	121.3	23.7
Cryptolabis sp.	4.45 ± 1.0	0.073	1.28	1.12	61.3	28.8
Helicopsyche mexicana	1.39 ± 0.3	0.039	3.17	3.09	35.3	228.1†
Cheumatopsyche arizonensis	1.51 ± 0.3	0.056	0.40	0.40	27.0	26.5
Total	120.9 ± 18.0	1.03	23.1	22.37	117.4	16.6‡

* Data for *B. quilleri* and *B. insignificans* are combined.

† See Materials and Methods: Measurement of Secondary Production, Emergence, and Adult Return, for explanation of emergence exceeding production.

‡ Data for *H. mexicana* excluded; see Materials and Methods: Measurement of Secondary Production, for explanation.

JOHN K. JACKSON AND STUART G. FISHER

TABLE 5. Annual emergence from various aquatic habitats. Taxa examined are (E) Ephemeroptera, (P) Plecoptera, (T) Trichoptera, (Ch) Chironomidae, and (C) whole community. Ranges (given in parentheses) indicate data from different years or sites which were averaged to give a single figure.

| | Emergence | | | |
Location	Numbers ($ind \cdot m^{-2} \cdot yr^{-1}$)	Dry mass ($g \cdot m^{-2} \cdot yr^{-1}$)	Taxa	Reference
Schreierbach Stream, Austria	*	3.63 (2.97–4.46)	E, P, T	Illies 1980
Teichbach Stream, Austria	*	5.04 (3.67–7.21)	E, P, T	Illies 1980
Costello Creek, Ontario, Canada	21 381 (10 842–40 446)	*	C	Ide 1940
Dundas Marsh, Ontario, Canada	4401	*	C	Judd 1953
Midway Creek, Ontario, Canada	4521 (2776–6198)	*	C	Judd 1962
Mud Creek, Ontario, Canada	6887 (2601–14 602)	*	C	Sprules 1947
l'Achigan River, Quebec, Canada	18 912	5.29†	C	Harper 1978
l'Achigan River, Quebec, Canada	22 793 (9118–48 300)	7.08† (2.2–15.2)	C	Harper 1978
Breitenbach Stream, F. R. Germany	32 182†	5.44†	C	Ringe 1974
Breitenbach Stream, F. R. Germany	3175† (2001–5204)	2.64† (1.8–3.9)	E, T, P	Illies 1978, 1980
Breitenbach Stream, F. R. Germany	4858	2.629	C	Gümbel 1976
Breitenbach Spring, F. R. Germany	8183	3.722	C	Gümbel 1976
Breitenbach Stream, F. R. Germany	4684	3.74 (2.7–6.3)	C	Illies 1971, 1975
Kalkbach Stream, F. R. Germany	5305	2.046	C	Gümbel 1976
Kalkbach Spring, F. R. Germany	7791	2.596	C	Gümbel 1976
Rohrwiesenbach Stream, F. R. Germany	7400†	3.17†	C	Ringe 1974
Kalengo Stream, Republic of Zaïre	938	0.474	T	Statzner 1976
Kalengo Stream, Republic of Zaïre	14 630	3.955	C	Böttger 1975
Lake Erken, Sweden	676† (418–896)	1.87† (1.7–2.2)	Ch	Sandberg 1969
Sycamore Creek, Arizona, USA	155 691	23.1	C	present study

* Data not available.
† Calculated for this paper from data contained in the original work.

uous reproduction generates a community composed of multiple cohorts. These factors combine with a long period of low, stable stream flow (204 d during this study year) to generate high secondary production.

Chironomids and ephemeropterans accounted for 95% of insect biomass produced. Total annual production for various taxa was similar, while the period of growth differed among taxa (Fig. 1, Tables 2 and 4). For example, three different mayflies contributed approximately equally to annual secondary production, but at different times. *Baetis quilleri* was most abundant during period III. *Leptohyphes packeri* was numerous in period IV, whereas there were many *Tricorythodes dimorphus* in late period III and early period IV (Fig. 1, Table 2). Chironomids were abundant and made large contributions to secondary production in periods I and III (Fig. 1, Table 2). Overall, the contribution to annual production by all species was greatest during period III.

Although annual secondary dry mass production estimated in this study approaches that found for Sycamore Creek between 1979 and 1980 ($135 \, g \cdot m^{-2} \cdot yr^{-1}$, Fisher and Gray 1983), percent contributions for some

taxa contrast markedly. Fisher and Gray (1983) showed *Cryptolabis* sp. to be a significant contributor to total production (39%, $52.6 \, g \cdot m^{-2} \cdot yr^{-1}$) and chironomid production to be only 13.6% ($18.3 \, g \cdot m^{-2} \cdot yr^{-1}$). In this study, the contribution of *Cryptolabis* sp. was small (3.7%, $4.5 \, g \cdot m^{-2} \cdot yr^{-1}$) and chironomid contribution was large (48.2%, $58.3 \, g \cdot m^{-2} \cdot yr^{-1}$). Mayfly production was similar in the two studies, $48.7 \, g \cdot m^{-2} \cdot yr^{-1}$ (Fisher and Gray 1983) and $54.8 \, g \cdot m^{-2} \cdot yr^{-1}$ (present study), yet *Baetis quilleri* was less important in results reported here. It is remarkable that no significant differences exist between total production estimates in these two studies, especially considering the different sites, different flood patterns, and changing taxonomic dominance in the two studies.

Cohort P/B was between 3 and 5 throughout this study, with deviations due mainly to changes in mortality rates. Waters (1979) predicted an average cohort P/B of 5.0 for freshwater benthic insects. Variation in annual P/B (27 to 124) reported here is a function of generation number (development time). High annual P/B's are characteristic of insects with rapid development and multiple cohorts (Fisher and Gray 1983,

TABLE 6. Annual ratios of emergence to secondary production (E/P) and estimates of return of emergent aquatic insects, for taxa in various habitats.

Taxon	E/P (%)	Emergence return (%)	Location	Reference
Ephemeroptera-Leptophlebiidae				
Leptophlebia vespertina	18.5	*	Øvre Heimdalsvatn, Norway	Brittain 1978
Odonata-Libellulidae				
Brachythemis contaminata	*	12.1†	Indumban Pond, India	Mathavan and Pandian 1977
Trichoptera-Glossosomatidae				
Agapetus fuscipes	4.0	*	Breitenbach Stream, F. R. Germany	Castro 1975
Diptera-Chaoboridae				
Chaoborus sp.	8.5	45.0	Lake Beloie, USSR	Borutsky 1939*b*
Diptera-Chironomidae				
Anatopynia dyaria	14.0	25.0	Root Spring, Massachusetts, USA	Teal 1957
Calopsectra dives	20.4	66.0	Root Spring, Massachusetts, USA	Teal 1957
Chironomus tendans	20.4	*	Cornell Experimental Ponds, New York, USA	Hall et al. 1970
Glyptotendipes barbipes	38.3	*	Primary sewage ponds, Oregon, USA	Kimerle and Anderson 1971
Glyptotendipes barbipes	40.4	*	Secondary sewage ponds, Oregon, USA	Kimerle and Anderson 1971
Tanytarsus jucundas	19.6‡	*	Sugarloaf Lake, Michigan, USA	Anderson and Hooper 1956
Tanypus sp.	15.0	28.1	Lake Beloie, USSR	Borutsky 1939*b*
Tendipes plumosus	11.7	9.7	Lake Beloie, USSR	Borutsky 1939*a*
Chironomidae	38.5	>50.0	Lake Char, Northwest Territory, Canada	Welch 1973, 1976
Chironomidae	52.9	*	Lake Esrom, Denmark	Jónasson 1972
Diptera	56.9	*	Lake Esrom, Denmark	Jónasson 1972
Diptera-Simuliidae				
Four species—1971	23.3	*	Streams in Oregon, USA	Speir and Anderson 1974
Four species—1972	20.8	*	Streams in Oregon, USA	Speir and Anderson 1974
Diptera-Stratiomyidae				
Hedriodiscus truquii	27.2	21.0	Ohanapecosh Hotspring, Washington, USA	Stockner 1971

* Data not available.
† Derived estimate based on measurement of eggs laid in the pond, not adults returning.
‡ Calculated using adult mass = 0.71 × pupae mass (Teal 1957).

Benke et al. 1984) and demonstrate a major difference between insects in desert streams and their temperate counterparts. Temperate stream insects rarely have more than two or three generations, while in Sycamore Creek there may be 5 to 20, depending on the species. Thus, a moderate invertebrate standing stock with rapid and repeated turnover annually produces 5–15 times the insect biomass common in temperate streams.

Emergence

In Sycamore Creek, chironomids dominated emergence dry mass (59.7%), while *Helicopsyche mexicana* and mayflies together accounted for another 33%. Total emergence in this study (23.1 g·m⁻²·yr⁻¹) was much higher than any previously reported rate (Table 5). Illies (1980) predicted emergence to range between 5 and 15 g·m⁻²·yr⁻¹, but most empirical estimates are 3–7 g·m⁻²·yr⁻¹. Previously reported emergence estimates would be even lower if emergence from riffles

and less productive pools were combined, as was done by us and by Harper (1978).

The relationship between emergence and production (E/P) combines insect metabolic activities (instar growth rates and production) and population dynamics (mortality schedule and final survivorship). Biotic and abiotic factors (e.g., predation and flash floods) influence the shape of survivorship curves to produce variation in the percent of accrued biomass that emerges. Sycamore Creek dipteran E/P ranged from 24 to 29%, which is within the range of published data (Tables 4 and 6). *Cheumatopsyche arizonensis* ($E/P = 27\%$) was similar to this, yet much higher than the trichopteran studied by Castro (1975). Mayfly E/P (2–15%) was consistently lower than the value of 18.5% reported by Brittain (1978). E/P in Sycamore Creek appears to have been reduced by flooding or by predators, as was found by Hall et al. (1970) and Illies (1975) in north temperate streams. Surface-dwelling benthic insects (e.g., mayflies) had lower E/P's than burrowing insects
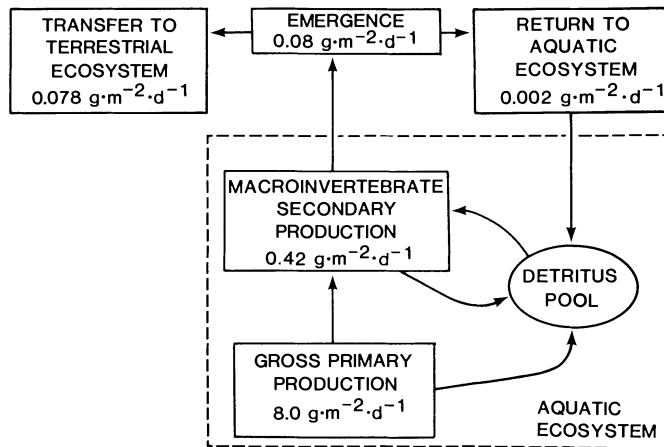
FIG. 2. Daily estimates of primary production (Busch and Fisher 1981), secondary production, emergence, and transfer to the terrestrial ecosystem at Sycamore Creek. All estimates are expressed as ash-free dry mass.

(e.g., chironomids and *Cryptolabis* sp.). Presumably, these surface-dwelling insects were more vulnerable to omnivorous fish (the cyprinid *Agosia chrysogaster*), predaceous insects, and minor floods.

Most E/P estimates in the literature are from single cohorts, and thus little is known about variation in E/P. In this study, multiple cohorts represent replications under different conditions and showed variation in E/P throughout the year. Annual E/P's for Sycamore Creek insects were similar to those reported elsewhere (Tables 4 and 6). As a result, emergence in Sycamore Creek was high by comparison because secondary production was elevated. This high emergence provides a potentially strong linkage between aquatic and terrestrial ecosystems.

Adult return and biomass transfer to the terrestrial ecosystem

The return of emergent adults to the stream is influenced by interactions among adult life histories, terrestrial environment, and chance. Environmental stress (e.g., desiccation, metabolic exhaustion from swarming or high temperatures, accidental injury) along with predation pressure from aerial and nonaerial insectivores influence adult insect mortality and return of adults to the stream (Corbet 1964, Dahl 1965, as cited in Tozer et al. 1981, Stockner 1971, Edmunds and Edmunds 1980).

Sycamore Creek insects conform in varying degrees to the prediction that the probability of return decreases with increasing adult longevity (exposure to predators and physical environment) and distance between swarming site and stream. Species that swarm over water and have brief adult lives (*Tricorythodes dimorphus*) have higher return than species that are longer lived, swarm over land, or return to the terrestrial environment after oviposition (*Baetis quilleri* and *Helicopsyche mexicana*).

The return of emergent insect biomass is also related to stream canopy. Insect biomass falling into streams is usually greatest where vegetation overhangs the stream (Mason and MacDonald 1982). The riparian zone at Sycamore Creek is 1–30 m from the stream edge, resulting in an open canopy and relatively low adult return; only 3.1% of emergent biomass returned to the stream by adult fall-in. Chironomidae and *Tricorythodes dimorphus* accounted for most of this return (59.2%). The few estimates of adult return available in the literature (Table 6) are usually <50% of emergence. Terrestrial insect import may equal or exceed aquatic insect export (Mason and MacDonald 1982) and can occasionally be important to stream insectivores (Hunt 1975, but see Schreiber and Minckley 1981). Very few terrestrial insects fell into our catch-nets; thus aquatic insect emergence from Sycamore Creek resulted in a net export of insect biomass.

Aquatic-terrestrial interactions

In the context of total organic matter or nutrient budgets, secondary production and emergence are small fluxes in both temperate and desert aquatic habitats (Vallentyne 1952, Teal 1957, Webster and Patton 1979, Davies 1980; Fig. 2). Although insects transferred from aquatic systems may be insignificant compared to terrestrial inputs (leaves and other organic matter), emergence can be a major part of that export which does occur (Likens and Loucks 1978).

Aquatic ecosystems represent sources of food and water for organisms in riparian habitats. The significance of water for terrestrial plant and wildlife use is clear, especially in the desert. In addition, insects from aquatic systems may represent important prey items for riparian insectivores. Large numbers of terrestrial insectivores (bats, birds, adult odonates, and spiders) that eat emerged aquatic insects feed and reproduce near Sycamore Creek and its riparian zone. Spiders

were constantly present, but bats, birds, and adult odo-
nates were opportunistic visitors, feeding intensely on
adult aquatic insects over the stream corridor when
these insects were numerous and moving into the ad-
jacent riparian vegetation when the insects were scarce
(Jackson 1984). Terrestrial invertebrate insectivores
(e.g., adult odonates and spiders) facilitate the transfer
of energy from aquatic to terrestrial ecosystems by con-
suming small aquatic insects while serving as prey for
large terrestrial vertebrate insectivores. Past studies
have correlated emergence and swarming of aquatic
insects with bird and bat population parameters such
as adult territoriality, feeding behavior, and reproduc-
tive success (e.g., Orians 1966, Davies 1976, Anthony
et al. 1981, Sjöberg and Danell 1982). Interactions be-
tween aquatic insects and riparian insectivores appear
to be strong, influencing the evolution of behaviors and
life history traits of both prey (Corbet 1964, Edmunds
and Edmunds 1980, Sweeney and Vannote 1982) and
predators (Orians 1966, Davies 1976, Anthony et al.
1981, Sjöberg and Danell 1982). These ecological and
evolutionary interactions are examples of the intricate
connections and intimate relationships between aquat-
ic and nearby terrestrial ecosystems.

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