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## SECONDARY PRODUCTION AND ORGANIC MATTER PROCESSING BY COLLECTOR MACROINVERTEBRATES IN A DESERT STREAM<sup>1</sup>

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**Abstract.** Secondary production (measured as dry mass) of collector macroinvertebrates of Sycamore Creek, Arizona, estimated by the size-frequency method, is  $135 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ . This high rate of production is attributed to a long growing season, continuous reproduction, rapid life cycles of major taxa, and small size at maturity. Assimilation efficiency for selected collector taxa is estimated to be 7–14% and gross growth efficiency 2–11%. At mean standing stock ( $3 \text{ g/m}^2$ ) collectors ingest 4.2 times their body mass per day. Ingestion exceeds gross primary production, dictating both fecal reingestion and rapid turnover of fine particulate organic matter in this desert stream.

**Key words:** *aquatic insects; Arizona; desert; macroinvertebrates; organic matter; secondary production; stream.*

### INTRODUCTION

The purpose of this paper is to evaluate macroinvertebrate secondary production in Sycamore Creek, a hot-desert stream in Arizona, and to discuss the consequences of that production to overall stream functioning. Annual macroinvertebrate secondary production has not heretofore been measured in Sonoran desert streams; however, rates range widely in streams of other regions. New England (USA) streams support secondary production (measured as dry mass) at a rate of  $10 \text{ g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  (Fisher and Likens 1973, Neves 1979), while in southeastern USA, secondary production may be five times this (Nelson and Scott 1962). Waters (1977) considers  $50 \text{ g/m}^2$  to be an upper limit for annual secondary production of benthic macroinvertebrates, yet acknowledges that higher rates may exist under special circumstances, as in streams with an extensive hyporheic zone (Hynes and Coleman 1968).

While the definitive predictive model of secondary production in streams is yet to be constructed, several features of hot-desert streams of the American Southwest appear especially favorable for high secondary production. Between catastrophic flash floods, primary production is high in Sycamore Creek, and food for consumer invertebrates is always ample (Busch and Fisher 1981). Even after major flooding, fine particulate organic matter (FPOM, 1–1000  $\mu\text{m}$ , as ash-free dry mass) associated with sediments does not drop below  $50 \text{ g/m}^2$ . Most invertebrates of the system are collector-deposit feeders which utilize algae or detritus derived from algae in this size-range (Fisher et al. 1982). Recolonization of the stream by invertebrates after flooding is rapid, and dry mass of standing stocks quickly reaches 2–9  $\text{g/m}^2$ , which is characteristic of most of the year, save high winter runoff periods (Gray

1980, Fisher et al. 1982). Water temperature ranges from  $5^\circ$  in winter to  $33^\circ\text{C}$  in summer; however, afternoon temperature rises to  $10^\circ$ – $15^\circ$  on even the coldest winter days. As a result, the growing season is long. Most aquatic insects of Sycamore Creek and other Sonoran Desert streams are multivoltine, producing several generations annually. The predominant mayfly and chironomid species of Sycamore Creek pass from egg to adult in 1–2 wk and reproduce continuously through the year (Gray 1980). Rapid development is related in part to small size at maturity and may be an adaptation to an uncertain environment which is subject to both periodic drying and catastrophic flooding (Gray 1981).

Secondary production in itself does not tell us much about the influence of invertebrates on ecosystem functioning since it is only one end product of organic matter processing. Even at  $50 \text{ g/m}^2$ , secondary production is small compared to total organic matter input, which may approach  $1 \text{ kg} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$  in both autotrophic (Naiman 1976, Minshall 1978, Busch and Fisher 1981) and heterotrophic streams (Fisher and Likens 1973, Fisher 1977). Thus while Fisher and Likens (1973) attributed just 1% of ecosystem respiration to macroinvertebrates in a New England stream, ingestion required to support this respiration is perhaps 10 times higher. Petersen and Cummins (1974) report shredder insects to be responsible for 25% of leaf litter processing in a Michigan stream. Short and Maslin (1977) have shown shredders to be important in generating fine particles consumed later by collectors and filter feeders. Manipulation of FPOM feeders may have pronounced consequences on FPOM transport as well (Wallace et al. 1982). Thus even modest rates of secondary production may be associated with potentially significant influences on organic matter processing and nutrient cycling in the ecosystem as a whole. We will thus attempt to place our secondary production estimates in the context of the stream eco-

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system to examine the consequences of consumer activities to desert stream structure and function.

## METHODS AND MATERIALS

### *Study site*

Sycamore Creek (33°45'N, 111°30'W) is a tributary of the Verde River in central Arizona. The stream drains a watershed of 505 km<sup>2</sup>, which ranges in elevation from 427 to 2164 m. Terrain is rugged and mountainous; however, at the elevation of our study (650 m), the stream channel is wide, sandy, and relatively unshaded. While the channel may be 50 m wide, water width at low summer flow is 1–4 m, mean depth is 7 cm, and velocity averages near 15 cm/s. Precipitation is low (40 cm/yr) and potential evaporation high (300 cm/yr); thus, in summer, discharge is low (0.03 m<sup>2</sup>/s), and the stream flows in and out of the coarse sandy substrate, dividing the stream into several discontinuous reaches of several hundred meters length, separated by long, dry sandy expanses. The stream is subject to flash flooding, especially in late summer.

Because of its wide channel and the high insolation characterizing central Arizona, Sycamore Creek displays high rates of algal primary production in summer (Busch and Fisher 1981). Aquatic macrophytes are abundant only after long periods without flooding. Aquatic insects dominate the benthic macroinvertebrate community. *Agosia chrysogaster* (longfin dace) and *Pantosteus clarki* (Gila Mountain sucker) are the predominant fish species present; however, the latter is abundant only during unusually wet years.

Sycamore Creek is characterized by moderately hard calcium and magnesium bicarbonate water, with specific conductance near 500  $\mu$ S/cm and total alkalinity as CaCO<sub>3</sub> averaging 250 mg/L. Summer pH varies diel between 7 and 8. Dissolved phosphorus is generally >50  $\mu$ g/L, and NO<sub>3</sub>-N usually exceeds 100  $\mu$ g/L. Except during floods, suspended solids are low, and the water is remarkably clear. In summer, mean daily temperature varies between 20° and 25°. Further description of Sycamore Creek may be found in Fisher and Minckley (1978) and Fisher et al. (1982).

### *Biomass and secondary production techniques*

The sampling program was designed to describe conditions in Sycamore Creek from 1 April to 1 November 1979. Prior to April and after 1 November, stream discharge was high, and benthic standing stock was negligibly low and, for calculations described here, assumed to be zero. On each of 15 dates (approximately twice monthly), 4–12 benthic samples were taken with an 80-cm<sup>2</sup> core to a depth of 10 cm. Few macroinvertebrates in Sycamore Creek are present deeper than 10 cm in sediments (Gray 1981). Samples were elutriated through a 270- $\mu$ m mesh sieve, preserved in Kahle's fluid, and later sorted in the laboratory under a dissecting microscope. Body length of individuals of five taxonomic categories (Table 1), rep-

resenting 89% of total collector biomass and numbers, was also measured to the nearest 1.0 mm with an ocular micrometer. Secondary production of each of these five groups was estimated by the size-frequency method (Hynes and Coleman 1968, Hamilton 1969, Benke 1979, Krueger and Martin 1980, Waters and Hokenstrom 1980). With this method, cohort distinction is not necessary, and several taxa can be combined provided they are similar in developmental times, food habits, and final size (Waters 1977). Calculated rates of cohort production were multiplied by the number of generations during the period based on average development times from hatching to adult emergence (Gray 1981). Production of those collector taxa not directly measured was estimated by applying to the remaining 11% the average production to biomass ratio (P/B) derived for the five major taxa. Unless otherwise indicated, all organic matter units reported in this paper are as dry mass (DM).

### *Individual energy budgets*

Organisms for lab studies were collected at Sycamore Creek from June to August 1980, when water temperature ranged from 20° to 28°. Organisms were placed in containers with sand substrates, a standard food (see below), and filtered stream water, and were held in constant-temperature incubators for 24–72 h until use.

Two size-classes of *Baetis quilleri*, a baetid mayfly, were used: I (2.0–3.0 mm body length excluding cerci and 40–110  $\mu$ g DM), and II (3.1–4.4 mm body length and 120–310  $\mu$ g DM). Chironomid dipterans (*Tribelos* sp.) were 2.1–4.4 mm long and weighed 30–140  $\mu$ g. Individuals of the grazing snail *Physa virgata* were 3–8 mm in shell height and 2–7 mg DM (without shells).

The standard food used in all experiments was a mixture of *Cladophora glomerata*, diatoms, detritus, and inorganic material collected from algal mats in June. This material was dried, ground, and sieved to obtain particle diameters <50  $\mu$ m. Organic matter of standard food was 23%, based on dichromate oxidation (Maciolek 1962), a method used to estimate organic matter in all egestion and ingestion experiments.

Energy budgets were calculated from the equations:

$$A = I - E, \quad (1)$$

$$A = P + R, \quad (2)$$

$$P = G + Ex, \quad (3)$$

where  $A$  = assimilation,  $I$  = ingestion,  $E$  = egestion,  $R$  = respiration,  $P$  = production,  $G$  = growth, and  $Ex$  = exuviae. Direct measures of  $E$ ,  $R$ , and  $P$  were made for *B. quilleri* and *Tribelos* sp., and  $I$ ,  $E$ , and  $R$  were measured directly for *P. virgata*. Ingestion could not be measured directly for small collectors because their feces were indistinguishable from their food. Ingestion and assimilation rates for these collectors were calculated with Eq. 1 and 2.

Continuously fed *B. quilleri* and *Tribelos* sp. larvae

TABLE 1. Biomass, production, and turnover of collector macroinvertebrates in Sycamore Creek. All mass units are dry mass.  $P_d$  and  $P_a$  refer to production on daily and growing season bases, respectively. Generations are based on development times (egg to adult) of 22 d for *Cryptolabis* sp. and 12 d for other taxa. Rates for "other collectors" estimated from means of the five major taxa.

Taxon	Average biomass (g/m <sup>2</sup> )	No. generations/yr	Secondary production		Residence time $B/P_d$ (d)	Turnover ratio $P_a/B$ (yr <sup>-1</sup> )
			$P_d$ (g·m <sup>-2</sup> ·d <sup>-1</sup> )	$P_a$ (g·m <sup>-2</sup> ·yr <sup>-1</sup> )		
<i>Baetis quilleri</i>	0.34	18	0.103	21.9	3.3	64
<i>Tricorythodes dimorphus</i>	0.19	18	0.07	14.3	2.7	75
<i>Leptohyphes packeri</i>	0.20	18	0.06	12.5	3.3	63
Chironomidae	0.28	18	0.09	18.4	3.1	66
<i>Cryptolabis</i> sp.	1.63	9	0.246	52.6	6.6	32
Other collectors	0.34	...	0.07	15.3	4.9	45
Total	2.98	...	0.63	135	4.7	45

were placed in clean petri dishes containing distilled water and sand to determine rates of egestion. The amount of time allowed for egestion was equivalent to gut-loading times previously determined using standard food mixed with powdered charcoal as a marker (McCullough et al. 1979). Gut-loading times were 20 min at 25°, 30 min at 20°, and 40 min at 10°. Dishes without organisms served as controls.

Ingestion and egestion by *P. virgata* were determined by placing four to six continuously fed snails (15–25 mg DM total) in petri dishes with a known amount of standard food (25–35 mg DM) and distilled water. Feeding was allowed for 3 h, then snails were transferred to clean petri dishes with distilled water for 1 h. Ingestion was calculated by subtracting organic matter of uneaten food and dissolved wastes (measured by dichromate oxidation) from initial amounts determined from controls incubated concurrently. Egestion was thus partitioned into two components: feces produced in feeding dishes, and dissolved wastes and mucus from clean dishes.

Respiration rates were determined by placing an

equivalent of 1–2 mg DM of *B. quilleri* and *Tribelos* sp., or a single snail, in a 10-mL syringe for 1–2 h depending upon temperature. Nitex mesh was added as substrate for insects. Samples in syringes were fixed without removing organisms, and oxygen content was determined by a micro-Winkler technique (azide modification). In none of the experiments did oxygen saturation drop below 50%. Respiration was estimated as the difference in oxygen between experimental syringes and controls (without organisms). Respiration rates in microlitres of oxygen per milligram per hour were converted to equivalent ash-free dry biomass (in micrograms per milligram per hour) by multiplying by 0.83, a value that represents the standard oxyenergetic equivalent of 20.5 mJ/μL O<sub>2</sub> divided by 24.7 mJ/μg AFDM for baetids and chironomids (these values were expressed in calories by Cummins and Wuycheck 1971; 1 cal = 4.184 J).

Growth rates of collectors were estimated by measuring body length with an ocular micrometer before and after a 3-d period at each temperature. Organisms were maintained in the lab in containers with aerated,

TABLE 2. Energy budgets for three Sycamore Creek macroinvertebrates. Values measured directly are given as mean (SE, n). Remaining terms calculated. Assimilation efficiency (AE) = (ingestion-egestion)/ingestion = assimilation/ingestion. Gross growth efficiency (GGE) = production/ingestion. All rates are reported in AFDM units of μg·mg<sup>-1</sup>·h<sup>-1</sup>. Dry masses of *Baetis* size-classes are I: 40–110 μg; II: 120–310 μg.

Species	Size-class	°C	Respiration	Production	Egestion	Ingestion	Assimilation	AE (%)	GGE (%)
<i>Baetis quilleri</i>	I	10	6.7 (1.6, 6)	2.5 (0.2, 7)	121 (28, 4)	130	9	7	1.9
		10	3.5 (0.9, 6)	2.0 (0.35, 4)	39 (3, 4)	44	5	11	4.5
	II	20	11.7 (1.1, 4)	4.8 (0.6, 6)	203 (21, 4)	219	16	7	2.2
		20	7.9 (1.0, 6)	3.9 (0.45, 5)	113 (23, 4)	125	12	10	3.1
	II	25	14.9 (3.4, 3)	15.6 (1.8, 6)	221 (8, 3)	251	30	12	6.2
		25	11.5 (1.0, 7)	12.0 (2.5, 12)	153 (15, 5)	176	23	13	6.8
<i>Tribelos</i> sp.		20	4.1 (0.5, 5)	11.0 (1.9, 10)	90 (26, 5)	105	15	14	10.5
		25	5.6 (0.5, 5)	13.4 (2.3, 4)	152 (40, 5)	171	19	11	7.8
<i>Physa virgata</i>		20	1.8 (0.2, 10)	6.2	34 (1.7, 5)*	53 (24, 5)	8	15	11.7
					11 (1.7, 5)†				
		25	4.7 (0.4, 10)	7.3	69 (8, 5)*	94 (42, 5)	12	13	7.8
					13 (1.8, 5)†				

\* Feces only.

† Dissolved wastes and mucus only.

TABLE 3. Annual secondary production of collectors in Sycamore Creek compared with other streams in which total benthic macroinvertebrate production has been calculated.

Stream	Trophic category	Dry mass production ( $\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$ )	Reference
Speed River, Ontario	All benthos	200	Hynes and Coleman (1968), recalculated by Waters (1977)
Sycamore Creek, Arizona	Collectors	135	This study
Middle Oconee River, Georgia	Primary consumers	56	Nelson and Scott (1962)
River Thames, England	Primary consumers	21.4	Mann et al. (1972)
	Predators	3.5	
Factory Brook, Massachusetts	All benthos	12.2	Neves (1979)
Bear Brook, New Hampshire	All benthos	4.8	Fisher and Likens (1973)

filtered stream water and standard food during this time. Lengths ( $L$ ) were converted to mass ( $M$ ), using empirical relationships derived for each taxon: *B. quilleri*,  $M = 5.17 L^{2.83}$  ( $r = .97$ ,  $n = 12$ ); *Tribelos* sp.,  $M = L^{4.16}/3.56$  ( $r = .98$ ,  $n = 12$ ). Growth rate was then estimated from these expressions and the time required to grow to maximum size. Exuviae were collected and their mass added to growth. For both species, exuviae comprised 1% of total production. All mass values generated from these expressions are as ash-free dry mass (AFDM).

## RESULTS

### *Secondary production of collectors*

Details on standing stocks and community composition in Sycamore Creek have been published elsewhere (Gray 1980, 1981, Gray and Fisher 1981, Fisher et al. 1982) and will not be repeated here. Dry biomass of collectors averaged nearly 3 g/m<sup>2</sup> during the study period (Table 1) but ranged from near zero after an early August flood to over 10 g/m<sup>2</sup> 2 mo later. The three small mayfly taxa present in the stream comprised  $\approx 25\%$  of biomass but contributed nearly 37% of total collector secondary production during the study period. *Cryptotabis* sp., a small tipulid dipteran, made up 55% of total biomass but contributed only 39% to secondary production, largely because its generation time (22 d) is twice that of the dominant mayflies and chironomids (10–13 d).

Mayflies and chironomids exhibited a mean turnover time of  $\approx 3$  d, the total collector fauna 4.7 d. This yields very high annual secondary production to mean biomass ratios (P/B) for these taxa (63–75) and for the total collector fauna (45). Thus while mean standing crop was a modest 2.98 g/m<sup>2</sup>, production was quite high at 135 g/m<sup>2</sup>.

### *Individual energy budgets*

Bioenergetic parameters for the three taxa examined in detail are presented in Table 2. These results are probably conservative, in that activity levels in the laboratory may underestimate those in nature. All five

metabolic parameters measured for all taxa increased with temperature over the range measured. Similarly, size-specific rates of metabolism decreased with body size in *Baetis quilleri*.

Respiration rates (expressed as loss of AFDM per unit dry mass) of *B. quilleri* and *Tribelos* sp. at 20° and 25° ranged from 4.1 to 14.9  $\mu\text{g} \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$ . These values are in the range reported for similar organisms at these temperatures (Edwards 1958, Rueger et al. 1969, McCullough et al. 1979). Respiration rates of *P. virgata* (1.8 and 4.7  $\mu\text{g} \cdot \text{mg}^{-1} \cdot \text{h}^{-1}$  at 20° and 25°, respectively) are similar to those reported for other pulmonate snails (Berg and Ockelmann 1959).

As expected from their short generation times, growth rates of *B. quilleri* and *Tribelos* sp. were high. At 25°, both species could complete larval development in the laboratory within 10–13 d. Growth rates of all species increased with temperature. *B. quilleri* exhibited the greatest temperature dependence with growth  $Q_{10}$  values of 6.1–6.4 between 20° and 25°. Large  $Q_{10}$ 's at high temperatures have been reported for other organisms in temporary habitats. Hillyard and Vinegar (1972) reported respiration  $Q_{10}$ 's between 4 and 12 at 26°–30° for larval phyllopod crustaceans in ephemeral ponds and postulated similar responses in growth rates.

At higher temperatures, ingestion rates were very high for *B. quilleri* and *Tribelos* sp. These organisms consumed an amount of food equivalent to their body mass every 4–6 h; however, assimilation efficiencies (AE) were consistently low on standard food (AE = 7–15%).

## DISCUSSION

### *Secondary production*

Secondary production of the collector component of the macroinvertebrate community of Sycamore Creek is high compared to other stream ecosystems (Table 3). Our estimated rate of 135 g/m<sup>2</sup> is exceeded only by Speed River, Ontario, where sediments of unconsolidated glacial till extend invertebrate habitat to nearly a metre into the stream bottom (Hynes and

Coleman 1968, Williams and Hynes 1974). On a substrate volume basis, secondary production of Sycamore Creek is several times that of Speed River.

Our calculations underestimate total invertebrate production in Sycamore Creek in that only collectors were considered. Beetles and hemipterans, many of which are predators, were omitted from the estimates. Noncollector taxa make up  $\approx 15\%$  of the invertebrate standing stock in Sycamore Creek, and most species in these groups are larger and have longer life cycles than the collector taxa considered here. Shredders are virtually absent, as are large particulate organic materials which serve as food for this group elsewhere.

Production is probably further underestimated by the substantial period of 1979 with high discharge (November–April). We assumed production during that time to be zero; it is surely insignificantly low compared to low-flow periods. In other, more normal years, low flow may typify a larger fraction of the year, permitting maintenance of larger standing stocks in winter. Lower growth rates would be expected at reduced winter temperatures, and annual secondary production is thus not directly proportional to the number of days with optimal flow. Perhaps a greater source of variation between years is the regime of summer flooding. Summer floods drastically reduce invertebrate standing stocks at a time of warm water temperature and thus maximal productivity. Sycamore Creek experiences an average of 2 flash floods/yr; however, in the past 15 yr, as few as none and as many as nine have occurred. While macroinvertebrate recovery from these events is rapid, and pre-flood standing stocks are regained in 2–4 wk, a year with several evenly spaced floods could lower annual productivity markedly.

Since only a few taxa contribute to the great bulk of total production in Sycamore Creek, species-specific production rates are also high compared to congeners in cooler temperate streams. For example, annual production of *B. quilleri* in Sycamore Creek during 1979 was 21.9 g/m<sup>2</sup>. This is about an order of magnitude greater than 2.1 g/m<sup>2</sup> for *B. vagans* in Valley Creek, Minnesota (Waters 1966), 1.4 g/m<sup>2</sup> for *B. bicaudatus* in Logan River, Utah (Pearson and Kramer 1972), and 0.9 g/m<sup>2</sup> for *B. rhodani* in Czechoslovakian trout streams (Zelinka 1973).

#### Individual energy budgets

None of the metabolic parameters measured for *B. quilleri*, *Tribelos* sp. or *Physa virgata* is markedly different from estimates reported for similar species of comparable size. Nor do these three otherwise quite different taxa differ markedly from each other in gross metabolism when results are reported on a mass-specific basis (Table 2).

The energy budget for *B. quilleri* (size-class II) at 20° can be compared with that of another multivoltine stream collector, the mayfly *Tricorythodes minutus* Traver (McCullough et al. 1979) (Table 4). The two

TABLE 4. Comparison of bioenergetics of *Baetis quilleri* (size-class II) and *Tricorythodes minutus* Traver (McCullough et al. 1979) at 20°C. All rates are reported in AFDM units.

Parameter	<i>B. quilleri</i>	<i>T. minutus</i>
Respiration ( $\mu\text{g}\cdot\text{mg}^{-1}\cdot\text{h}^{-1}$ )	7.9	2.1
Production ( $\mu\text{g}\cdot\text{mg}^{-1}\cdot\text{h}^{-1}$ )	3.9	4.5
Ingestion ( $\mu\text{g}\cdot\text{mg}^{-1}\cdot\text{h}^{-1}$ )	125	24
Assimilation Efficiency (%)	9.4	27.5

species have similar growth rates, but *B. quilleri* has a higher respiration and ingestion rate, and much lower assimilation efficiency on similar foods. In these respects, *B. quilleri* is similar to terrestrial insect larvae in temporary habitats. Rapidly growing beetle larvae in dung exhibit high ingestion rates and very low assimilation efficiencies (Holter 1974). Low assimilation efficiencies have been found for other aquatic detritivores, but these result from feeding on low-quality food (McDiffett 1970, Nilsson 1974, Wotton 1978). Assessment of food quality is somewhat subjective. While assimilation efficiencies of all organisms and sizes we studied ranged from 7 to 15%, both individual and community production rates were quite high. In the laboratory on standard food, both *B. quilleri* and *Tribelos* sp. complete their life cycles and emerge as rapidly as they do in the field. As a result, we are confident that our laboratory estimates of AE adequately reflect field AE. Furthermore, individual production rates for the three taxa estimated in the laboratory at 25°C range from 175 to 331  $\mu\text{g}\cdot\text{mg}^{-1}\cdot\text{d}^{-1}$ . Field measures of secondary production by the size-frequency method yield an estimate of 0.63 g·m<sup>-2</sup>·d<sup>-1</sup>, which at laboratory growth rates would require a standing stock of 1.9–3.6 g/m<sup>2</sup>. This range neatly encompasses the mean empirically determined standing crop of 2.98 g/m<sup>2</sup>.

Rapid growth of small collectors in Sycamore Creek is achieved by high rates of ingestion combined with low assimilation, in parallel to organisms of other temporary habitats (Holter 1974). Low assimilation efficiencies seem incongruous, especially when compared to the much higher efficiencies of other stream collectors, such as *Tricorythodes minutus* (McCullough et al. 1979). It is unlikely, however, that collectors in Sycamore Creek are food limited, because of large amounts of detritus in sediments ( $\approx 10$ – $100$  times that of collector biomass). Thus it may be energetically less costly to continue feeding and assimilate only the most labile fraction in food, rather than to increase gut retention time and assimilate additional fractions. Therefore, low AE may be a viable physiological strategy when food abundance offsets low quality per mouthful (Taghon 1981).

Finally, gross growth efficiency (GGE, growth/ingestion) can be computed from laboratory data (Table 2). These values are lower than AE, the difference

TABLE 5. Energetic parameters of collectors in Sycamore Creek based on laboratory measures of metabolism of *Baetis quilleri* and *Tribelos* sp. at 20° and 25°C.

	Daily rate				
	Ingestion	Egestion	Assimilation	Respiration	Growth
g/g	4.2	3.7	0.46	0.22	0.24
% of ingestion	100	89	11	5.2	5.7
Rate at standing crop of 3 g/m <sup>2</sup>	12.6	11.1	1.38	0.66	0.72

due to respiration. At 25° GGE for the three taxa ranges from 6.2% (*B. quilleri*, size-class I) to 7.8% (*P. virgata*, *Tribelos* sp.). Lower temperatures widen the range of GGE to 1.9–11.7%, yet we are confident that 10% does not overestimate GGE of the collector fauna as a whole. What this means, of course, is that one unit of production requires 10 units of ingested food, nearly 90% of which is released to the environment by egestion, as fecal matter.

#### Role of collectors in desert stream metabolism

The impact of collectors on energy flow in Sycamore Creek in summer can be illustrated by the following simplified scenario. First we will assume that metabolism of collectors in Sycamore Creek can be described as the simple average of *B. quilleri* (two size-classes) and *Tribelos* sp. at 20° and 25°C (Table 5). Other mayflies in the system grow to the same maximum size (4–5 mm) as *B. quilleri* at the same rate. Twelve other chironomid taxa are present, 11 that grow to the same maximum length as *Tribelos* sp. (7 mm) and 1 that is slightly smaller (Gray 1980). Mean size-specific metabolic rates can then be applied to mean standing stock during the study period (3 g/m<sup>2</sup>). Based on these simplifications, daily secondary production is 0.72 g/m<sup>2</sup>, respiration is slightly less (0.66 g·m<sup>-2</sup>·d<sup>-1</sup>), and ingestion is 12.6 g·m<sup>-2</sup>·d<sup>-1</sup>. The ratio of ingestion: growth is 17.5:1 and ingestion: biomass is 4.2:1. Thus collectors ingest 4.2 times their body mass per day. This latter ratio is striking in itself but becomes even more significant when compared to the rate of gross primary production in Sycamore Creek, which in summer averages 8.5 g·m<sup>-2</sup>·d<sup>-1</sup> (Busch and Fisher 1981). Thus at mean standing stock, collectors ingest organic matter at a faster rate than it is being produced in the ecosystem; under mean conditions, ≈50% more.

Both collector standing stock and primary production vary, however, and respond to flooding, by declining dramatically. In August 1979, a catastrophic flash flood scoured Sycamore Creek and removed over 95% of the biota. Recovery from the flood is described in Fisher et al. (1982). During the 2-mo recovery period, gross primary production ( $P_g$ ) increased from 0 to 7.4 g·m<sup>-2</sup>·d<sup>-1</sup> and insect biomass from 0 to 10.4 g/m<sup>2</sup>, the highest biomass values attained during the

study period. These data and the fraction of  $P_g$  ingested by collectors are presented in Fig. 1. Using these data, we estimate that collectors ingested organic matter equivalent to from 2.5 to 6.2 times gross primary production during the postflood, recovery period. These rates are considerably higher than the 1.6 ratio which describes the entire year. Collector ingestion of primary production increased through the 2-mo recovery period, until another flood reset the system in early November.

These high rates of organic matter ingestion are accentuated when we consider that the predominant primary producer, *Cladophora glomerata*, is unavailable to collectors until it dies and enters the detritus pool of the system. About half of  $P_g$  during the recovery period contributes to increased standing crop of algae, and the remainder is available to consumers. As a result, production of new FPOM is even lower than  $P_g$  would imply.

Substrates present immediately after flooding contain allochthonous FPOM at a concentration of ≈50 g/m<sup>2</sup>, and early primary producers are predominantly diatoms (Fisher et al. 1982). Later, FPOM derived from *C. glomerata* makes up the bulk of fine organic particles in the system. Based on gut analyses, collectors switch between these materials in sequence. Nevertheless, by day 20 following flooding, collectors are ingesting each day the equivalent of 30% of the organic matter present (Fig. 2).

Of course, ingested organic matter is not lost from the ecosystem; only the respired fraction is. Macroinvertebrate respiration accounts for just 21% of total ecosystem respiration. Much of secondary production also remains in the system and eventually augments the FPOM pool. Only emergent adults which do not return to the stream after death represent a net output via secondary production.

Even allowing for large errors of estimation, these data dictate reingestion of fecal material by collectors. There is simply insufficient organic matter available from other sources (nor, we suspect, plausible mechanisms to avoid reingestion). Gray (1981) reports that FPOM comprises 60–90% of total organic matter in Sycamore Creek. At this level, the mean time between egestion and reingestion is 2–3 d. Ladle and Griffiths

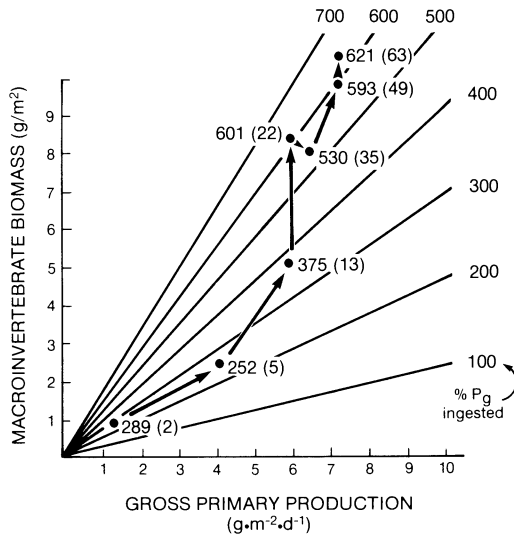


FIG. 1. Relationship between macroinvertebrate biomass and gross primary production ( $P_g$ ) in Sycamore Creek. Isoleths indicate the percentage of gross primary production ingested per day at different biomass and productivity rates. The vector plotted follows the path of each during a 63-d flood recovery sequence in August–October 1979. The percent of  $P_g$  ingested per day is shown numerically at each point along with days since flooding (in parentheses).

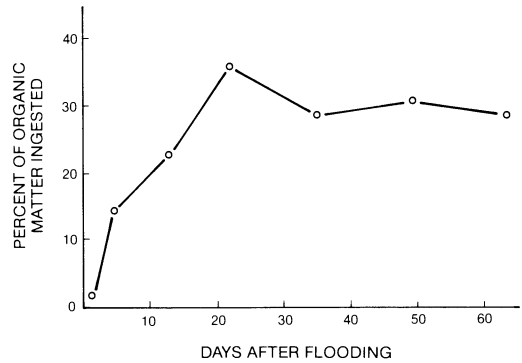


FIG. 2. Percent of total organic matter that was ingested daily by collector macroinvertebrates during a 63-d flood-recovery period in Sycamore Creek, August–October 1979.

(1980) estimate FPOM turnover in a chalk stream at 71–102 d, based on defecation by *Gammarus pulex* and simuliids and reuse by tubificids.

Given this scenario, the strategy of low AE assumes a new complex. If organisms egest a large percentage of ingested food and thus do not process the refractory fraction, what changes in food quality must occur in the environment to warrant the energetic expense of re-collecting and reprocessing, perhaps within a day's time? We propose that bacterial colonization and conditioning improve the quality of feces both in terms of digestibility and nitrogen content, much as terrestrial leaves are conditioned by bacteria and fungi in temperate streams, albeit at slower rates (Triska et al. 1975, Suberkropp and Klug 1976). This idea is not, of course, original to us. Many lotic insects consume feces (Hynes 1970), and fecal matter has been shown to be an adequate food for collectors (Ward and Cummins 1979, Shepard and Minshall 1981). Anderson and Sedell (1979) suggest blackflies strip bacteria from particles and derive nutrition therefrom. Bird and Kaushik (1981) emphasize the importance of bacterial colonization of feces in the cycle of coprophagy.

In Sycamore Creek and by inference in many streams of the desert Southwest, macroinvertebrate communities are dominated by collectors. Not only is their secondary production rate among the highest reported, but their metabolism and food-handling tactics are largely responsible for the rapid turnover of fine par-

ticulate organic matter. The collector macroinvertebrate–FPOM subsystem is thus central to organic matter processing in these ecosystems and a major determinant of desert stream structure and function.

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