Secondary Production of Epilithic Fauna in a Woodland Stream

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ABSTRACT: Epilithic fauna were sampled by placing three sets of 40 cobbles in transects across a riffle in Factory Brook, Massachusetts. One set was sampled monthly from September 1973 to August 1975, allowing 3 months for recolonization. Three Surber samples were collected concurrently during the last 12 months to provide biomass estimates of infauna. Length-wet weight regression equations and dry weight conversion factors were computed for genera; caloric equivalents were obtained from the literature. Surface area of cobbles was determined by a foil-areagraph technique. Secondary production on cobbles was calculated mainly by genus with the modified Hynes method.

Mean standing stock in dry weight (DW) was 0.65 gDW/m² of cobble surface in 1974 and 0.61 gDW/m² in 1975. Insect production on cobbles in 1974 was 4.80 gDW/m²-year and 4.32 gDW/m²-year in 1975, or between 22.3-24.7 kcal/m²-year. Approximately half of the mean biomass and production on cobbles was attributed to four genera, *Epeorus*, *Ephemerella*, *Hydropsyche* and *Acroneuria*. Dipterans constituted 56% of the organisms collected but less than 20% of production; mayflies represented 53% of epilithic production. Annual turnover ratios were 7.4 and 7.1 in 1974 and 1975, respectively, and are a first estimate of community-based P/B̄ for stream benthos in New England. Trophic level production efficiency between primary and secondary consumer groups agreed closely with previous studies on benthic communities in streams and may provide a simplified method for estimating secondary production. Total benthic production on the riffle, based on Surber and cobble sampling, was approximately 12.2 gDW/m²-year.

INTRODUCTION

Research in stream ecology has recently emphasized the productivity of biota to quantify the functional relationships and energy flow between trophic levels. Production studies of invertebrates have generally lagged behind those of algae and fish in streams (Waters, 1969), and this has limited our understanding of the impact and role of invertebrate consumers in detrital and grazing food webs. Estimates of benthic productivity in streams vary widely among regions due to differences in substrate type, food imports, water chemistry, temperature and biota. Community composition and structure is influenced by invertebrate predator/prey interactions, distinct from the more obvious effect of fish predation on invertebrate mortality. However, the significance of invertebrate predation within the benthic community has not been adequately examined (Benke, 1976; Macan, 1977). Productivity of predacious species has often been combined with other consumer groups and has masked the production dynamics between invertebrate predators and their prey. Biological factors such as high diversity and different life cycles in the benthos have

generally impeded a detailed study of all species separately, but community analysis by trophic structure can provide useful generalizations about complex biotic associations (Coffman et al., 1971).

Adequate sampling is a major obstacle to most benthic production work. Limitations of substrate samplers in depth (Coleman and Hynes, 1970; Williams and Hynes, 1974), mesh size (Zelt and Clifford, 1972) and extreme variability among replicate samples (Needham and Usinger, 1956; Chutter, 1972) are best overcome by sampling small quadrats of similar substrate across the stream (Cummins, 1962, 1975; Coffman et al., 1971; Resh, 1975). Artificial substrates can provide quantitative replicates but will not duplicate natural community composition or abundance. These sampling limitations, as well as the high diversity, incomplete taxonomy and habitat specificity of immature aquatic insects, have restricted most production studies to either single species or community treatment by trophic or taxonomic group (Waters, 1977). No previous attempt has been made to estimate total consumer production in a benthic community on a genus-by-genus basis.

In this study, I estimate the production of aquatic insect genera living on cobbles in a Massachusetts stream and compare the relationship between predator/prey productivity in this subcommunity with benthic communities in other lotic systems.

STUDY AREA

Factory Brook (lat 42°21′ N, long 73°01′ W) is a 13-km tributary of the West Branch, Westfield River in Hampshire Co., Mass. This second-order softwater stream drains 22 km² and has a gradient of 18.6 m/km. Stream discharge during the year varies from 0.004 to 2.6 m³/s; mean annual precipitation for the region is 114 cm/year. Land use in the drainage basin is as follows: woodland 90%, cropland and pasture 8%, wetland 1% and urban land 1% (MacConnell, 1975). The forest canopy is a typical mixed northern hardwood-hemlock forest, dominated by yellow birch (*Betula alleghaniensis*), bigtooth aspen (*Populus grandidentata*), red maple (*Acer rubrum*), American elm (*Ulmus americana*), white ash (*Fraxinus americana*) and eastern hemlock (*Tsuga canadensis*). No aquatic macrophytes occur along the stream. Soils are predominantly shallow glacial tills, underlaid by gneiss bedrock.

The study riffle, located 1.4 km above Factory Brook mouth, is 16 m long and 3.9 - 5.6 m wide except during spates and spring runoff. Riffle substrate is composed primarily of coarse particle sizes, ranging from pebbles to boulders. The stream does not freeze over in winter, although ice shelves nearly cover pools and slow riffles; anchor ice is common in February. The fish community in Factory Brook is typical of New England trout streams.

MATERIALS AND METHODS

To sample the biomass and productivity of epilithic fauna, three sets of 40 cobbles were placed in transects across the riffle. Cobbles of approximately 15 cm diam were obtained from adjacent riffles and set in transects of 10 cobbles per row in July 1973. Each 40-cobble set had a volume displacement of 40 liters to approximate equal surface area and was marked with a different-colored, fluorescent paint spot for identification during sampling. Rows were 1 m apart; cobbles were spaced roughly 0.5 m apart and moved closer together during low flow periods to prevent exposure. One 40-cobble set was sampled each month about mid-month from September 1973 to August 1975, allowing 3 months for recolonization.

During each sampling date, cobbles were retrieved using a backup net (nine threads/cm), placed in a bucket and scrubbed underwater with a stiff brush. The backup net was initially fitted with an outer nitex bag (16 threads/cm) to check for small organism losses. Nearly all dislodged invertebrates were retained by the coarser mesh which was used thereafter. Bucket contents were poured into a #100

(149 u) U.S. Standard Sieve and organisms preserved in 70% isopropanol. From September 1974 to August 1975, three Surber samples (nine threads/cm) were taken concurrently for biomass comparison, using a hand cultivator. I collected these samples in transects across the upper riffle, which was denuded of boulders and cobbles, and represented mainly substrate infauna. Ten substrate samples were collected from this upper riffle section with a Proctor soil corer for dry weight particle size analysis.

A 30-day thermograph monitored water temperature at this riffle for the 2-year period, supplemented by maximum-minimum thermometer readings. Mean water velocity during each sample period was based on 10 section readings with a pigmy flowmeter at slightly below mid-depth. Dissolved oxygen, alkalinity, total hardness and pH were monitored with a portable Hach Kit (Hach Chemical Co., Ames, Iowa). Stream discharge was determined from a rating curve for an upstream bridge.

Upon completion of the 2-year sampling period, 10 cobbles from each set were randomly selected and brought to the laboratory for surface area measurements. Heavy-duty aluminum foil was cut to fit each cobble, flattened to conform with surface area covered, and measured with a Bruning areagraph (Bruning Div., Needham, Mass.). The grand mean for the three samples was expanded to a 40-cobble area.

Epilithic organisms were initially sorted to order and placed into 1 mm length classes, each size class being $\pm$ 0.5 mm of the median length. Specimens larger than 2.5 mm total length were identified to genus, counted and measured (excluding cerci and prolegs) under a dissecting microscope with either a millimeter ruler or an ocular micrometer. Organisms less than 2.5 mm and all chironomids were pooled and enumerated by size class from a 10% subsample. Each sample was diluted to a workable density (10-20 organisms/ml), and 10 aliquots, constituting 10% by volume, were withdrawn with a large-bore pipette. Identifications, measurements and counts of taxa were made on a sectioned petri dish under 30 X magnification, and the number expanded to the entire volume.

I obtained wet weight per size class by weighing a series of organisms in each genus. Live specimens were killed in hot water, measured, placed on tissue paper for 1 min to remove surface moisture and weighed on a Mettler balance to the nearest 0.1 mg. Length-weight regression equations for genera were used to convert lengths to weights in monthly samples. To obtain conversion factors for dry weight, the above procedure was followed; representative specimens from each size class were then dried at 50 C for 48 hr and reweighed to obtain a percent wet-weight value. Wet- and dry-weight equivalents for uncommon genera were obtained from closely related taxa (Neves, 1977). Wet weights for Chironomidae were computed according to Hynes and Coleman (1968), assuming a cylindrical shape and a density of 1.05 g/cm.^{3} A mean body length to width of 11:1 was computed from 40 chironomids withdrawn from each of two monthly samples.

Epilithic production was computed mainly by genus using the Hynes and Coleman (1968) method as modified by Hamilton (1969), hereafter called the Hynes method. This method circumvents the problem of species identification by treating the average size frequency distribution of populations over the year as an "average cohort." Numerical losses between adjacent size classes are assigned the organism's weight at midlength point. The number of average cohorts in a year equals the number of size classes (i); average cohort production is therefore multiplied by i to obtain annual production. The sum of the annual productivity values for all taxa approximates net production for the epilithic subcommunity.

Each genus was considered a community resident (cohort component) for only that portion of its life cycle spent on cobbles. Most genera were annual residents while a few uncommon taxa occurred there only as early instars. Maximum length

class values (i) are therefore commensurate with residency times and are assumed constant between years. Tendency for productivity values by the Hynes method to vary with maximum instar size used in computations (Waters and Crawford, 1973) was addressed by assigning i values intermediate for the genus. For example, four species of *Ephemerella* were common epilithic residents with last instar sizes ranging from 7 - 11 mm. For the "ith" class, a length of 9 mm was used in computing production for this genus. Uncommon genera were lumped by maximum size class and similar weights when possible. The production of miscellaneous orders on cobbles was minor and estimated by using their mean biomass and assuming a turnover ratio of five (Waters, 1977). Production estimates for non-univoltine genera and families were corrected for length of larval periods (Cushman *et al.*, 1975; Benke, 1979). Intensive field collections of adults (Neves, 1977, 1978), temporal patterns in the size frequencies of immatures, and the first appearance of early instars in field collections provided enough data to approximate the mean cohort production interval (CPI) in days for multivoltine populations. A production estimate for infauna was obtained by using the mean biomass from Surber sampling and the $P/\overline{B}$ ratio for the cobble subcommunity.

I partitioned consumers into two categories, primary (algae-detritus) and secondary (carnivore), according to Grafius and Anderson (1973) and Shapas and Hilsenhoff (1976). Dry weight values of production were converted to kilocalories with the equivalents of Davis and Warren (1971) for Plecoptera and the values of Cummins and Wuycheck (1971) for other major orders; miscellaneous taxa were assigned the equivalent for Insecta.

RESULTS

Physicochemical.—Weekly maximum and minimum water temperatures for the combined 2-year period ranged from 0 C in February to 21.7 C in mid-August (Fig. 1), with an annual mean of 8.3 C. Several weekly temperature ranges represent single year values due to mechanical failure of the thermograph. Water chemistry values showed only minor fluctuations during the year. Alkalinity (9 - 10 mg/liter) and total hardness (14 - 24 mg/liter) were low, but typical for streams in the area (U. S. Geological Survey, 1973). Dissolved oxygen (9 - 14 mg/liter) was near saturation throughout the year, and *p*H (6.5 - 7.6) fluctuated around neutrality.

Mean water velocity on the riffle was 49 cm/sec (10 - 89 cm/sec); mean depth was 28 cm (21 - 56 cm). Cobble density in adjacent riffles was 6 cobbles/m², and
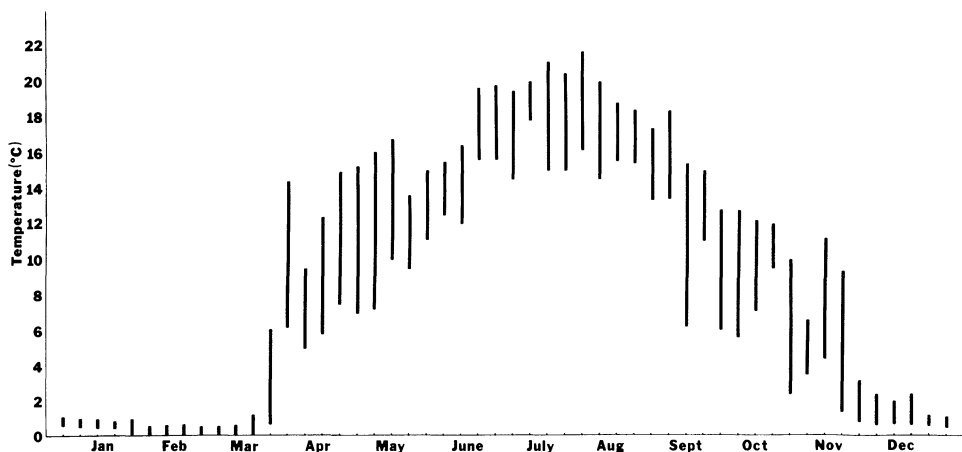

Fig. 1.—The combined weekly range of water temperatures in Factory Brook, 1974 and 1975

riffle substrate, excluding boulders and cobbles, was composed of the following size categories (according to Cummins, 1962): pebble (46.2%), gravel (25.1%), mixed sand (27.0%), silt-clay (1.2%) and organic matter (0.5%).

Mean surface area per cobble from the three 10-cobble samples was 547.5, 534.2 and 551.0 cm², yielding an overall mean of 2.18 m²/40-cobble set. This value included areas of contact with the stream bottom inaccessible to invertebrates, estimated at 5 - 10%. Colonizable surface area was therefore reduced to 2 m²/40 cobbles. No aquatic mosses or filamentous algae colonized the cobbles in this riffle.

Faunal composition.—Insect orders ranked according to numerical abundance on cobbles were Diptera (55.8%), Ephemeroptera (31.9%), Trichoptera (7.3%), Other (3.2%) and Plecoptera (1.8%) for the 2-year period, with little variation between years (Table 1). The two consecutive field seasons, September to August, are designated as 1974 and 1975, respectively. Aquatic insects were most abundant in the autumn, diminishing to minimal numbers by late winter; spring and summer densities were intermediate. The mean number of organisms collected in 1974 was 3917/m² and 3613/m² in 1975. The dipteran peak in July of both years (Table 1) was due to a cohort of *Rheotanytarsus* sp.

The mean standing stock of infauna based on Surber sampling in 1975 was 3088 organisms/m² or 743.5 mgDW/m² (DW = dry weight); mean epilithic density during that year was 3613 organisms/m² or 610.6 mgDW/m² of cobble surface (Table 2). The coarse Surber mesh underestimated numerical abundance, but indicated that a greater biomass existed in the mixed substrate. However, Surber samples represented 1 m² of stream bottom and, consequently, a much larger surface area than that measured on cobbles. Community composition was qualitatively similar between these substrates, although the relative abundance of genera differed. *Glossosoma, Apatania, Agapetus, Epeorus* and *Stenonema* were more abundant on cobbles, while *Pycnopsyche, Isoperla, Leuctra* and *Alloperla* preferred the mixed substrate.

Epilithic biomass and production.—Seasonal changes in epilithic biomass (Table 2) generally reflected differences in numerical abundance during the year (Table 1). Mayflies dominated cobble biomass, followed by caddis flies, stone flies and dipterans; the occurrence of other orders was extremely variable but significant during several months (Table 2). Computations for each taxon within the cobble subcommunity are summarized by mean biomass and production (Table 3). Dry weights of organisms ranged between 18 and 28% of wet-weight values. Miscellaneous orders included Neuroptera, Coleoptera, Odonata, Acarina and Basommatophora, with *Nigronia, Ectopria, Ferrissia* and Hydracarina as the major gravimetric components. Miscellaneous Plecoptera included *Isoperla, Alloperla, Taeniopteryx, Allocapnia, Paracapnia, Leuctra* and *Paraleuctra;* miscellaneous Trichoptera included *Helicopsyche, Psilotreta, Ceraclea, Mystacides, Micrasema* and *Oecetis;* miscellaneous Diptera included *Atherix,* Tipulidae and Blepharoceridae. The length-weight relationship of an intermediate-sized taxon was used to calculate weights for these uncommon taxa, *Alloperla, Lepidostoma* and Tipulidae, respectively.

Several genera of low abundance were paired with closely related genera of similar length-weight and maximum size; these pairs included *Stenonema-Stenacron, Heptagenia-Rhithrogena, Neureclipsis-Polycentropus* and *Paragnetina-Phasganophora.* The length-weight relationship of the dominant pair member was used in computing dry weights. Immature and adult collections from Factory Brook (Neves, 1977) indicated that the following taxa had more than one generation per year: *Glossosoma, Baetis* and *Pseudocloeon* were bivoltine; Simuliidae was trivoltine, and the Chironomidae had approximately four generations per year. *Rheotanytarsus* sp. was the dominant chironomid and had two major and two minor peaks during the year. Although number of generations and generation times for chironomids are highly

TABLE 1.—Monthly composition of epilithic fauna (organisms/m² of cobble surface) in
Factory Brook during the two field seasons (columns 1 and 2)

Month	Diptera		Ephemeroptera		Trichoptera		Plecoptera		Other		Total	
September	4530	4040	1155	1123	1028	1032	169	193	355	375	7237	6763
October	3047	3770	3927	891	572	297	241	89	150	185	7937	5232
November	1498	1000	2049	1504	156	156	92	96	37	17	3832	2773
December	1123	2705	701	1633	104	289	27	70	16	45	1971	4742
January	978	715	510	869	105	134	14	22	9	10	1616	1750
February	880	715	618	935	114	160	6	21	13	10	1631	1841
March	847	1290	571	829	103	173	10	13	17	26	1548	2331
April	957	829	527	564	74	78	8	3	6	20	1572	1494
May	2255	1095	608	779	141	188	19	6	198	239	3221	2307
June	2040	735	1105	2013	93	299	133	254	90	159	3461	3460
July	6530	4320	2453	1536	363	499	27	25	201	146	9574	6526
August	2155	2440	874	1053	74	333	6	84	295	227	3404	4137
Mean	2237	1971	1258	1144	244	303	63	73	116	122	3917	3613
Percent	57.1	54.5	32.1	31.7	6.2	8.4	1.6	2.0	3.0	3.4	100	100

TABLE 2.—Monthly standing stock (mgDW/m²) of epilithic fauna on Factory Brook
cobbles during the two field seasons (columns 1 and 2)

Month	Diptera		Ephemeroptera		Trichoptera		Plecoptera		Other		Total	
September	82.9	147.8	266.1	283.3	263.2	230.1	56.3	192.5	7.3	60.2	675.8	913.9
October	16.2	130.8	1043.7	261.9	272.8	142.7	367.3	137.2	34.8	7.3	1734.8	679.9
November	7.8	18.2	638.7	426.5	120.8	66.1	54.9	113.9	24.7	2.1	846.9	626.8
December	38.9	30.8	215.9	420.9	109.9	169.6	13.1	38.1	....	......	377.8	659.4
January	28.8	7.6	213.8	217.2	90.1	84.7	11.4	195.8	4.9	38.8	349.0	544.1
February	18.6	7.6	226.2	293.8	98.8	135.8	6.5	105.1	....	2.4	350.1	544.7
March	8.8	22.5	191.1	237.9	138.2	152.0	98.2	71.1	40.6	4.0	476.9	487.5
April	25.9	30.5	235.2	213.6	128.5	128.3	140.9	21.5	5.8	0.8	536.3	394.7
May	12.4	3.9	232.8	301.8	244.4	160.9	107.5	81.7	1.1	12.9	598.2	561.2
June	90.4	13.5	247.3	346.9	173.8	130.7	72.2	70.9	13.8	151.6	597.5	713.6
July	20.9	17.4	485.9	301.9	179.0	211.8	73.5	20.9	74.3	......	833.6	552.0
August	39.0	40.0	179.5	197.9	19.4	150.5	95.1	141.4	51.5	120.2	384.5	650.0
Mean	32.5	39.2	348.0	292.0	153.2	146.9	91.4	99.1	21.6	33.4	646.7	610.6
Percent	5.0	6.4	53.8	47.8	23.7	24.1	14.1	16.2	3.4	5.5	100.0	100.0

variable, I treated this family according to its most abundant representative. Hemivoltine genera included *Acroneuria, Paragnetina* and *Phasganophora,* while *Allonarcys* appeared to have a 3-year life cycle. Production values for these nonunivoltine taxa (Table 3) are corrected for mean length of immature life, according to my field collections (Neves, 1977, 1978).

Total mean biomass on cobbles amounted to 646.7 mgDW/m² in 1974 and 610.6 mgDW/m² in 1975 (Table 3). Ephemeroptera, Trichoptera, Plecoptera and Diptera were ranked in order of biomass importance. Estimated annual production on cobbles during 1974 was 4804.9 mgDW/m²-year and 4315.1 mgDW/m²-year in 1975 (Table 3). Most of the invertebrate production on cobbles was attributed to relatively few abundant and common species, although many more uncommon and rare species were collected over the 2-year sampling period. A complete list of Trichoptera,

TABLE 3.—Mean standing stock (mgDW/m²) and production (mgDW/m²-yr) of epilithic fauna in Factory Brook, 1974 and 1975

Taxa	Standing stock		Production		Mean Annual
	1974	1975	1974	1975	P/B̄
Trichoptera					
Hydropsyche spp.	51.6	50.0	320.9	308.0	6.2
Neophylax spp.	43.6	20.8	170.5	80.3	3.9
Glossosoma nigrior	26.3	26.0	303.9	304.1	11.6
Apatania incerta	13.4	18.4	19.3	26.6	1.4
Lepidostoma spp.	6.3	7.3	46.0	60.5	7.8
Rhyacophila spp.	4.3	5.8	19.6	22.9	4.2
Neureclipsis-Polycentropus spp.	3.0	3.4	16.5	19.3	5.6
Hydroptilidae	2.1	2.2	7.3	7.4	3.4
Cheumatopsyche spp.	1.2	9.9	6.8	69.5	6.9
Dolophilodes distinctus	0.6	0.7	2.6	2.4	3.8
Agapetus pinatus	0.3	1.1	0.7	3.2	2.8
Misc. Trichoptera	0.5	1.3	1.5	4.8	3.5
Subtotal	153.2	146.9	915.6	909.0	6.1
Ephemeroptera					
Epeorus spp.	184.1	113.1	1212.8	759.0	6.6
Ephemerella spp.	80.4	94.4	747.9	774.7	8.7
Stenonema-Stenacron spp.	36.3	22.0	243.6	154.8	6.8
Baetis levitans	25.5	33.2	243.6	349.1	10.1
Pseudocloeon carolina	12.4	14.0	128.0	144.1	10.3
Paraleptophlebia spp.	6.4	9.6	18.7	30.6	3.1
Heptagenia-Rhithrogena spp.	2.9	5.7	9.9	21.4	3.6
Subtotal	348.0	292.0	2604.5	2233.7	7.6
Plecoptera					
Acroneuria spp.	54.8	55.2	195.2	199.9	3.6
Allonarcys biloba	14.7	26.6	40.1	72.8	2.7
Paragnetina-Phasganophora spp.	9.2	1.1	23.2	2.9	2.5
Taenionema atlanticum	1.5	4.0	4.9	12.8	3.2
Misc. Plecoptera	11.2	12.2	58.6	69.0	5.5
Subtotal	91.4	99.1	322.0	357.4	3.6
Diptera					
Simuliidae	21.6	6.5	375.8	84.7	16.4
Chironomidae	7.1	10.2	467.4	487.4	55.2
Misc. Diptera	3.8	22.5	11.6	75.9	3.3
Subtotal	32.5	39.2	854.8	648.0	21.0
Misc. orders					
	21.6	33.4	108.0	167.0	5.0
Total	646.7	610.6	4804.9	4315.1	7.3

Ephemeroptera and Plecoptera collected from Factory Brook is available elsewhere (Neves, 1977, 1978). Mean annual $P/\overline{B}$ values for the major insect orders were as follows: Diptera 21.0, Ephemeroptera 7.6, Trichoptera 6.1 and Plecoptera 3.6. Turnover ratios for the various species were in agreement with $P/\overline{B}$ values from previous studies in inland waters (Waters, 1977). The unusually low value (1.4) for *Apatania incerta* was attributed to late instar aggregation on cobbles for pupation; this behavior exaggerated mean biomass estimates in both years (Table 3).

Community composition was similar for both years but shifts in population abundance were also evident. *Neophylax, Epeorus, Stenonema-Stenacron, Paragnetina-Phasganophora* and Simuliidae were more abundant in 1974, whereas *Cheumatopsyche, Paraleptophlebia, Heptagenia-Rhithrogena, Taenionema* and miscellaneous Diptera were more common in 1975 (Table 3). In spite of these intra-order fluctuations, subtotals for each year were in agreement. Approximately half of the mean biomass and production on cobbles was attributed to four genera, *Epeorus, Ephemerella, Hydropsyche* and *Acroneuria*. The relative importance of each insect order in the subcommunity depended on the mode of analysis (Table 4). For example, dipterans contributed more than half of the insect numbers but less than 20% of the production. Conversely, mayflies were less than one-third of the organisms collected but comprised more than half of all production (Table 4). Subcommunity $P/\overline{B}$ values were 7.4 in 1974 and 7.1 in 1975.

Production by trophic level.—Based on the food habits review of Grafius and Anderson (1973) and laboratory observations, the following genera were considered entirely carnivorous: *Rhyacophila, Neureclipsis, Polycentropus, Acroneuria, Paragnetina* and miscellaneous Plecoptera. *Hydropsyche* and *Cheumatopsyche* were omnivores and treated as 50% carnivorous. Miscellaneous orders, because of two large *Nigronia serricornis*, were also treated as half carnivorous (by weight). Based on my primary and secondary consumer categories, predators made up 18.5 - 20.4% of the biomass and contributed 11.1 - 13.6% of invertebrate production on cobbles (Table 5). The remaining biomass (79.6 - 81.5%) and production (86.4 - 88.9%) was attributed to herbivores and detritivores. The contribution of epilithic primary consumer production to secondary consumer production was not assessed. Annual energy output, according to the caloric equivalents of Cummins and Wuycheck (1971) and Davis and Warren (1971), was 24.7 kcal/m²-year in 1974 and 22.3 kcal/m²-year in 1975.

TABLE 4.—Relative importance of insect orders in the epilithic subcommunity by number, biomass and production

Order	% by Number 1974/1975		% by Biomass 1974/1975		% by Production 1974/1975	
Ephemeroptera	32.1	31.7	53.8	47.8	54.1	51.6
Trichoptera	6.2	8.4	23.7	24.1	19.0	21.0
Diptera	57.1	54.5	5.0	6.4	17.8	15.0
Plecoptera	1.6	2.0	14.1	16.2	6.9	8.5
Other	3.0	3.4	3.4	5.5	2.2	3.9

TABLE 5.—Composition of the epilithic subcommunity based on primary (herbivore-detritivore) and secondary (carnivore) consumer groups

Trophic level	Mean biomass (mgDW/m²) 1974	1975	Production (mgDW/m²-year) 1974	1975
Primary consumers	527.0 (81.5%)	486.2 (79.6%)	4273.9 (88.9%)	3728.8 (86.4%)
Secondary consumers	119.7 (18.5%)	124.4 (20.4%)	531.0 (11.1%)	586.3 (13.6%)
Total	646.7	610.6	4804.9	4315.1

DISCUSSION

Epilithic sampling.—The composition of epilithic fauna in streams has worldwide similarity (Hynes, 1970) and is influenced by water velocity, temperature, food availability and the life history stages of organisms (Meadows and Campbell, 1972). Although I did not quantify differences in biomass among cobbles in a transect, it was evident during sampling that midstream cobbles supported the greatest biomass. This study and others (Cummins, 1962; Resh, 1975) reiterate the importance of using average insect densities determined by transect sampling for production estimates. The use of large unimpacted cobbles across the stream provided the following advantages in sampling: measurable surface area, uniform substrate type and stability, mean water velocity effects and colonization sites for all epilithic fauna. This sampling method was also more reliable in density estimates than mixing substrate types, due partly to the competitive spacing of aquatic insects by aggression (Scott, 1958; Edington, 1965). Coincident to this study, Stout and Vandermeer (1975) found that 40 rock samples from streams approached the asymptotic value of epilithic species diversity in riffles.

Areagraph use for surface area determinations provided consistent values for similar-sized cobbles and in replicate trials. Initial area measurements on geometric figures of known surface area were helpful in perfecting the foil-areagraph technique. Other methods of determining surface area were tested (Schrader, 1932; Calow, 1972) but proved more variable.

Benthic productivity.—Most secondary production methods for invertebrates (for review of methods, *see* Edmondson and Winberg, 1971; Emondson, 1974; Waters, 1977) are only applicable to populations with identifiable cohorts. The Hynes method provided the only feasible means of treating such a diverse subcommunity and has been used in other benthic studies to overcome the cohort identification problem (*e.g.*, Fisher and Likens, 1973; Benke and Waide, 1977). My treatment of the subcommunity by generic components followed as closely as possible the five assumptions of the method (Hamilton, 1969) in an attempt to improve the accuracy of production values and reduce the likelihood of overestimation. Slight overestimates would compensate for small organism losses in sampling (Waters, 1969; Waters and Crawford, 1973) and exuvial losses, which are neglected in most production estimates. These cuticle losses at molting can reach 4 - 16% of dry body weight (McDiffett, 1970).

The only other estimate of community production in a stream riffle was obtained from Bear Brook, New Hampshire (Fisher, 1970; Fisher and Likens, 1973). Monthly Surber sampling over a 6-month period yielded a benthic invertebrate productivity of 4.8 gDW/m²-year. I believe that Fisher's estimate is low by roughly a factor of two, since Surber sampling is approximately 50% efficient in biomass collection (Radford and Hartland-Rowe, 1971; Kroger, 1972). To obtain a comparable estimate of total benthic production for my study riffle, mean Surber standing stock, corrected for sampler inefficiency (X 2), was multiplied by the annual turnover ratio (7.1) for the epilithic subcommunity in 1975. Hyporheal biomass was not significant in this riffle because of shallow bedrock, which limited sample depth to approximately 15 cm with the hand cultivator. This estimate of infaunal production, determined in an area with no cobbles, plus epilithic production based on cobble density in Factory Brook riffles, gave a total invertebrate production of 12.2 gDW/m²-year. Estimates of benthic biomass and productivity in these two New England streams are considerably less than available data would indicate for other streams in the U.S.A. (Waters, 1977), but indicate the low aquatic productivity at all trophic levels in this region (Brooks and Deevey, 1963; Webster and Wallace, 1975; Fisher and Carpenter, 1976).

    Numerous studies have correlated biotic productivity with water alkalinity (Waters and Ball, 1957; Neel, 1973) and conductivity (Rawson, 1960; O'Connor and Power, 1976). These two chemical parameters may be indicative of nutrient levels available for primary production (Hall *et al.*, 1971; Brylinsky and Mann, 1973) or be related to the degree of microbial activity for decomposition or dissolved organic matter uptake (Willoughby, 1974). Most heterotrophic, softwater streams in deciduous forests are unproductive (Mackay and Kalff, 1969; Fisher and Likens, 1973), and softwater streams through coniferous forests are even less productive (Woodall and Wallace, 1972; O'Connor and Power, 1976). Regional geology, hydrology and vegetation control the availability of chemical constituents to running waters and appear to play a significant role in defining a woodland stream's productive capacity at all trophic levels.

    Trophic relationships.—Cummins (1975) defined four functional trophic groups among stream invertebrates; grazers and scrapers, shredders, collectors and predators. All of these consumers are predominantly polyphagous (Cummins, 1973), with feeding mechanisms adapted to food availability and particle size rather than specific food type. Most macroconsumers feed on detritus during at least part of their life cycle (Coffman *et al.*, 1971), much of it allochthonous in origin. The seasonal input of leaf litter into woodland streams serves not only as an energy reservoir for all organisms in early life or during periods of food scarcity, but also determines the optimal growth periods of herbivore and detritivore populations (Petersen and Cummins, 1974). The temperature-compensated activity and production of primary consumers during the autumn and winter (Cummins, 1974) may have an effect on predatory population development as well. Most stream predators are feeding generalists and serve in part as a biological control on primary consumers. Brocksen *et al.* (1968) demonstrated that benthic carnivores had a greater feeding efficiency and effect on prey density than seasonal or environmental factors. Although prey size and size of insect predator are correlated (Siegfried and Knight, 1976), the staggered life cycles of potential prey species in Factory Brook resulted in seasonal availability to predators. This seasonality may have had as much effect on food choice as size selection. Vulnerable prey may be the surplus beyond carrying capacity, cropped initially by invertebrate predators and secondarily by fishes. Invertebrate predators were therefore potential prey and competitors with many stream fishes in Factory Brook.

    Trophic studies of aquatic communities have focused on energy transport through food webs to discern predictable relationships between populations of different trophic levels (Grodzinski *et al.*, 1975). To compare invertebrate production at the primary (algae-detritus) and secondary consumer levels, I partitioned production estimates for several stream communities into these two categories (Table 6). The trophic level production efficiency (TLPE), defined as the ratio between secondary consumer production and primary consumer production (Odum, 1971), was computed. This production ratio tends to average and summarize various types of ecological efficiencies between and within trophic levels. I emphasize that TLPE is just a ratio and not a conversion efficiency. All values are in caloric equivalents except for Hynes (1961); his index units are based on the relative abundance of species, corrected for size differences among organisms.

    Ecological efficiency among ecosystems is not constant (Turner, 1970), but production efficiency of similar communities within the same type of ecosystem appears to be relatively constant (Table 6). The interaction between predator and prey populations is a consequence of local variables (Slobodkin, 1972), but has a relationship that appears fairly consistent for stream benthos (13 - 14%). The range of TLPE for Cone Spring and Root Spring results from the speculated energy budget

TABLE 6.—Estimates of invertebrate production efficiency between primary and secondary consumers in lotic systems

Ecosystem	Substrate	1° Consumer (P_{n-1}) kcal/m²-year	2° Consumer (P_n) kcal/m²-year	Production efficiency (P_n/P_{n-1}) %	Reference
Streams					
Middle Oconee River, Georgia	rock outcrop	278.0	36.6	13.2	Nelson and Scott, 1962
Thames River, England	mixed	127.1	17.4	13.7	Mann, 1972
Factory Brook, Massachusetts	cobble	20.65	2.84	13.8	This study
Afon Hirmant, Wales	mixed	941[1]	122[1]	13.0	Hynes, 1961
Springs					
Cone Spring, Iowa	sand	643.1	77.2-160.8	12-25	Tilly, 1968
Root Spring, Massachusetts	mud	208.0	32.0-121.0	15-58	Teal, 1957
Silver Springs, Florida	mixed	1478.0	67.0[2]	4.5	Odum, 1957[3]

[1] Index units
[2] Mainly fishes
[3] As corrected in Kormondy, 1965

of the flatworm predator, *Phagocata* sp. The efficiency value depends upon how this predator's role as both a secondary and tertiary consumer is partitioned and whether mucus production is considered true tissue elaboration or represents a form of energy expenditure for mobility and prey capture. If mucus production is not considered a form of tissue production, then TLPE for streams and these springs are in agreement. Production studies in lentic environments are too incomplete for comparison, although a mean TLPE of 13% for zoobenthos was obtained in three Russian lakes (Winberg *et al.*, 1972). These data suggest that invertebrate predator/prey relationships play a dominant role in structuring benthic communities.

Estimating benthic production.—The relative constancy of trophic level production efficiency in benthic communities (Table 6) suggests a possible shortcut method for estimating invertebrate productivity in streams. Annual production of invertebrate carnivores in steady-state communities could be used to compute herbivore-detritivore production, assuming a TLPE of *e.g.*, 13%. Considering the sampling, sorting, identification and other potential errors in any estimate of benthic production, even small deviations around this efficiency value would provide good estimates with minimal effort. Obviously, more detailed studies are necessary to test the validity of this "trophic constant" in other streams and the effect of environmental disturbances on trophic structure. The treatment of predator-resistant consumers such as bivalve mollusks and polytrophic crayfish needs evaluation; predator/harvestable prey may be the more appropriate production ratio for trophic relationships. Predatory fishes may be the key species in defining the contribution of large invertebrates to benthic community structure (Stein and Magnuson, 1976).

Another potential estimator of benthic production is the annual turnover ratio for the community. Trophic models of streams which use functional groups in energy flow diagrams presently lack enough data on community-based food webs and trophic efficiencies to predict the net productivity of a benthic community. A search of regularities in the turnover ratio to circumvent the involved procedures of computing secondary production shows some promise (Winberg, 1971; Zaika, 1973; Waters, 1977). An annual $P/\overline{B}$ ratio of 3.5 - 5 for univoltine freshwater invertebrates (Waters, 1969, 1977) can be used to approximate species productivity from mean biomass data, but no community-based $P/\overline{B}$ ratios are available. Annual turnover in a community depends on species composition, cohort voltinism, chemical parameters of the stream and many other biotic and abiotic factors. Year-round sampling is essential for accuracy, since seasonal changes in standing stock and production must be considered. Multivoltine species were more abundant than hemivoltine species in Factory Brook; the annual $P/\overline{B}$ ratio was therefore larger than the 3.5 - 5 values for univoltine species. Chironomidae had the highest $P/\overline{B}$ ratio (55.2) in the subcommunity; bivoltine species had $P/\overline{B}$ ratios between 10.1 and 11.6. The mean annual $P/\overline{B}$ ratio of ca. 7.3 for the cobble subcommunity is a first estimate for benthos in the Northeast and will hopefully lead to similar studies in other geographic regions. Both trophic level production efficiency and annual $P/\overline{B}$ ratios are likely candidates for simplifying the estimation of benthic production and deserve further consideration along with other indirect methods currently available (Illies, 1971; Spier and Anderson, 1974).

LITERATURE CITED

BENKE, A. C. 1976. Dragonfly production and prey turnover. *Ecology*, **57**:915-927.

————. 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. *Limnol. Oceanogr.*, **24**:168-171.

———— AND J. B. WAIDE. 1977. In defense of average cohorts. *Freshwater Biol.*, **7**:61-63.

BROCKSEN, R. W., G. E. DAVIS AND D. E. WARREN. 1968. Competition, food consumption, and production of sculpins and trout in laboratory stream communities. *J. Wildl. Manage.*, **32**:51-75.

BROOKS, J. L. AND E. S. DEEVEY, JR. 1963. New England, p. 117-162. *In:* D. G. Frey (ed.). Limnology in North America. Univ. Wis. Press, Madison.

BRYLINSKY, M. AND K. H. MANN. 1973. An analysis of factors governing productivity in lakes and reservoirs. *Limnol. Oceanogr.*, **18**:1-14.

CALOW, P. 1972. A method for determining the surface areas of stones to enable quantitative density estimates of littoral stonedwelling organisms to be made. *Hydrobiologia*, **40**: 37-50.

CHUTTER, F. M. 1972. A reappraisal of Needham and Usinger's data on the variability of a stream fauna when sampled with a Surber sampler. *Limnol. Oceanogr.*, **17**:139-141.

COFFMAN, W. P., K. W. CUMMINS AND J. C. WUYCHECK. 1971. Energy flow in a woodland stream ecosystem: I. Tissue support trophic structure of the autumnal community. *Arch. Hydrobiol.*, **68**:230-276.

COLEMAN, M. J. AND H. B. N. HYNES. 1970. The vertical distribution of the invertebrate fauna in the bed of a stream. *Limnol. Oceanogr.*, **15**:31-40.

CUMMINS, K. W. 1962. An evaluation of some techniques for the collection and analysis of benthic samples with special emphasis on lotic waters. *Am. Midl. Nat.*, **67**:477-504.

————. 1973. Trophic relations of aquatic insects. *Annu. Rev. Entomol.*, **18**:183-206.

————. 1974. Structure and function of stream ecosystems. *BioScience*, **24**:631-641.

————. 1975. Macroinvertebrates, p. 170-198. *In:* B. A. Whitton (ed.). River ecology. Univ. Calif. Press, Berkeley.

———— AND J. C. WUYCHECK. 1971. Caloric equivalents for investigations in ecological energetics. *Verh. Int. Ver. Limnol.*, **18**:1-158.

CUSHMAN, R. M., J. W. ELWOOD AND S. G. HILDEBRAND. 1975. Production dynamics of *Alloperla mediana* Banks (Plecoptera: Chloroperlidae) and *Diplectrona modesta* Banks (Trichoptera:Hydropsychidae) in Walker Branch, Tennessee. *Oak Ridge Natl. Lab. Environ. Sci. Div. Publ.*, **785**:1-66.

DAVIS, G. E. AND C. E. WARREN. 1971. Estimation of food consumption rates, p. 227-248. *In:* W. E. Ricker (ed.). Methods for assessment of fish production in fresh waters. Blackwell Sci. Publ., Edinburgh.

EDINGTON, J. M. 1965. The effect of water flow on populations of net-spinning Trichoptera. *Verh. Int. Ver. Limnol.*, **13**:40-48.

EDMONDSON, W. T. 1974. Secondary production. *Ibid.*, **20**:229-272.

———— AND G. G. WINBERG. 1971. A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17. 358 p.

FISHER, S. G. 1970. Annual energy budget of a small stream ecosystem: Bear Brook, West Thornton, New Hampshire. Ph.D. Dissertation, Dartmouth College, Hanover, N.H. 97 p.

———— AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. *Ecol. Monogr.*, **43**:421-439.

———— AND S. R. CARPENTER. 1976. Ecosystem and macrophyte primary production of the Fort River, Massachusetts. *Hydrobiologia*, **47**:175-187.

GRAFIUS, E. AND N. H. ANDERSON. 1973. Literature review of foods of aquatic insects. Int. Rep. 129, Coniferous Forest Biome. 52 p.

GRODZINSKI, W., R. Z. KLEKOWSKI AND A. DUNCAN. 1975. Methods for ecological bioenergetics. IBP Handbook No. 24. 367 p.

HALL, D. J., W. E. COOPER AND E. E. WERNER. 1971. An experimental approach to the production dynamics and structure of freshwater animal communities. *Limnol. Oceanogr.*, **15**: 839-928.

HAMILTON, A. L. 1969. On estimating annual production. *Ibid.*, **14**:771-782.

HYNES, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. *Arch. Hydrobiol.*, **57**:344-388.

————. 1970. The ecology of running waters. Univ. Toronto Press, Toronto. 555 p.

————— AND M. J. COLEMAN. 1968. A simple method of assessing the annual production of stream benthos. *Limnol. Oceanogr.,* **13**:569-573.

ILLIES, J. 1971. Emergenze 1969 on Breitenbach (Schlitz studies on productivity, no. 1). *Arch. Hydrobiol.,* **69**:14-59.

KORMONDY, E. J. 1965. Readings in ecology. Prentice-Hall, Inc., Englewood Cliffs, N.J. 219 p.

KROGER, R. L. 1972. Underestimation of standing crop by the Surber sampler. *Limnol. Oceanogr.,* **17**:475-478.

MACAN, T. T. 1977. The influence of predation on the composition of fresh-water animal communities. *Biol. Rev.,* **52**:45-70.

MACCONNELL, W. P. 1975. Remote sensing 20 years of change in Hampshire County, Massachusetts, 1952-1972. *Mass. Agric. Exp. Stn. Res. Bull.,* **627**:1-91.

MACKAY, R. J. AND J. KALFF. 1969. Seasonal variation in standing crop and species diversity of insect communities in a small Quebec stream. *Ecology,* **50**:101-109.

MANN, K. H. 1972. The analysis of aquatic ecosystems, p. 1-14. *In:* R. B. Clark and R. J. Wootton (eds.). Essays in hydrobiology. Townsend and Sons, Ltd., Great Britain.

MCDIFFETT, W. F. 1970. The transformation of energy by a stream detritivore, *Pteronarcys scotti* (Plecoptera). *Ecology,* **51**:975-988.

MEADOWS, P. S. AND J. I. CAMPBELL. 1972. Habitat selection by aquatic invertebrates. *Adv. Mar. Biol.,* **10**:271-382.

NEEDHAM, P. R. AND R. L. USINGER. 1956. Variability in the macrofauna of a single riffle in Prosser Creek, California, as indicated by the Surber sampler. *Hilgardia,* **24**:383-409.

NEEL, J. K. 1973. Biotic character as related to stream mineral content. *Trans. Am. Microsc. Soc.,* **92**:404-415.

NELSON, D. J. AND D. C. SCOTT. 1962. Role of detritus in the productivity of a rock-outcrop community in a Piedmont stream. *Limnol. Oceanogr.,* **7**:396-413.

NEVES, R. J. 1977. Species composition, epilithic faunal production, and movements of *Pycnopsyche guttifer* (Trichoptera:Limnephilidae) in Factory Brook, Westfield River, Massachusetts. Ph.D. Dissertation, Univ. of Massachusetts, Amherst. 177 p.

————. 1978. Seasonal succession and diversity of stoneflies (Plecoptera) in Factory Brook, Massachusetts. *J. N.Y. Entomol. Soc.,* **86**:144-152.

O'CONNOR, J. F. AND G. POWER. 1976. Production by brook trout (*Salvelinus fontinalis*) in four streams in the Matamek Watershed, Quebec. *J. Fish. Res. Board Can.,* **33**:6-18.

ODUM, E. P. 1971. Fundamentals of ecology. Saunders Co., Philadelphia. 574 p.

ODUM, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. *Ecol. Monogr.,* **27**:55-112.

PETERSEN, R. C. AND K. W. CUMMINS. 1974. Leaf processing in a woodland stream. *Freshwater Biol.,* **4**:343-368.

RADFORD, D. S. AND R. HARTLAND-ROWE. 1971. Emergence patterns of some Plecoptera in two mountain streams in Alberta. *Can. J. Zool.,* **49**:657-662.

RAWSON, D. S. 1960. A limnological comparison of twelve large lakes in northern Saskatchewan. *Limnol. Oceanogr.,* **5**:195-211.

RESH, V. H. 1975. The use of transect sampling in estimating single species production of aquatic insects. *Verh. Int. Ver. Limnol.,* **19**:3089-3094.

SCHRADER, T. 1932. Uber die moglichkeit einer quantitativen undersuchung der uferund bodentierwelt flussender gewasser. *Z. Fisch. Deren Hilfswiss,* **30**:105-127.

SCOTT, D. 1958. Ecological studies on the Trichoptera of the River Dean, Cheshire. *Arch. Hydrobiol.,* **54**:340-392.

SHAPAS, T. J. AND W. L. HILSENHOFF. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera, and Trichoptera. *Great Lakes Entomol.,* **9**:175-188.

SIEGFRIED, C. A. AND A. W. KNIGHT. 1976. Prey selection by a setipalpian stonefly nymph, *Acroneuria (Calineuria) californica* Banks. *Ecology,* **57**:603-608.

SLOBODKIN, L. B. 1972. On the inconstancy of ecological efficiency and the form of ecological theories. *Trans. Conn. Acad. Arts Sci.,* **44**:293-305.

SPEIR, J. A. AND N. H. ANDERSON. 1974. Use of emergence data for estimating annual production of aquatic insects. *Limnol. Oceanogr.,* **19**:154-156.

STEIN, R. A. AND J. J. MAGNUSON. 1976. Behavioral response of crayfish to a fish predator. *Ecology,* **57**:751-761.

STOUT, J. AND J. VANDERMEER. 1975. Comparison of species richness for stream-inhabiting insects on tropical and mid-latitude streams. *Am. Nat.,* 109:263-280.

TEAL, J. M. 1957. Community metabolism in a temperate cold spring. *Ecol. Monogr.,* 27: 283-302.

TILLY, L. J. 1968. The structure and dynamics of Cone Spring. *Ibid.,* 38:167-197.

TURNER, F. B. 1970. The ecological efficiency of consumer populations. *Ecology,* 51:741-742.

U. S. GEOLOGICAL SURVEY. 1973. Water resources data for Massachusetts, New Hampshire, Rhode Island, Vermont — Parts 1 and 2. Surface water records; water quality records, 1971. 401 p.

WATERS, T. F. 1969. The turnover ratio in production ecology of fresh-water invertebrates. *Am. Nat.,* 103:173-185.

———. 1977. Secondary production in inland waters. *Adv. Ecol. Res.,* 10:91-164.

——— AND R. C. BALL. 1957. Lime application to a soft-water, unproductive lake in northern Michigan. *J. Wildl. Manage.,* 21:385-391.

——— AND G. W. CRAWFORD. 1973. Annual production of a stream mayfly population: a comparison of methods. *Limnol. Oceanogr.,* 18:286-296.

WEBSTER, J. R. AND J. B. WALLACE. 1975. Productivity of southeastern stream ecosystems, p. 64-77. *In:* U.S. Forest Service, Symposium on trout habitat research and management proceedings. SE Forest Exp. Stn., Asheville, N.C.

WILLIAMS, D. D. AND H. B. N. HYNES. 1974. The occurrence of benthos deep in the substratum of a stream. *Freshwater Biol.,* 4:1-23.

WILLOUGHBY, L. G. 1974. Decomposition of litter in fresh water, p. 659-681. *In:* C. H. Dickinson and G. J. F. Pugh (eds.). Biology of plant litter decomposition, Vol. 2. Academic Press, New York.

WINBERG, G. G. 1971. Methods for the estimation of production of aquatic animals. Academic Press, New York. 175 p.

———, V. A. BABITSKY, S. I. GAVRILOV, G. V. GLADKY, I. S. ZAKHARENKOV, R. Z. KOVALEVSKAYA, T. M. MIKHEEVA, P. S. NEVYADOMSKAYA, A. P. OSTAPENYA, P. G. PETROVICH, J. S. POTAENKO AND O. F. YAKUSHKO. 1972. Biological productivity of different types of lakes, p. 383-404. *In:* Z. Kajak and A. H. Ilkowska (eds.). Productivity problems of freshwaters. IBP-UNESCO Symposium, Poland.

WOODALL, W. R. AND J. B. WALLACE. 1972. The benthic fauna in four small southern Appalachian streams. *Am. Midl. Nat.,* 88:393-407.

ZAIKA, V. E. 1973. Specific production of aquatic invertebrates. John Wiley and Sons, New York. 154 p.

ZELT, K. A. AND H. F. CLIFFORD. 1972. Assessment of two mesh sizes for interpreting life cycles, standing crop, and percentage composition of stream insects. *Freshwater Biol.,* 2:259-269.