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INVERTEBRATE PRODUCTIVITY IN A SUBTROPICAL BLACKWATER RIVER: THE IMPORTANCE OF HABITAT AND LIFE HISTORY[1]

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Abstract. Habitat and life history are critical elements in assessing the production dynamics of invertebrates and their role in aquatic ecosystems. We studied invertebrate productivity at two sites in a subtropical blackwater river (the Satilla) in the Lower Coastal Plain of Georgia, USA, and found that submerged wooden substrates, or snags, are heavily colonized by aquatic insects. We compared invertebrate productivity on the snag habitat with productivity in the sandy benthic habitat of the main channel, and the muddy benthic habitat of the backwaters. The size-frequency method was applied to individual taxa in order to determine total invertebrate productivity. Emphasis was placed on the importance of the length of larval life, or the cohort production interval, in determining biomass turnover rates.

The diversity of taxa was much higher on the snag habitat than in either of the benthic habitats. Filter-feeding caddisflies (especially *Hydropsyche* spp.) and black flies (*Simulium* spp.) were the major consumers on the snag habitat. Several species of midges, mayflies, and beetles also were abundant. Total densities, standing stock biomass, and production were very high for primary consumers on snags. Annual production was 51.9 and 67.1 $g\cdot m^{-2}\cdot yr^{-1}$ (dry mass per surface area of snag, or effective habitat) for the two sites. Hellgrammites, dragonflies, and stoneflies were the major insect predators colonizing snags, and their production was 5.5 and 5.2 $g\cdot m^{-2}\cdot yr^{-1}$ (effective habitat). Annual production/biomass ratios ($P/\bar{B}$) were usually 5–10 for insects that had univoltine or bivoltine life cycles. Annual $P/\bar{B}$ estimates were very high for midges (>100) and black flies (>70), since length of larval life was estimated to be very short.

The sandy-substrate benthos consisted almost exclusively of very small midges with oligochaetes of lesser abundance. Densities were quite high ($>20\,000/m^2$), but biomass was very low ($\approx$ 100 mg/m^2 or less). Production of primary consumers was >11 $g\cdot m^{-2}\cdot yr^{-1}$ with a very high estimate of annual $P/\bar{B}$ (166–227). The major predators were Ceratopogonidae (biting midges) larvae with an annual production of 1.6–2.6 $g\cdot m^{-2}\cdot yr^{-1}$. The muddy-substrate benthos consisted primarily of oligochaetes (*Limnodrilus*) and midges. Annual production was $\approx$7–10 $g\cdot m^{-2}\cdot yr^{-1}$ for primary consumers. The major predators were larger Tanypodinae midges.

On a substrate surface area basis, standing stock biomass on snags was 20–50 times higher than in the sandy habitat and 5–10 times higher than in the muddy habitat. Production on snags was only 3–4 times higher than production in the benthic habitats, with higher annual $P/\bar{B}$ in the latter. The production estimates for the snag habitat are among the highest yet reported for lotic ecosystems, and it appears that production on snags is limited by available substrate. Habitat areas per length of shoreline were estimated so that we could approximate relative amounts of biomass and production for a stretch of river. Although the snag habitat accounted for only $\approx$6% of the effective habitat substrate over a stretch of river, it was responsible for over half of invertebrate biomass, and $\approx$15–16% of production.

Taxa within each habitat were categorized to functional feeding groups, and habitat-specific functional groupings were evaluated using numbers, biomass, and production. Filtering collectors predominated on snags, and gathering collectors in benthic habitats. When corrected for habitat abundance, the distribution of biomass among filtering collectors, gathering collectors, and predators was very close. However, the distribution of production was $\approx$12% filtering collectors, 71% gathering collectors, and 17% predators. We suggest that production is the most meaningful parameter to consider in functional group analysis and that the use of numbers or biomass alone can sometimes result in misleading conclusions. As a middle order (5th–6th) stream, the distribution of production or biomass among functional groups in the Satilla River differs considerably from that predicted by the river continuum concept, predicting a high percentage of grazing consumers.

Key words: Aquatic invertebrates; blackwater river; functional groups; habitat; life cycle; secondary production; snags; spatial distribution; streams; turnover rates; United States coastal plain.

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INTRODUCTION

Recent studies have provided many new insights to our understanding of stream function and the qualitative role of invertebrates in processing organic matter (e.g., Cummins 1973, Fisher and Likens 1973, Boling et al. 1975, Fisher 1977, Liaw and MacCrimmon 1977, Wallace et al. 1977, Vannote et al. 1980, and Wallace and Merritt 1980). In spite of these advances, there has been relatively little detailed quantification of the overall role played by stream animals, particularly the invertebrates. An important aspect of such quantification is estimating the secondary production of the various species, or at least production of the functional feeding groups (e.g., see Cummins and Klug 1979), but sampling problems and difficulties in applying production methods have frustrated benthic ecologists for years. The present study represents an attempt to assess, on a taxon-specific basis, the production of the entire invertebrate community and its distribution among the major habitats of a subtropical blackwater river in the Coastal Plain of Georgia, USA. Besides addressing the ecology of a relatively little known type of river, our study suggests a strategy for estimating production that should be useful for others concerned with understanding the complexity of consumer production dynamics. We also combine our taxon-specific production estimates into functional group categories within each habitat to provide insight into the strategies used by organisms in processing organic matter in blackwater rivers.

Most detailed studies of secondary production in streams have been limited to one or a few species at a time, with little attempt to assess their role in the entire stream system. Most of these population studies have been conducted only recently, with ≈60 single-species estimates of production made through early 1976 (Waters 1977*a*). There have been relatively few attempts to estimate production of all invertebrates separately (to the species or at least the functional group level) in a given stream, and subsequently to obtain an overall production estimate of the invertebrate community. Some of these community studies are on rather atypical spring systems (Odum 1957, Teal 1957, Tilly 1968), and some are limited to a particular substrate type such as rock surfaces (Nelson and Scott 1962, Flössner 1976, Neves 1979). One major study was on a large regulated river (Mann et al. 1972, Mann 1975), and another was on two small streams (Hopkins 1976). Although the single-species production studies frequently provided detailed information on population dynamics and other production statistics, the more holistic approaches characteristically are lacking in species-specific details and are difficult to assess fully on that basis.

In order to evaluate accurately the ecological roles of coexisting invertebrates, we believe it is essential to consider differences in production statistics among taxa, particularly turnover rates, which can vary greatly among groups. Waters (1979) and Benke (*in press*) have emphasized the importance of life history information in accurately quantifying biomass turnover. Thus, we feel that any estimates of secondary production should include life history information when possible. When life history data are unavailable, a careful documentation of other data or assumptions used in estimating important parameters (such as length of larval life) should be presented. Otherwise, it is not possible to evaluate the production estimate critically.

Although the number of studies of secondary production in streams has increased greatly in recent years, relatively little is known about secondary production in subtropical rivers, such as the blackwater rivers with shifting sandy substrates in the Coastal Plain of the Southeastern United States. In fact, there is relatively little knowledge on the ecological characteristics of such blackwater rivers in general. These rivers seem to share many physical-chemical characteristics with those found in the Amazon Basin (Beck 1967), and Amazonian blackwaters apparently have a relatively low species diversity and secondary production (Janzen 1974, Fittkau et al. 1975). Interestingly, the limited information on Southeastern blackwater streams suggests a relatively high animal diversity (Dahlberg and Scott 1971, Peters and Jones 1973). Southeastern blackwater rivers also bear certain similarities to the bog-stained brownwater streams of the northern USA and Canada. Although some of these streams have high alkalinity and seem reasonably diverse and productive (Clifford 1978), many others have low alkalinity and appear to have low productivity (Waters 1977*b*).

A thorough assessment of secondary production in streams can only be accomplished if the spatial distribution of invertebrates among habitats is taken into account (Resh 1977). One habitat which seems of considerable importance in many rivers, and which we will emphasize in the present study, is composed of the submerged natural wood substrates often found along the river banks. These substrates, hereafter referred to as "snags," include fallen trees, plus trunks, roots, and branches of living trees which periodically become inundated. D. C. Scott (*personal communication*) and Peters and Jones (1973) identified snags as a major invertebrate habitat in Southeastern blackwater rivers. Snags have also been identified as major sites for invertebrates in other large rivers and as major sources of fish-food organisms (e.g., Berner 1951, Morris et al. 1968, Modde and Schmulbach 1973, Nilsen and Larimore 1973, Nord and Schmulback 1973). More recently, wood substrates have been identified as important attachment sites in some small streams (Anderson et al. 1978, Kovalak 1978). Sometimes the importance of such solid substrates in running waters is only recognized when a higher diversity of organisms is found drifting in the current than can be accounted for by benthic sampling (Berner 1951, Morris et al.

1968, Modde and Schmulbach 1973, Kovalak 1978). Only a few attempts have been made to quantify populations on snags (Nilsen and Larimore 1973, Nord and Schmulbach 1973, Cudney and Wallace 1980), and their importance in lotic systems is not widely recognized. This is especially unfortunate, since snags are commonly removed from running waters as part of a range of channel modification procedures from simple "snagging" to much more intensive channelization. Marzolf (1978) recently summarized the potential effects of snagging on streams and pointed out the need for research in this area.

The present paper dealing with distribution of secondary production represents one of three relatively independent approaches that we have used to assess the population and trophic dynamics of invertebrates found in the major habitats of the Satilla River, Georgia, USA (Benke et al. 1979). The second approach is concerned with invertebrate drift dynamics (Hunter 1980), and the third involves the relative contribution of invertebrates from the major habitats to the diets of the predominant fish species (Henry 1979). The latter two approaches are consistent with the findings that we will present herein: that snags are a significant habitat type, sufficiently abundant to be colonized by a large proportion of the invertebrate biomass and production for the entire river. This production is the source of the majority of animals found in the drift, and provides much of the foundation for the entire riverine food web. Furthermore, the snags provide the only significant habitat for the filtering-feeding community.

Study Area

The Satilla River basin lies almost entirely in the Lower Coastal Plain (the Coastal Flatwoods) of Georgia and flows a total of 362 km to the Atlantic Ocean near Brunswick, Georgia (Fig. 1). The drainage basin is 9143 km^2 and contains soils that are poorly drained and highly leached. Our study sites were in the topographic region known as the Coastal Terraces, an area covered by Pleistocene sands and sandy loams, except in swamps where sands are overlain by muck or peat (LaForge et al. 1925).

There is relatively little development along the course of the river and relatively little pollution. Cypress–black gum swamps are adjacent to the river along much of its length and may extend >1 km from the main channel. Pine forests and to a lesser extent agriculture occupy most of the drainage basin. The swamps are apparently the source of fine allochthonous detritus utilized by the many filter-feeding invertebrates in the river.

The Satilla is characterized by poorly buffered waters with low pH, low ionic strength, and a high mean temperature (Table 1). Water temperatures fluctuate between 10° and 16°C in the coldest months and between 25° and 30° in the warmest months (Fig. 2). Beck et al. (1974) conducted detailed chemical analyses on Satilla River water collected on two dates in 1970. They point out that while the concentration of dissolved organic carbon (they estimate a mean value of 23 mg/L in the Satilla) is about twice the figure for the average world river water, the ratio of dissolved organic carbon to total dissolved inorganics (1:1 in the Satilla) is much greater than the ratio found in the average world river water (1:10). The bulk of the river water organic matter was shown to resemble soil humic substances containing acidic functional groups. The predominance of this acidic organic matter during periods of high to moderate discharge is apparently responsible for pH values usually in the 4.3–5.2 range (Table 1). The organic matter is apparently derived from the river swamps, particularly during flooding, which usually occurs at least once a year. It also may come from soil organic matter in the drainage basin which is leached by percolating rain water (Beck et al. 1974). The dissolved humic substances impart a tea-like color (Table 1) to the water, resulting in a "blackwater" appearance. The effect of swamp drainage, with its high content of acidic humus, on water chemistry almost vanishes during low flow conditions when the swamps are dry and the river flows over its bed of white sand. During these periods, flow is maintained from the ground water, pH rises to 6 or higher, and color and total organic carbon concentration decrease (Georgia Department of Natural Resources, Environmental Protection Division 1977).

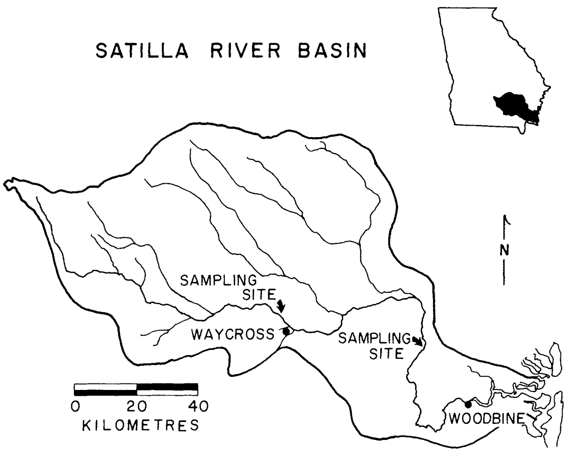

Fig. 1. Satilla River Basin. Lower sampling site is 129 river km from Atlantic Ocean; Upper site is 290 km from ocean.

Sampling was conducted at two widely separated river sites in order to get some idea of intrabasin variation and possibly a longitudinal shift in invertebrate composition and production dynamics (Fig. 1). The upper site is ≈13 river km upstream of Waycross, the largest city in the drainage basin, and 290 km upstream from its mouth at the Atlantic Ocean. The drainage area of the upper sampling site is ≈3100 km^2, and the

TABLE 1. Chemical and physical parameters of the Satilla River water.

Parameter	Units	Mean	Max	Min	Source
Color	Pt*	152	320	80	E.P.D.†
Turbidity	JTU‡	4.7	7	2	USGS§
Temperature	°C	19.0	29.5	8.5	USGS
Dissolved oxygen	mg/L	8.0	11.6	4.7	USGS
Specific conductivity	μS	44.9	63	28	USGS
Acidity	pH	5.1	6.7	4.3	E.P.D.
Hardness (Ca + Mg carbonate)	mg/L	11	20	7	USGS
Hardness (noncarbonate)	mg/L	8	13	3	USGS
Alkalinity ($CaCO_3$)	mg/L	3.8	9.0	0.0	USGS
Total nitrogen (N)	mg/L	.79	1.4	.54	USGS
Total phosphorus (P)	mg/L	.07	.16	.01	USGS
Total organic carbon (C)	mg/L	17	25	14	USGS
Dissolved silica (SiO_2)	mg/L	8.2	11.0	6.1	USGS

* 1000 Pt units = color from 2.492 g K_2PtCl_6, 2 g $CoCl_2 \cdot 6H_2O$, and 200 mL conc. HCl in 800 mL water (Wetzel 1983).
† Georgia Department of Natural Resources, Environmental Protection Division (1975).
§ United States Geological Survey (1976).
‡ Jackson Turbidity Units.

stream gradient at this point is ≈19 cm/km (United States Study Commission, Southeast River Basins 1963). The lower site is ≈16 river km downstream from the Highway 84 bridge near Atkinson and 129 km upstream from the mouth. At this site, the river drains an area of ≈7300 km^2. Here, the river is only ≈9 m above sea level and the gradient is only 8 cm/km. The mean gradient from the headwaters to the site downstream of Atkinson is 36.4 cm/km. Mean annual rainfall is ≈125 cm, with summer months the wettest (≈17 cm/mo) and fall-winter the driest (≈8 cm/mo).

River discharge is monitored continuously by the United States Geological Survey near the upper site (at Waycross) and near the lower site (Highway 84). Discharge from December 1974 through November 1975 at the upper site ranged from 2.9 to 280 m^3/s with an annual mean of 44.7 m^3/s (Fig. 3). This was somewhat higher than the 38-yr average discharge of 28.4 m^3/s. Discharge at the lower site ranged from 6.9 to 504 m^3/s with an annual mean of 87.2 m^3/s. The 45-yr average discharge was 62.4 m^3/s. Current velocity in the channel during our sampling period varied from ≈0.2 to 0.7 m/s at the upper site, and from 0.2 to 0.9 m/s at the lower site.

MATERIALS AND METHODS

We identified three major habitat types from which to estimate invertebrate production: (1) the snag habitat described above, (2) the sandy benthic habitat of the main channel, and (3) the muddy depositional habitats found in backwaters. Identical sampling strategies were followed at both river sites (Fig. 1).

Snag samples were taken from December 1974 through November 1975. Six snag samples per site were collected every 2 wk from May through August, and monthly for the remainder of the year. We felt that more frequent sampling in summer months would better enable us to identify cohorts of certain groups such as Hydropsychidae that are known to complete a generation during the summer. The increased sampling frequency was fortunate in another respect; we could not always obtain reliable snag samples due to rapidly rising water (see below). Samples were taken from a boat in the main river channel along the bank where water velocities were at least 20 cm/s. Snags could usually only be retrieved from the top metre of the water column, but artificial substrate sampling demonstrated that the same snag community was usually found at all depths (Van Arsdall 1977). A specially designed longitudinal sieve (45 cm long) was placed under a section of the snag while the snag was cut and quickly transferred to a bucket. Relatively few animals dropped into the sieve, and thus few were believed to have been lost during this procedure. The sample was then preserved in 10% Formalin until further processing.

Samples were returned to the laboratory where the contents were placed in a white porcelain pan. Animals were rinsed from snags into the pan with running water, and sieved from the excess water with a 100-μm sieve. Snags were then carefully picked through (e.g., loose bark removed) under a magnifying light and any remaining animals were removed. All animals were preserved in 80% ethanol for later counting and identification. Body length and head widths (at widest point) were measured using an ocular micrometer accurate to 10 μm.

Habitat surface area was calculated by measuring the length and mean diameter of each segment of snag after all animals were removed. Surface area per snag sample usually was between 100 and 400 cm^2. Animal densities and standing stock were then converted to amount per square metre of habitat surface for each snag sample, or amount per "effective habitat" area (Neves 1979, Resh 1979).

Benthic samples of both the sandy substrate in the main channel and muddy substrate in the backwater were taken monthly at each site. We did not sample

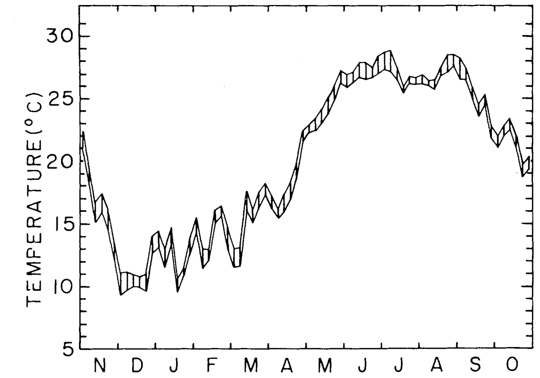

FIG. 2. Five-day means of daily maximum and minimum water temperatures near the lower site (Water Year 1975, United States Geological Survey 1976).

biweekly during summer months as we did for snags, since we were pessimistic about being able to follow cohorts of benthic species. All samples were collected with a ponar grab (Wildlife Supply Company, Saginaw, Michigan; sampling area ≈ 15 × 15 cm). We originally employed a stratified sampling strategy in which three ponar samples were taken in a relatively straight part of the river channel, three at a sharp bend in the river, and three from a backwater area. The substrate from both main channel locations consisted of loose sand with little organic matter, and subsequent analyses showed that both locations contained similar fauna. Therefore, all sandy substrate samples from the main channel were treated as a single habitat in the analyses.

Sand samples were placed in buckets, and concentrated Formalin was added. After several minutes, contents of the bucket were stirred so that the organisms were suspended and the sand would settle. The suspended organisms were poured through a Nitex sieve with a 100-μm mesh opening. This process of elutriation was repeated several times until no animals were observed in the supernatant. This simple procedure was not possible for backwater samples due to the fine organic particles clogging the 100-μm sieve. These samples were preserved in 10% Formalin, and returned to the laboratory in sealed buckets. Here the samples were gently rinsed in a Number 60 brass sieve (250-μm opening) to remove fine silt. From the filtered material, organisms were separated from debris and sand using a sugar flotation technique (Anderson 1959). They were then stored in 80% ethanol for later processing.

Dry mass for the common larger species (i.e., most size classes >0.05 mg) were obtained by placing fresh specimens in an oven at 60° for 24 h. Biomass conversion factors of instars or length classes were usually estimated by regressions of log dry mass on log head width (or total length). For smaller animals (such as the Diptera), less common species, and oligochaetes, dry mass was usually estimated from volume calculations using length and width measurements, assuming a cylindrical shape, and a wet-to-dry mass conversion factor of 0.2. Although percent dry mass varies considerably within an individual as well as between species, it usually ranges between 10 and 30%, with a mean close to 20% (Waters 1977*a*, Neves 1979, Driver 1981, A. C. Benke, *personal observation*).

The size-frequency method (Hynes 1980, Waters and Hokenstrom 1980), formerly called the Hynes method

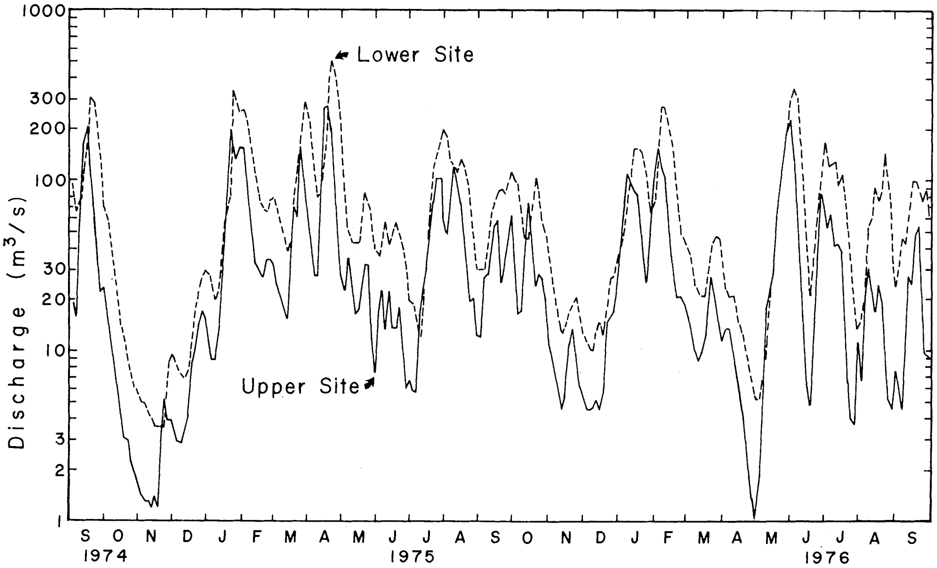

FIG. 3. Discharge at the upper and lower sites on the Satilla River (based on data in United States Geological Survey 1976, 1977). Note logarithmic scale of ordinate.

TABLE 2. Number of insect and oligochaete genera commonly found in snag, sandy benthic, and muddy benthic habitats (both sites).

Taxon	Number of genera		
	Snags	Sand	Mud
Diptera	17	15	11
Ephemeroptera	5	0	0
Plecoptera	2	0	0
Trichoptera	9	0	3
Coleoptera	3	1	1
Megaloptera	1	0	0
Odonata	3	1	0
Oligochaeta	0	3	2

(Hynes 1961, Hynes and Coleman 1968, Hamilton 1969), was used to estimate production directly for most of the populations in each habitat. Although the size-frequency method was originally conceived to apply to entire faunal assemblages, in this study it was used separately for each of the major species. The less numerous species were grouped into families or other common taxonomic units for production calculations. The most accurate estimates would be expected when the method is applied to single species.

To calculate population production, the average size-frequency distribution is determined from samples collected throughout the year. This size distribution is assumed to approximate the survivorship of an "average cohort" (Hamilton 1969, Benke and Waide 1977, Benke 1979). Production of the average cohort is calculated as the sum of production losses between size classes, and then is multiplied by the number of size classes. See Benke and Wallace (1980) for a more complete description of method rationale. Benke and Wallace referred to the production value obtained after multiplication by number of size classes as the "Hynes" estimate. To be more consistent with Waters and Hokenstrom (1980), we now refer to this as uncorrected annual production, or simply uncorrected *P*. Unless the individuals in a population take a full year to complete development, this uncorrected *P* estimate must be further multiplied by 365/CPI, where CPI is the mean cohort production interval in days (Benke 1979). For aquatic insects, the CPI is the average larval development time. For some Satilla River invertebrates, CPI could be approximated from life history data. However, it was necessary to utilize a combination of field data and literature values for several taxa.

Although only six (snag and sand habitats) or three (mud habitat) samples were collected on each date at each site, samples across all dates serve as replicates in calculating production by the size-frequency method. For example, production calculations for animals collected on snags were based upon 108 separate samples for each site. Krueger and Martin (1980) recently developed a procedure for estimating confidence intervals for size-frequency estimates of production. As an example, they presented data for a mayfly which was sampled on 13 dates with 10 samples per date. Their 95% CI was <±20% of the mean. We have not utilized their procedure since it does not take into account potential errors associated with snag sampling and quantification, and CPI estimation (also see Hynes 1980). If our CPI estimates are reasonable, we suspect that with our somewhat lower amount of replication and additional sources of sampling errors, our 95% CI values would probably be no better than ±30–40% of the production estimate. Although we have chosen not to provide CI values which could be misleading, we have provided some standard error estimates for mean standing stock biomass of most groups.

RESULTS

Invertebrate fauna and habitats

The diversity of taxa on snags was much greater than that of either the sandy or muddy benthos (Table 2 and Appendix). Seven insect orders were each represented by at least one common species on the snags. The orders with the largest numbers of taxa (Diptera and Trichoptera) were also the most productive, and were dominated by filter-feeding forms.

The sandy benthos consisted almost entirely of dipterans and oligochaetes of very small size inhabiting the interstitial spaces of the sand grains. Most of the dipterans were midge larvae (Chironomidae), although the largest dipteran was a predator in the family Ceratopogonidae. The only large invertebrate predator, an odonate, was generally found along sand bars at low water, and in very low densities.

The muddy benthos consisted primarily of dipterans and oligochaetes, but included larger species than those found in the sand. The most conspicuous dipterans were predaceous chironomids (subfamily Tanypodinae) which presumably fed on oligochaetes, chironomids, and benthic microcrustaceans such as ostracods. Low densities of tube-dwelling caddisflies were also found regularly. Some large predators (dragonflies and hellgrammites) were found here infrequently.

Snag production

Trichoptera.—The net-spinning caddisflies of the family Hydropsychidae (*Hydropsyche*; *Cheumatopsyche*, and *Macronema*) were by far the most conspicuous consumers on the snag habitat. They are generally regarded as filtering-feeding omnivores, with actual consumption being a function of net mesh size and seston composition. *Hydropsyche* and *Cheumatopsyche* have relatively large mesh openings for river species (>100 μm for final instars) (Wallace and Sherberger 1974, Wallace 1975). Wallace et al. (1977) showed that animals comprised a significant portion of the diet of *Hydropsyche* species in the Altamaha River of the Georgia Coastal Plain. *Macronema* nets are much finer and they feed primarily on detritus. The philopotamid *Chimarra* was also common at both Sa-

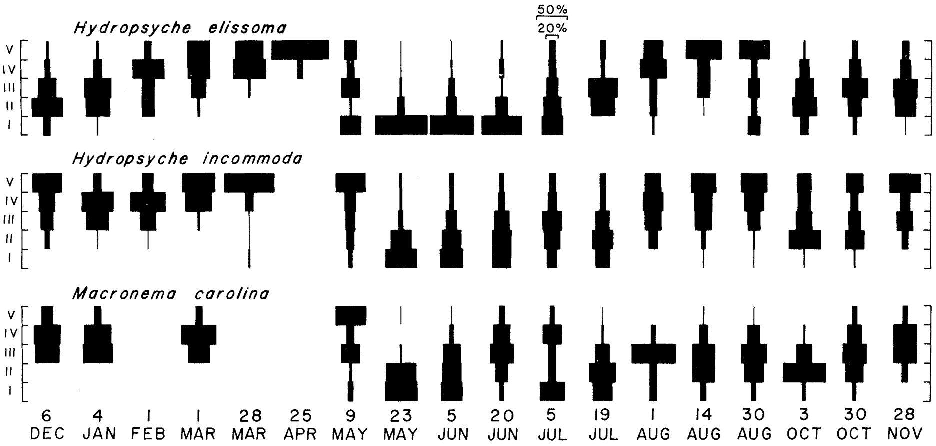

FIG. 4. Instar-frequency distributions on each sample date for the dominant caddisfly species on the snag habitat in the Satilla River. Instars designated as I through V. Width of each bar represents percentage of total animals found in an instar. *H. elissoma* are from the upper site; *H. incommoda* and *M. carolina* are from the lower site.

tilla River sites. *Chimarra* constructs extremely fine nets (<1 × 9 μm mesh openings for final instars, Wallace and Malas 1976) and also consumes fine detritus (Wallace et al. 1977). The less common snag caddisflies consisted of Polycentropodidae (net-spinning species) and Leptoceridae (grazers or predators).

At the upper site, the predominant species was *Hydropsyche elissoma,* with smaller *Cheumatopsyche* spp. a distant second in abundance. *Macronema carolina* and *Hydropsyche incommoda* (called *H. orris* by Benke et al. 1979; but now regarded as *H. incommoda* by Flint et al. 1979) were found infrequently and in much lower densities. However, at the lower site (≈160 river km downstream), *H. incommoda* was the predominant species, and *M. carolina* was also very abundant. *Hydropsyche elissoma* and *Cheumatopsyche* were only rarely found on snags at the lower site. Gordon and Wallace (1975) found a somewhat similar distribution for Hydropsychidae on the Savannah River (Georgia-South Carolina border). *Hydropsyche incommoda* and *M. carolina* were the major species where the Savannah flows through the Coastal Plain, but in the lower Piedmont-upper Coastal Plain *H. rossi* (rather than *H. elissoma*) and *Cheumatopsyche* predominated.

In at least one respect, caddisflies are ideal organisms for life history and production analyses. They generally have five distinct instars which can be easily separated by head width (Van Arsdall 1977). Series of instar-frequency histograms for each sample date were constructed for each of the common caddisfly species at both sites. However, only the three most abundant species displayed reasonably consistent trends (Fig. 4).

Both *Hydropsyche incommoda* at the lower site and *H. elissoma* at the upper site appeared to have two generations per year. A major recruitment period was evident for both species from late May through June (Fig. 4). The histogram patterns indicate that a second recruitment period apparently occurred for both species in September. Unfortunately, this recruitment peak was not actually observed, since no samples were taken between 30 August and 3 October. Pupae of both species were found predominantly during May and August, at their respective sites, coinciding with recruitment periods. These life cycles are almost identical to that found by Cudney and Wallace (1980) for *H. incommoda* on snags in the Savannah River.

The instar-frequency histograms indicated the presence of at least one generation per year for *Macronema carolina* (lower site), also consistent with the findings of Cudney and Wallace (1980) in the Savannah River. Pupae appeared in May and recruitment was highest from late May through early June. The presence of first instars throughout the summer and fall again indicates an extended recruitment period. It is possible that some individuals recruited in May are able to complete development during the summer, emerge, and produce a second generation.

For the rest of the Trichoptera, either there was not enough information to obtain adequate life histories, or there was no consistent pattern. However, Cudney and Wallace (1980) observed two generations per year for *Cheumatopsyche, Chimarra,* and some Polycentropodidae in the Savannah River. For these taxa, we therefore assumed two generations per year in our production analyses. For *Macronema* and Leptoceridae we assumed only one generation per year.

Our findings and assumptions regarding Trichoptera life cycles are reasonably consistent with the literature. Although many studies of the Trichoptera have indicated that univoltine life cycles are the most common for this order (Wiggins 1977), several cases of bivoltinism in addition to those reported here have now been found for hydropsychids (e.g., Fremling 1960, Oswood 1976, Rhame and Stewart 1976, Lapchin and Neveu 1979, Mackay 1979, Cudney and Wallace 1980).

Standing stock values for Trichoptera and other in-

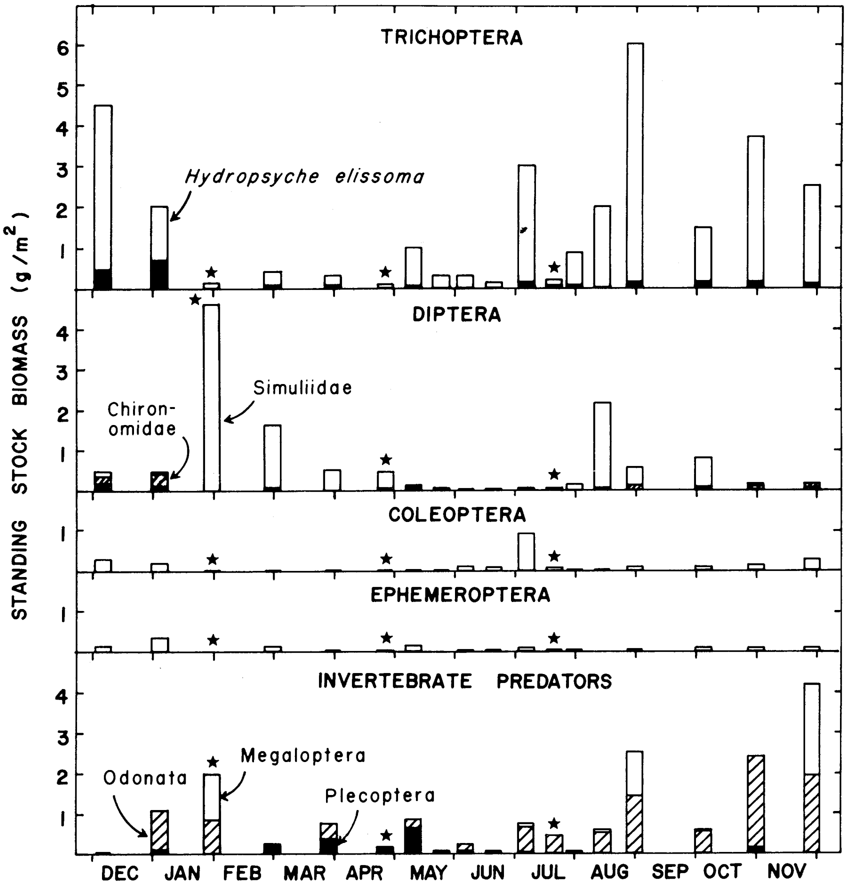

FIG. 5. Standing stock biomass (dry mass) trends for major taxa on snags at the upper site (habitat surface area basis). Stars associated with bars indicate dates on which water level was rapidly rising. Identities of the solid, hatched, and open portions of histogram bars for each taxon apply to all months of the year. Note all values on a given date are cumulative.

vertebrates on snags appeared extremely variable (Figs. 5 and 6). Some of the trends are real ones due to life history and population dynamics characteristics, but some of the variation is due to a particularly high statistical sampling error. The coefficient of variation (CV) for caddisfly biomass on a given day at a single site averaged ≈95% with the standard error (SE) ≈40% of the mean ($\bar{x}$). For total invertebrate biomass the CV averaged ≈90% with the SE ≈37% of the mean. Some extremely low standing stock values observed on Figs. 5 and 6 are clearly due to our inability to collect well-colonized snags during periods of rapidly rising water. Since all these sources of variation are superimposed on one another, it is difficult to separate out the effects for any given date. Thus we cannot place a great deal of confidence in a standing stock value on a single date. However, these figures do give us some idea of annual trends when considered in conjunction with life history information, and they also illustrate some particularly high standing stock biomass values.

Our ultimate goal is to estimate production of the major groups, and since we are using the size-frequency method, the reliability of biomass estimates on any given date is not crucial. Since the size-frequency method uses a mean size distribution, and samples from all dates serve as replicates, normal sampling variation among dates should have little effect on the production estimate. For example, the SE was ≈13–16% of the mean caddisfly biomass using all snag samples on all dates at a site. The most serious sampling error as far as calculating production for most groups is the low numbers collected during periods of rising water, which are known to be underestimates. These dates are indicated by stars on Figs. 5 and 6. It should be noted that certain groups such as Chironomidae seem little affected by high water, and the Simuliidae are frequently found in great quantities during flood stage. At least these two groups must be regarded as fast colonizers, and because of this observation, we have retained these otherwise inadequate snag samples in our figures.

Hydropsyche elissoma clearly comprised the highest standing stock biomass on snags at the upper site (Fig. 5). Mean numerical density and dry biomass were 4017

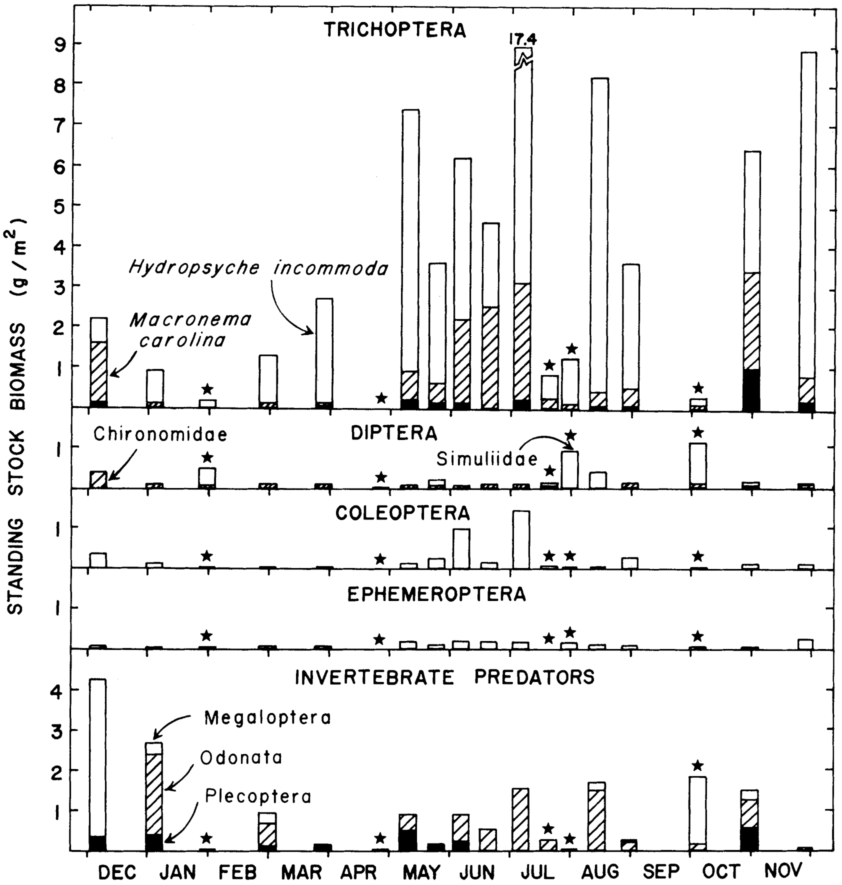

FIG. 6. Standing stock biomass (dry mass) trends for major taxa on snags at the lower site (habitat surface area basis). Symbols as in Fig. 5. Identities of the solid, hatched, and open portions of histogram bars for each taxon apply to all months of the year. Note all values on a given date are cumulative.

animals /m² and 1462 mg/m² of snag surface, respectively. Maximum numerical density and biomass were 16 474 animals/m² in December and 5832 mg/m² on 30 August. All other Trichoptera averaged only 693 individuals/m² and 119 mg/m², of which more than half was attributed to *Cheumatopsyche.*

At the lower site, *Hydropsyche incommoda* dominated the biomass on snags (Fig. 6). Mean numerical density and biomass were 8149 larvae/m² and 3287 mg/m² of snag surface, respectively. Maximum values of 41 997 larvae/m² and 14 200 mg/m² of snag surface were reached on 5 July. *Macronema carolina* averaged 1637 animals/m² and 810 mg/m² with maxima of 10 037 animals/m² and 2902 mg/m² on 5 July. All other Trichoptera averaged only 700 animals/m² and 125 mg/m².

The limited data reported from other rivers indicate that the extremely high numbers and biomass of hydropsychids reported in our study should not be considered unusual. Investigators commonly find densities of several thousand individuals/m² and dry biomass >2 g/m² (e.g., Cushing 1963, Nilson and Larimore 1973, Nord and Schmulbach 1973, Flössner 1976, Rhame and Stewart 1976, Cudney and Wallace 1980).

Although numbers and biomass values give some idea of the relative importance of species in ecosystems, an evaluation of their production provides a much better basis for evaluating their trophic-dynamic contributions. The size-frequency method of calculating consumer production is illustrated for *Macronema carolina* in Table 3. The second column represents the annual mean instar frequency distribution. This distribution is assumed to represent the survivorship for an average cohort, but because animals probably do not spend equal amounts of time in each instar, it is only a rough approximation. This "error" does not seem seriously to affect the production calculation (Hamilton 1969, Benke and Waide 1977). The remaining columns represent the calculations for production (biomass) lost between each pair of successive instars of the average cohort. Each value in column 7 must be multiplied by 5, the number of instars, before the column is summed to obtain uncorrected P (Hamilton 1969). The useful pieces of information from this

TABLE 3. Calculation of production for *Macronema carolina* at the lower site in the Satilla River using the size-frequency method. $\bar{N}$ = annual mean density, $\bar{B}$ = annual mean standing stock biomass, P = cohort production = annual production. Biomass values are mg dry mass.

Instar	Annual mean density (no./m^2)	Mean individual biomass (mg)	Annual mean standing stock (mg/m^2)	No. lost/m^2	Individual biomass at loss (mg)	Biomass loss (mg/m^2)	Biomass correction factor (loss × 5)
I	479.6	.03	14.4	10.2	.07	0.7	3.5
II	469.4	.11	51.6	81.1	.24	19.5	97.5
III	388.3	.37	143.7	161.6	.90	145.4	727.0
IV	226.7	1.43	324.2	154.2	2.62	404.0	2020.0
V	72.5	3.81	276.2	72.5	3.81	276.2	1381.0
	$\bar{N}$ = 1636.5		$\bar{B}$ = 810.1				P = 4220.0

table are: (1) the average cohort, since it is an approximation of survivorship, (2) the sum of column 2, which represents the annual mean numerical density, (3) the mean biomass of each size class (column 3), (4) the sum of column 4, which represents annual mean standing stock biomass, and (5) the sum of column 8, which represents uncorrected P. The ratio of uncorrected P to mean standing stock biomass is equal to cohort $P/\bar{B}$, and is a production parameter of particular interest. Waters (1977*a*) has observed that the cohort $P/\bar{B}$ is frequently ≈5, and this is the case for *M. carolina* (Table 3). Since the mean larval development time (or CPI, see Materials and Methods) is about a year for *M. carolina*, the uncorrected P required no CPI correction and equals annual production. Furthermore, cohort $P/\bar{B}$ = annual $P/\bar{B}$.

Hereafter, the average cohort and production statistics indicated above are presented for each of the common species on which separate production calculations were made. Only production summaries ($\bar{N}$, $\bar{B}$, P) are presented when densities for a species are low, and species are sometimes grouped into families when all members of the family are in low abundance (Tables 4 and 5). Both of the *Hydropsyche* species have two consecutive generations per year (Fig. 4), which means that the CPI is ≈6 mo. Thus, the uncorrected P value is multiplied by 2 (i.e., 12 mo/6 mo, using months instead of days in the CPI correction factor) to obtain the annual production values presented in Table 4. Note that the annual $P/\bar{B}$ values for *Hydropsyche* spp. in Table 4 are twice the cohort $P/\bar{B}$ values.

Hydropsyche incommoda and *Macronema carolina* occurred infrequently or in low numbers at the upper site, insufficient for estimating production with the size-frequency method. Therefore, in order to estimate their production at the upper site, we multiplied their annual mean biomass there by the annual $P/\bar{B}$ values calculated from the lower site. For the Leptoceridae and Polycentropodidae, a reliable $P/\bar{B}$ value could not be calculated from the data collected at either site. There-

TABLE 4. Average cohorts and production statistics for Satilla River Trichoptera on snags at the upper site. Numbers in parentheses are mean individual dry mass (mg).

Taxon	Instars I	II	III	IV	V	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	Annual P (mg/m^2)	Annual $P/\bar{B}$
	No. larvae/m^2 habitat surface area								
Hydropsyche incommoda						11	3	19	6.4†
Hydropsyche elissoma	881 (0.02)	1187 (0.07)	979 (0.21)	498 (0.62)	472 (1.71)	4017	1462	10 830	7.4*
Macronema carolina						49	21	109†	5.2†
Cheumatopsyche sp.		11 (0.02)	184 (0.07)	108 (0.21)	42 (0.74)	345	67	656	9.8*
Chimarra (*socia*)	37 (0.003)	57 (0.01)	80 (0.04)	32 (0.21)	17 (0.50)	223	19	200	10.6*
Leptoceridae						16	3	15‡	5‡
Polycentropodidae						49	6	60*,‡	10*,‡
Total Trichoptera						4710	1581	11 889	7.5

* Two generations per year (cohort production interval = 6 mo).

† Assumed same $P/\bar{B}$ as for lower site; see Table 5.

‡ Assumed cohort $P/\bar{B}$ = 5.

TABLE 5. Average cohorts and production statistics for Satilla River Trichoptera on snags at the lower site. Numbers in parentheses are mean individual dry mass (mg).

Taxon	Instars					$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	Annual P (mg/m^2)	Annual $P/\bar{B}$
	I	II	III	IV	V				
	No. larvae/m^2 habitat surface area								
Hydropsyche incommoda	1866 (0.02)	1939 (0.06)	1649 (0.15)	1077 (0.42)	1618 (1.50)	8149	3287	21030	6.4*
Hydropsyche elissoma						139	47	348†	7.4†
Macronema carolina	480 (0.03)	469 (0.11)	388 (0.37)	227 (1.43)	73 (3.81)	1638	810	4229	5.2
Cheumatopsyche sp.						0	0	0	
Chimarra (*socia*)	43 (0.003)	103 (0.01)	120 (0.04)	93 (0.21)	37 (0.50)	396	43	420	9.8*
Leptoceridae						72	21	105‡	5‡
Polycentropodidae						93	14	140*,‡	10*,‡
Total Trichoptera						10486	4222	26272	6.2

* Two generations per year (cohort production interval = 6 mo).
† Assumed same $P/\bar{B}$ as upper site, see Table 4.
‡ Assumed cohort $P/\bar{B} = 5$.

fore, we assumed, based on our own data on other caddisflies, and literature values (e.g., Waters 1977*a*), that the cohort $P/\bar{B}$ was 5.

Production of *Hydropsyche elissoma* was 10 830 mg/m^2 of snag surface and represented almost 95% of Trichoptera production on snags at the upper site. Numerically, *H. elissoma* represented ≈85% of all caddisflies found on snags at the upper site. It should be noted that the smallest size category in the average cohort frequently will not have the highest numbers, as seen for *H. elissoma* (Table 4). When this occurred, we did not include the resulting negative value in the production calculation, since it is probably due to poorer sampling efficiency for the smallest animals, as well as a shorter amount of time spent in early instars (see Benke and Wallace 1980 for rationale).

Trichoptera production at the lower site was more than twice that of the upper site (Table 5). *Hydropsyche incommoda* and *Macronema carolina* comprised 81 and 16% of total Trichoptera production, respectively. Numerically, the two comprised 93% of all caddisflies on snags at the lower site.

We have included the snag samples taken during periods of higher water (Figs. 5 and 6) in our calculations of annual production, and because these snags were collected near the surface and were not fully colonized, the production estimates are probably conservative. Exclusion of these dates from our calculations would raise our estimate of total Trichoptera production of 11.9 g/m^2 at the upper site by roughly 20% (to ≈14 g/m^2), and our estimate of 26.3 g/m^2 at the lower site by roughly 30% (to ≈34 g/m^2). However, for the sake of objectivity in making comparisons with other snag organisms (such as black flies), we have included all snag samples in our analyses.

In addition to the results presented here, there is relatively little information on Trichoptera production in other rivers, but the high densities and standing stock biomass values mentioned above indicate that production in these other rivers could be comparable to that found in the Satilla. Of the few estimates of Trichoptera production made in smaller streams, most are much lower than values found in the Satilla (Otto 1975, Cushman et al. 1977, Resh 1977, Neves 1979, Benke and Wallace 1980, Iverson 1980, Haefner and Wallace 1981, Ross and Wallace 1981). Trichoptera production values comparable to our own have been found by Hopkins (1976) in the enriched Horokiwi stream (New Zealand), Flössner (1976) in the Saale River (East Germany), and Cudney and Wallace (1980) on snags from the Savannah River.

Diptera.—Black fly (Simuliidae) and midge (Chironomidae) larvae were the most common dipteran families represented on the snags. Black fly larvae are filter feeders which strain fine particulate organic matter with specialized mouthparts called cephalic fans. They commonly feed on particles varying in length from 20 to 100 μm, but they can also capture particles as small as 0.1 μm (Wotton 1976), including bacteria (Fredeen 1964). Midge larvae, on the other hand, possess an enormous variety of feeding strategies (Coffman 1978). Among midges found on Satilla snags, species in the Tribe Tanytarsini (primarily *Rheotanytarsus* and *Tanytarsus*) are fine-particle filter-feeders. The *Polypedilum* species, our *Cricotopus* "group" (primarily *Rheocricotopus* and *Cricotopus*), and the small *Corynoneura* and *Thienemanniella* are generally considered gathering collectors. The largest chironomid found on snags, *Stenochironomus* sp., is considered to be a wood borer. Tanypodinae species, which include *Ablabesmyia* spp. and species in the *Thienemannimyia* group are usually predaceous.

The black flies appeared to consist primarily of two species: *Simulium taxodium,* and an unnamed *Si-*

TABLE 6. Average cohorts and production statistics for Satilla River Diptera on snags at the upper site. Numbers in parentheses are mean individual dry mass (mg). CPI = cohort production interval.

Taxon	Total length (mm) 1	2	3	4	5	6	7	8	$\bar{N}$ (no./m²)	$\bar{B}$ (mg/m²)	Uncorrected P (mg/m²)	365/CPI	Annual P (mg/m²)	Annual $P/\bar{B}$
	No. larvae/m² habitat surface area													
Chironomidae									7565	69.5			9509	137
Cricotopus group	826	438	215	55	9				1542	12.7	78.2	16	1251	99
	(.001)	(.007)	(.023)	(.054)	(.105)									
Thienemannimyia group/ *Ablabesmyia*	333	225	49	27	11	1	1		647	9.4	63.7	20	1274	136
	(.002)	(.010)	(.035)	(.083)	(.163)	(.280)	(.446)							
Polypedilum spp.	505	572	357	148	82	13	3	2	1682	20.5	148.4	23	3413	166
	(.0005)	(.004)	(.014)	(.033)	(.066)	(.114)	(.181)	(.27)						
Tanytarsini	1001	878	232	21					2132	13.6	79.9	30	2397	176
	(.001)	(.007)	(.023)	(.054)										
Corynoneura/ Thienemanniella	1012	101							1113	2.0	8.7	46	400	200
	(.001)	(.007)												
Chironomini sp. A									53	1.0	5.0*	16	80	80
Stenochironomus									41	6.5	32.5*	13	423	65
Tribelos/ Xenochironomus									4	2.2	11.0*	13	143	65
Miscellaneous Chironomidae									351	1.6	8.0*	16	128	80
Simuliidae	6309	5760	5350	2098	267				19783	603	2390	18	43020	71
	(.01)	(.02)	(.04)	(.08)	(.16)									
Miscellaneous Diptera									382	22.6	113*	13†	1469	65

* Assumed cohort $P/\bar{B} = 5$.

† Assumed to be the same as the largest chironomids.

mulium species. Identifications were based upon pupae, and no attempt was made to separate larvae. Abundance of black flies on snags was extremely variable both between dates and on a given date (Figs. 5 and 6). The CV on a given date averaged 137% and the SE/$\bar{x}$ averaged 57%. Abundance was frequently associated with high or rapidly rising water levels, as mentioned above, and indicated by stars in the figures. Maximum numbers (102 000 larvae/m² of snag surface) and biomass (4.56 g/m²) of black flies were found on 1 February at the upper site. At the lower site, maximum values (42 000 larvae/m² and 1.0 g/m²) were found on 3 October. In a few cases, such as 24 April—lower site, the water was rising so rapidly that not even the black flies had yet colonized the snags nearest the surface. However, they were very abundant in the drift on this date (Benke et al. 1979). Furthermore, observations of high and dry snags at low water showed a vertical stratification of caddisfly larval cases and black fly pupal cases, with the latter only found high on the substrate. We interpret this as evidence that most black fly production (and subsequent pupation) occurs as water rises, before other species such as caddisflies have a chance fully to colonize the new substrate. Whether this strategy is a response to predation, crowding, or microhabitat conditions is an interesting question we cannot answer at this time.

Average cohorts for black flies are easily calculated using length classes (Tables 6 and 7) with mean numbers and biomass of 19 783 larvae/m² and 603 mg/m² at the upper site and 7038 larvae/m² and 163 mg/m² at the lower site. The uncorrected P calculations are 2390 mg/m² and 717 mg/m² at the upper and lower sites, respectively. These values must be multiplied by 365/CPI, where CPI is larval development time. Although we have no direct estimate of CPI, it is possible to make what we feel is a reasonable approximation from both our own field observations and the literature. Black flies are commonly reported to be multivoltine, and Stone and Snoddy (1969) have reported some Alabama species to have as many as seven generations per year. Laboratory growth studies and field observations show that black fly larvae can develop to pupation in as few as 8 d and usually <30 d at water temperatures >15°C (Wu 1930, Fredeen 1959, Tarshis 1968, Becker 1973, Reisen 1975, Colbo and Thompson 1978). Ross and Merritt (1978) and Brenner et al. (1981) present evidence that the number of degree-days required for black fly larval development is often <300 (e.g., at 15°, larval development would require 20 d).

TABLE 7. Average cohorts and production statistics for Satilla River Diptera on snags at the lower site. Numbers in parentheses are mean individual dry mass (mg). CPI = cohort production interval.

Taxon	Total length (mm) 1	2	3	4	5	6	7	8	9	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	Uncorrected P (mg/m^2)	$\frac{365}{\text{CPI}}$	Annual P (mg/m^2)	Annual $P/\bar{B}$
	No. larvae/m^2 habitat surface area														
Chironomidae										7014	70.1			9721	139
Cricotopus group	777 (.001)	184 (.007)	77 (.023)	10 (.054)	7 (.105)					1054	5.1	37.5	16	600	118
Thienemannimyia group/ *Ablabesmyia*	304 (.002)	183 (.010)	21 (.035)	10 (.083)	10 (.163)	3 (.280)				530	6.6	46.2	18	832	126
Polypedilum spp.	553 (.0005)	725 (.004)	494 (.014)	289 (.033)	100 (.066)	14 (.114)	4 (.181)	1 (.270)	2 (.390)	2182	32.6	207.7	23	4777	147
Tanytarsini	1368 (.001)	738 (.007)	166 (.023)	36 (.054)	1 (.105)					2308	12.5	76.9	30	2306	184
Corynoneura/ Thienemanniella	493 (.001)	78 (.007)	2 (.023)							573	1.1	8.5	46	391	355
Chironomini sp. A										61	1.0	5.0*	16	80	80
Stenochironomus										99	7.1	35.5*	13	462	65
Tribelos/ Xenochironomus										10	3.7	18.5*	13	241	65
Miscellaneous Chironomidae										197	.4	2.0*	16	32	80
Simuliidae	3282 (.01)	1982 (.02)	1529 (.04)	310 (.08)	34 (.16)					7038	163	717	18	12906	79
Miscellaneous Diptera										256	10.3	51.5*	13†	670	65

* Assumed cohort $P/\bar{B} = 5$.

† Assumed to be the same as the largest chironomids.

Our own field observations indicate that larvae appear to develop to pupation within 30 d (our sample interval) in the winter and within 14 d in the summer (i.e., on one sampling date there would be few black flies; on the next date, with water level much higher, larval densities would not only be extremely high, but many individuals would be pupating). Pupae were found at all times of the year except late spring–early summer, but we could easily have missed them during that period. Based upon the above information, a reasonable and probably conservative estimate of CPI is 20 d. The multiplication factor is thus 365/20 = 18 (Tables 6 and 7). This results in annual production at the upper site of roughly 43 g/m^2 and an annual $P/\bar{B}$ ratio of 71 (Table 6). At the lower site, production and $P/\bar{B}$ were 12.9 g/m^2 and 79, respectively (Table 7). While these annual $P/\bar{B}$ ratios may seem unusually high, it should be kept in mind that the CPI used in the production correction does not include the egg or adult stage (Benke 1979). Even a univoltine species, if its larval stage were present for only 30 d out of the year, could have an annual $P/\bar{B} \approx 60$.

Black fly larvae have often been found to occur in high densities (> 10 000/m^2), especially below lake outlets (e.g., Chutter 1968, Pearson and Franklin 1968, Ulfstrand 1968, Carlsson et al. 1977, Sheldon and Oswood 1977). Our mean values for the year on snag surfaces were in this range, 19 783 and 7038 black flies/m^2 at the upper and lower sites, respectively. Our value of > 100 000 black flies/m^2, which we found on a single date, is among the highest ever reported for black flies on a solid substrate. The few previous estimates of black fly production have been fairly low (e.g., Waters 1977*a*, Wotton 1978), although Ulfstrand (1968) reports an annual wet mass production, actually for ≈ 1 mo, of 1 kg/m^2 below a Swedish lake outlet. Except for Ulfstrand's estimate, our dry mass production values of 43 and 12.9 g/m^2 of snag surface are considerably higher than has been reported for black flies to date. Based upon studies in which high densities have been reported without production estimates (see above), we suspect that high productivity of black flies is more common than the production literature indicates.

Carlsson et al. (1977) have suggested that very dense populations are due to the abundance of extremely fine organic particles (< 2 μm). Wotton's (1976, 1977) feeding studies tend to support this possibility, and Ross and Craig (1980) have described the mechanism for capturing such fine particles using a mucosubstance. It seems likely that black fly production in the Satilla River may be supported by such fine particles, including bacteria (Fredeen 1964), and particles in the colloidal size range (0.1–1 μm). Although we did not characterize seston in the Satilla River, Wallace and his colleagues (Georgian and Wallace 1981, Wallace et al. 1982, J. B. Wallace, *personal communication*) have found that in other Coastal Plain rivers in Georgia typically 80% of total seston is in the 0.45–25 μm size class. Furthermore, R. T. Edwards (*personal communication*) has found that ≈95% of sestonic bacteria are unattached, with densities of 10^9–10^{11} cells/L in the Ogeechee, another Georgia Coastal Plain river.

Standing stock biomass for the Chironomidae was as consistent throughout the year as that of any group on snags (Figs. 5 and 6). This presumably was due to their short life cycles, rapid colonization and high turnover rates (see below). Unlike the black flies, they maintained their numbers and biomass in the presence of other consumers. Even the variation on a given date was the lowest of all major groups, with a CV averaging 86% and the SE/$\bar{x}$ averaging 36%. Maximum biomass and numbers were 313 mg/m^2 and 26 655 chironomids/m^2 of snag surface at the upper site and 377 mg/m^2 and 16 846 chironomids/m^2 at the lower site.

Among the most abundant species were members of the Tanytarsini and Orthocladiinae, all very small species which rarely exceeded 4 mm in length (Tables 6 and 7). Several species of *Polypedilum* (Chironominae) were abundant on snags, and as a group, were responsible for most of the chironomid biomass. The larger species, such as Chironomini sp. A, *Stenochironomus, Tribelos,* and *Xenochironomus,* were relatively low in abundance and very discontinuous in their temporal distribution.

As with the Simuliidae, the major problem in calculating production for the Chironomidae is determining the CPI for each group. Enormous variation apparently exists in both potential and actual development times for Chironomidae, and we were unable to estimate CPI from our field data. In some species of *Chironomus,* generation times of 1 or 2 yr have been reported in the colder lakes of Europe (Jonasson 1972, 1975) and up to 7 yr in an arctic pond (Butler 1982). However, for many chironomids, multivoltine populations have been reported in both lakes and rivers. For example, in Poland, Kajak and Rybak (1966) estimated 30-d development times for multivoltine populations in summer and 60 d in spring and autumn in lakes. Zieba (1971) estimated even shorter times in ponds. In the Canadian Northwest Territories, Rosenberg et al. (1977) found at least three generations per year for two *Cricotopus* species in lotic systems, and suggested a generation time of 4–6 wk during warm months (15°–20°). Gray (1981) found that chironomids (such as *Cricotopus* sp.) completed larval development in 1–2 wk in both laboratory and field studies on a desert stream. As far as we are aware, no one has done as detailed a laboratory/field study of chironomid development as Mackey (1976*a, b,* 1977*a, b, c*) on midges from the Thames River in England. Mackey (1977*c*) measured growth from hatching to pupation in the laboratory for several species at temperatures of 10°, 15°, and 20°, and also obtained independent estimates from field data. Species-specific regression equations were then calculated for predicting larval development from temperature. Development time at 15° varied from only 5 d for small Orthocladiinae to 60 d for larger Chironominae. Mackey's short development times are in general agreement with other laboratory growth studies of chironomids (e.g., Konstantinov 1958, Menzie 1981). We utilized Mackey's equations for closely related species in the Satilla River using our annual mean temperature of 19.0°. When Mackey's equations were based solely on laboratory growth, we arbitrarily doubled predicted development to account for some degree of "environmental resistance," such as competition, food shortage, etc. These values were then utilized in the production conversion 365/CPI, and multiplied by the uncorrected P (Tables 6 and 7). We are obviously assuming that food is not a major factor in limiting midge growth, and we discuss this assumption below.

The results show that chironomid species of relatively small size had moderate mean densities (for chironomids) and a fairly low standing stock biomass (Tables 6 and 7) compared to other groups such as caddisflies (Tables 4 and 5). However, due to short larval development times, annual $P/\bar{B}$ ratios are extremely high, and estimated production is among the higher estimates reported for midges (Waters 1977*a*). At the upper site, chironomid production (9.5 g/m^2) was almost as high as caddisfly production, but less than a quarter of black fly production. At the lower site, chironomid production (9.7 g/m^2) was somewhat less than black fly production and less than half of caddisfly production. The greatest chironomid production at both sites was attributed to the *Polypedilum* species. Our production estimates were somewhat less than Mackey's (1977*b*) estimates for total chironomid production in littoral zones of the Thames River. Some of Mackey's estimates (dry mass) were >30 g/m^2, but these figures are not strictly comparable to our own, since they were for a square metre of littoral zone bottom rather than substrate surface. Recent studies of chironomid production in streams much cooler than the Satilla demonstrated annual $P/\bar{B}$'s of ≈20 to >50 when short development times are taken into account (Mackey 1977*b*, Neves 1979, Menzie 1981). While not as high as our estimates for warm-water animals, they are clearly supportive of much higher values than investigators have estimated in the past.

The remaining miscellaneous dipterans (Tables 6 and 7) consisted primarily of *Atherix* sp. (Athericidae), *Hemerodromia* sp. (Empididae), and the ceratopogonids *Atrichopogon* sp. and species of the *Palpomyia* group. Total densities, biomass, and production were

TABLE 8. Modified average cohort (see text) and production statistics for Satilla River Ephemeroptera on snags. Numbers in parentheses are mean individual dry mass (mg).

	Head width (mm)					$\bar{N}$	$\bar{B}$	Annual P*	Annual
Taxon	0.5	1.0	1.5	2.0	2.5	(no./m²)	(mg/m²)	(mg/m²)	$P/\bar{B}$*
	No. larvae/m² habitat surface area								
Stenonema spp.†									
Upper site	67 (0.001)	114 (0.034)	36 (0.29)	17 (1.33)	5 (4.36)	239	54	576	10.7
Lower site	105	192	121	39	1	458	88	1148	13.0
	Total length (mm)								
	1	2	3	4	5				
	No. larvae/m² habitat surface area								
Other Ephemeroptera‡									
Upper site	9 (0.003)	22 (0.021)	11 (0.072)	3 (0.170)	1 (0.331)	46	2	22	11.0
Lower site	107	87	22	13	8	237	9	84	9.3

* Assumed two generations per year or an average larval development time of 6 mo for each group.

† *Stenonema* species include *S. exiguum, S. integrum,* and at least two other species.

‡ Other Ephemeroptera primarily include unknown species of *Eurylophella* and *Caenis.*

low in comparison to the midges and black flies on the snags. We have assumed cohort $P/\bar{B} = 5$, and CPI to be the same as for the large chironomids (28 d). This is probably too long for some (e.g., *Hemerodromia*), and too short for others (e.g., *Atherix*).

Our annual $P/\bar{B}$ ratios, particularly 355 for *Corynoneura/Thienemanniella,* seem unbelievably high in comparison to the literature (e.g., Waters 1977*a*, Banse and Mosher 1980). These high ratios are entirely due to our use of short CPI estimates, such as 8 d for *Corynoneura/Thienemanniella.* However, Mackey's (1977*c*) estimate of development time for *Corynoneura coronata* was 5 d at 15°. *Microcricotopus bicolor,* a species twice as long and many times the biomass of *Corynoneura,* was reared in <6 d at 15°. Gray's (1981) field studies in a desert stream are entirely consistent with these laboratory studies. The theoretical maximum annual $P/\bar{B}$ ratio for animals capable of completing larval development in 5 d and having a cohort $P/\bar{B}$ ratio of ≈8 (see *Corynoneura/Thienemanniella,* Table 7) is thus (365/5) × 8 = 584. Such a potential for high $P/\bar{B}$'s has never been recognized by aquatic ecologists, as far as we are aware. Clearly our somewhat lower $P/\bar{B}$ estimates are possible. The question is, do the midges in nature really complete their development in times that approach the minimum? Mackey's (1977*b*) estimates of combined daily chironomid $P/\bar{B}$ ratios were as high as 0.7 in the *Nuphar* habitat on the Thames River during warm months (when temperature approached 20°), and he estimated annual $P/\bar{B}$ was at least 30. Mackey observed several months of no growth due to temperatures <5°. However, since the Satilla River is a warm environment (mean = 19°, usual summer range = 25°–30°, usual winter range = 10°–16°) in which temperatures probably never drop below critical development temperatures, it would appear that low temperature would not generally be a major factor in limiting growth rates. This would appear to leave food as the major factor that could potentially limit individual growth rates (Anderson and Cummins 1979, Ward and Cummins 1979). Certainly food quality can be a major growth factor for some species in some streams, as Ward and Cummins (1979) found for *Paratendipes albimanus.* However, the following observations indicate that food does not usually limit growth rates in the Satilla. Snag substrates near the water surface may be inundated for relatively short periods of time due to fluctuating water levels. Yet such substrates are rapidly colonized by midges as water levels rise. Numbers and biomass of midges at high water can approach values observed at low water, even though the amount of substrate inundated is much higher in the former. This unpredictable habitat would appear to favor *r*-selected species, and the observations of rapid growth by black flies further supports this notion. Finally, as Cudney and Wallace (1980) point out, snag organisms in large Coastal Plain rivers are able to exploit various food materials produced elsewhere (e.g., flood plain swamps) that are carried to them by the current, and they do not appear to be food-limited.

Ephemeroptera.—At least four species of *Stenonema* (Heptageniidae) comprise the majority of mayflies found on snags (Table 8). Since separation of even late instars into species is very time consuming, and separation of early instars virtually impossible, we have combined these *Stenonema* species for all our analyses. All remaining species (primarily *Eurylophella* and *Caenis*) were combined into a second group for production analysis. All of these mayflies are generally considered as scrapers or gathering collectors (Cummins 1973, Shapas and Hilsenhoff 1976, Edmunds 1978).

Although few mayflies were found on snags during high water, at most other times the standing stock bio-

TABLE 9. Mean annual size distribution, standing stock biomass, and production for Satilla River Coleoptera (Elmidae) on snags (assumed annual $P/\bar{B} = 5$). Numbers in parentheses are mean individual dry mass (mg).

Taxon	Larval length (mm)				Total larvae	Adults	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	Annual P (mg/m^2)
	2	3	4	5					
	No. individuals/m^2 habitat surface area								
Upper site									
Stenelmis spp.	52 (0.028)	69 (0.095)	72 (0.23)	16 (0.44)	209	175 (0.46)	384	112	560
Total Elmidae					224	175	399	117	585
Lower site									
Stenelmis spp.	21	14	17	8	60	395	455	191	955
Ancyronyx variegata	16	14	33	14	77	22	99	27	135
Total Elmidae					137	417	554	218	1090

mass was relatively consistent, from 50 to 200 mg/m^2 of snag surface (Figs. 5 and 6). On a given date the CV averaged 112% and the SE/$\bar{x}$ averaged 46%. Production was calculated for the mayflies using the size-frequency method by grouping *Stenonema* species together, and all remaining mayflies into a second group. Head width was used as an index of size category for *Stenonema,* with roughly 20 size categories. A condensed representation of the average cohort is presented in Table 8. For the other genera, total larval length, exclusive of caudal filaments, was used to group individuals into size categories. There was no clear indication of length of larval development time from our size distributions. Therefore, we rely entirely upon the literature to approximate CPI for mayflies.

Length of larval life varies greatly among the mayflies, and within a species is strongly influenced by temperature (e.g., Brittain 1982, Clifford 1982). It is becoming increasingly evident that many species, especially those living in warm-water streams, can complete development rapidly. For example, Gray (1981) found four species in a desert stream (with annual temperature patterns similar to that of the Satilla) that could complete development in <2 wk. Of the limited life history studies conducted on *Stenonema* species, a 1-yr period of growth seems most common (e.g., Richardson and Tarter 1976, Flowers and Hilsenhoff 1978), but Kondratieff and Voshell (1980) have recently documented the existence of two generations per year for *S. modestum* in a Piedmont river in Virginia (with annual temperature pattern similar to that of the Satilla, but colder in the winter). In view of the warm-water environment of the Satilla River, we have assumed a CPI of 6 mo for *Stenonema,* as well as the other snag mayflies.

With densities of several hundred per square metre of snag surface, *Stenonema* spp. reached a production of 576 mg/m^2 at the upper site and 1148 mg/m^2 at the lower site (Table 8). Total density of other mayfly species was higher at the lower site, but individuals were very small and production was only 84 mg/m^2.

These production values, although low in comparison to other invertebrate groups on snags, are in the range of values reported for other mayflies. Waters's (1977*a*) review of secondary production showed mayfly annual dry mass production ranging from 120 to 4450 mg/m^2 in a variety of habitats. A few estimates for total mayfly annual dry mass production have exceeded 10 g/m^2 (Zelinka 1977, Welton et al. 1982). Hall et al. (1980) reported the highest mayfly annual production to be 8.56 g/m^2 for *Tricorythodes atratus* in northern Minnesota. The annual $P/\bar{B}$ ratio was 26, and in view of this and the short CPI's reported by Gray (1981), we may find eventually that mayflies in the Satilla have a shorter CPI (thus a higher $P/\bar{B}$) than we have assumed.

Coleoptera.—Riffle beetles (Elmidae) comprised the bulk of the Coleoptera present on snags. The *Stenelmis* species were by far the most abundant group, and *Ancyronyx variegatus* was commonly found (Appendix). Both *Stenelmis* and *Ancyronyx* are generally found on submerged wood, feeding on algae and the decayed, waterlogged wood (Brown 1972).

Standing stock biomass and densities were extremely variable from date to date at both sites (Figs. 5 and 6). Even on a given date, the CV averaged 128% and SE/$\bar{x}$ averaged 53%. The only pattern seems to be that high beetle densities are usually associated with high caddisfly densities. These dates also happen to be when water levels are low or have been dropping for some time. These are the times when the more decayed logs are likely to be collected as snags, and coincide with the observations above on the habitat and feeding preference of riffle beetles.

Mean larval length distributions, mean adult densities, and mean standing stocks are presented in Table 9. There is no obvious "average cohort" survivorship pattern, as one needs for using the size-frequency method. In fact, adult densities are almost as high as larval densities at the upper site, and adult densities are considerably higher than larval densities at the lower. Although this creates problems for estimating production, it does coincide with Brown's (1972) observations that the adults can live for long periods of time. Another

TABLE 10. Summary of density, standing stock biomass, and annual production for large invertebrate predators on snags (assumed cohort $P/\bar{B} = 5$). All mass units are dry mass.

Predator	Upper site			Lower site		
	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	P (mg/m^2)	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	P (mg/m^2)
Neurocordulia molesta	22	458	2290	27	351	1755
Macromiidae	0.3	0.6	3	0.2	27	135
Boyeria vinosa	3.0	115	575	3.0	149	745
Zygoptera	3.5	4.5	23	1.8	1.8	9
Total Odonata	29	578	2891	32	529	2644
Perlesta placida	110	88 (175)*	875	81	59 (119)*	595
Acroneuria mela	5.4	20	100	10	75	375
Other Plecoptera	2.5	1	5	0.4	3	15
Total Plecoptera	118	109	980	91	137	985
Corydalus cornutus	44	259	1295	41	379	1895
Total predators	191	946	5166	164	1045	5524

* Mean biomass for the part of the year during which larvae were present. See text.

possible explanation is that most larvae develop in the sandy benthic habitat (see below), but spend their adult life on the snags. Although little is published on elmid life histories, a typical life cycle would be 11 mo as larvae and several months to several years as adults (Reisen 1977, White 1978, H. P. Brown, *personal communication*). In view of the complexities involved for this group, we are simply assuming an annual $P/\bar{B}$ ratio of 5, in the absence of detailed information. One might note that on one date at each site, standing stock biomass exceeds our production estimate. With high SE's on these dates, we are assuming that these high values are anomalies due to sampling error. Even though this estimate for riffle beetle production is especially crude, it is the only production estimate of this group to date, as far as we are aware.

Large invertebrate predators.—The large invertebrate predators consisted primarily of the larvae of dragonflies (Odonata), stoneflies (Plecoptera), and dobsonflies (Megaloptera). The most important dragonfly was a large corduliid, *Neurocordulia molesta* (dry mass of final instar ≈62 mg/individual), always found clinging by its long legs to the outside of the snags. The large fast-swimming aeshnid *Boyeria vinosa* (final instar ≈154 mg) was found on occasion in low densities, but because of its extremely large size, it made a fairly large contribution to biomass. The small perlid *Perlesta placida* (final instar ≈4 mg) was the most abundant stonefly, and was found either on the outside of snags or beneath loose bark. The larger *Acroneuria mela* (final instar ≈55 mg) was much less common, and was particularly noted beneath the bark of snags. The large hellgrammite (larval dobsonfly) *Corydalus cornutus* (final instar ≈250 mg) was the only megalopteran found on snags, and it also was usually found under loose bark.

Dragonfly larvae are regarded as general predators, feeding on any available animals of the appropriate size (Pritchard 1964). Thus, *Neurocordulia* and *Boyeria* would be expected to feed on all snag organisms except large stoneflies and hellgrammites. Perlid stonefly larvae such as *Acroneuria* and *Perlesta* are also general predators and would be expected to concentrate on dipterans, mayflies, and caddisflies, as found by Sheldon (1969), Shapas and Hilsenhoff (1976), and Siegfried and Knight (1976) for *Acroneuria* species. *Perlesta placida,* as a smaller species, likely concentrates on smaller individuals (Shapas and Hilsenhoff 1976). The hellgrammites (*Corydalus cornutus*), like the dragonflies, can be expected to feed on any available invertebrate up to a fairly large size. Stewart et al. (1973) found that *C. cornutus* concentrated on black fly larvae and pupae, hydropsychid larvae, and to a lesser extent midge and mayfly larvae.

Although mean densities of invertebrate predators were relatively low, they comprised a large portion of total invertebrate standing stock biomass on snags at both sites (Table 10). However, since the low densities were associated with a relatively large sampling error, there was a very spotty temporal distribution of this standing stock (Figs. 5 and 6). Given these sampling difficulties, we were unable to approximate a reasonable "average cohort" for any of the predators to use in the size-frequency method of estimating production. Rather, we have assumed a cohort $P/\bar{B}$ of 5 and multiplied this times the mean standing stock value over the estimated time interval of the cohort (see Waters 1979).

For *Perlesta placida,* size-frequency data indicated a fairly synchronous univoltine development, a pattern consistent with the literature for this species (e.g., Snellen and Stewart 1979). Newly hatched recruits appeared in late autumn and grew throughout the winter. Adults emerged in early June. Only standing stock values over this interval were utilized in calculating production using a cohort $P/\bar{B}$ ratio of 5 (Table 10). Most of the Plecoptera standing stock observed during this time was due to *Perlesta* (Figs. 5 and 6). Apparently eggs are laid soon after emergence and remain in a dormant condition from June through November. *Acroneuria mela* was found in much lower densities than *Perlesta,* but since they are much larger, their mean standing stock sometimes was significant, especially at the lower site. Although *Acroneuria* and most other Perlidae take 2–3 yr to complete larval development (Hynes 1976), we are unaware of any life history studies on *Acroneuria* in streams as warm as the Satilla. Siegfried and Knight (1976) found a CPI of 18 mo for *Acroneuria* (*Calineuria*) *californica* and an annual $P/\bar{B}$ of 4.2 in a California stream (4–22.5°). In the absence of good evidence on their length of larval development, we have assumed an annual $P/\bar{B}$ of 5 for *Acroneuria* (Table 10). Total annual stonefly dry mass production at both sites was almost 1 g/m^2.

There are very few estimates of stonefly production (Waters 1977*a*). Only Winterbourne (1974) and Siegfried and Knight (1978) have presented comparable values for a predaceous stonefly. Winterbourn's estimate of 2.1 g/m^2 (dry mass) for *Stenoperla prasina* in a New Zealand river and Siegfried and Knight's 2.3 g/m^2 for *Acroneuria californica* are roughly twice our values for total stonefly production.

Neurocordulia molesta, like many dragonflies, showed a fairly synchronous univoltine development. Adult emergence probably occurred in late spring, although densities were so low by then, it was difficult to pinpoint the exact time. Small instars were found in early summer, and by autumn they had reached the penultimate or final instar, in which they overwintered. Since larval development was close to a full year, mean annual standing stock was multiplied by 5, resulting in the very high predator dry mass production values of 2290 mg/m^2 of snag surface at the upper site and 1755 mg/m^2 at the lower site. The aeshnid *Boyeria vinosa* like the stonefly *Acroneuria,* was large enough to have a relatively high mean standing stock, even though densities were very low. We have assumed an annual $P/\bar{B}$ of 5 for this species, although it is possible life history may be >1 yr.

There are few estimates of dragonfly production with which to compare our data. Lawton (1971) reported dry mass production of a British damselfly species to be 0.7 g/m^2 in a pond littoral zone. Kamlyuk (1973) found dragonfly production in the littoral zone of a Russian lake to be about 2 g/m^2, and Benke (1976) estimated dragonfly production in the littoral zone of a South Carolina pond to be 8 g/m^2. Our production values for *Neurocordulia* are comparable to the single-species estimates in the South Carolina pond.

Corydalus cornutus also appeared to have a fairly synchronous development. Early instars were found from late June through August in densities as high as 200 *C. cornutus*/m^2 of snag surface. This was responsible for a low but consistent level of standing stock during this period (10–60 mg/m^2). An increase in average larval size was obvious through the autumn from our size-frequency data. However, only a few large animals were found in the winter, and none was found in the spring. This probably indicates a univoltine development, as Brown and Fitzpatrick (1978) found for the same species in a north-central Texas stream. In the absence of further information, such as emergence period, we assumed an annual $P/\bar{B}$ ratio of 5. Based upon this analysis, *Corydalus* was the second most productive predator at the upper site (dry mass 1295 mg/m^2 of snag surface) and the most productive at the lower site (1895 mg/m^2, Table 10). This is somewhat less than the 2.5 g/m^2 found by Brown and Fitzpatrick (1978) for *C. cornutus,* which is apparently the only other estimate of a member of the Corydalidae. However, Brown and Fitzpatrick found an annual $P/\bar{B}$ ratio of almost 10, and if this is true for our population, we have underestimated *Corydalus* production to some extent. Production estimates for some lake-dwelling megalopterans have been reported, and they are much lower than reported here (Yamamoto 1972, Giani and Laville 1973).

Although standing stock values for large predators at each site are extremely variable on a date-by-date basis (Figs. 5 and 6), there is some degree of complementarity among the orders that can be partially explained by temporal separation of life histories. Larval development of *Neurocordulia* and *Corydalus* begins in late spring and probably ends with emergence in early to mid-spring. *Perlesta* larvae hatch in late autumn and emerge in early summer (late spring). This temporal separation is also reflected in the drift, where dragonflies and hellgrammites are most common in summer, and stoneflies most common in winter (Benke et al. 1979). In spite of the temporal variability in estimated standing stock, it is rather remarkable that such close correspondence in production results is found between the sites (Table 10). Total dragonfly production values are only ≈10% apart and stonefly estimates are virtually identical. The largest discrepancy is for *Corydalus,* where the production estimate at the upper site was 68% of that at the lower site. Total production values of large predators differed by only 7% between sites.

Snag production summary.—Of the major invertebrate groups on snags, black flies are clearly the most productive primary consumer at the upper site, comprising more than two-thirds of the total, with net-spinning caddisflies (primarily *Hydropsyche elissoma*) and midges sharing much of the remainder (Table 11). At the lower site, net-spinning caddisflies (primarily *H. incommoda*) comprise more than half the production of primary consumers, with black flies and midges sharing much of the rest. Total production of primary consumers is comparable at the two sites, and total production of large invertebrate predators is nearly identical. The dominance of black flies at the upper site and of caddisflies at the lower site appears to be real, but we currently have no explanation for this

TABLE 11. Mean annual density and standing stock biomass, annual production, and $P/\bar{B}$ ratios of major invertebrate groups on the snag habitat at two sites on the Satilla River. All biomass units are mg dry mass.

	Upper site				Lower site			
Taxon	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	P (mg/m^2)	$P/\bar{B}$	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	P (mg/m^2)	$P/\bar{B}$
Trichoptera	4710	1581	11889	7.5	10486	4222	26272	6.2
Chironomidae	7565	70	9509	137	7014	70	9721	139
Simuliidae	19783	603	43020	71	7038	163	12906	79
Other Diptera	382	23	1469	65	256	10	670	65
Ephemeroptera	285	56	598	11	695	97	1232	14
Coleoptera	399	117	585	5	554	218	1090	5
Total primary consumer	33124	2450	67070	27	26043	4780	51891	11
Large insect predators	191	946	5166	5.5	164	1045	5524	5.3

observation. The importance of the major taxa in influencing the total $P/\bar{B}$ ratio of primary consumers can be seen by comparing values at the two sites. At the upper site, where black flies predominated, annual $P/\bar{B}$ was 27. At the lower site, where caddisflies assumed the major production, total annual $P/\bar{B}$ was 11.

Since Nelson and Scott's (1962) production study on a rock-outcrop community on the Oconee River (Georgia Piedmont) included some of the same and many closely related species as found on Satilla snags, it is interesting to compare the two. Nelson and Scott's dry mass production estimate for primary consumers of 33.4 g/m^2 was roughly half that found at our upper site and two-thirds of that at our lower site. Their estimate for large predators, which included *Corydalus cornutus* and *Perlesta placida,* was 4.3 g/m^2, roughly 80% of our predator values. The correspondence between total production for the two studies is remarkable considering the fact that they are two different types of rivers (Coastal Plain and Piedmont), two different types of substrates, and that the production methodology used by Nelson and Scott was very different from ours. The common features of the two rivers are that both are warm-water and in both cases, production was measured on a solid substrate. Another interesting comparison is that 60% of the primary consumer production in the Oconee River was by filter-feeders, whereas on the Satilla snags, 85 and 80% were by filter-feeders at the upper and lower sites, respectively.

Sandy benthos production

Small dipterans and oligochaetes were the most common inhabitants in the sandy benthos, and the most abundant organism was a tiny midge, an unnamed species of *Parakiefferiella.* This species, as well as *Corynoneura* sp. and some small oligochaetes, attained a maximum length of no more than 2–3 mm. These organisms would not have been retained with the United States Standard Number 30 sieve (opening = 0.6 mm) used in most stream survey studies. Even with our mesh opening of 0.1 mm, it is unlikely that we retained first instars with much efficiency. Fortunately, although densities are highest in early instars, most of the production for aquatic insects occurs in later larval stages (Kimerle and Anderson 1971).

The feeding behavior of these very small invertebrates is unknown, but based upon feeding of related organisms, they probably consume extremely fine detritus mixed with the sand, microorganisms associated with detritus or sand particles, or diatoms attached to sand particles. At the lower site, several additional chironomid taxa comprised a more significant component of the sandy benthos than at the upper site. These chironomids primarily included Chironomini sp. B, *Cladotanytarsus, Cryptochironomus, Demicryptochironomus, Harnischia* complex, *Polypedilum, Rheotanytarsus, Tanytarsus,* and *Thienemanniella* (Appendix). Also found were elmid beetle larvae, primarily the genus *Stenelmis.* Very few adult beetles were found, and in view of the greater number of adult *Stenelmis* on snags, it is possible that these animals migrate from the sand to the snags as they mature.

There were two abundant predators which presumably preyed upon the smaller midges: the midge *Robackia claviger* and one or more species of the *Palpomyia* group (Ceratopogonidae). A gomphid dragonfly, *Progomphus obscurus,* was qualitatively collected by hand along the sandbars (when possible) on some sampling dates. Stomach analyses (A. C. Benke, *personal observation*) indicate that *Progomphus* feeds upon most of the midges collected from the sand, but we rarely collected the dragonflies in our grab sampler due to low densities, and have no way to estimate their production. A predaceous mayfly, *Dolania americana* (Behningiidae), is known to occur in the shifting sand of blackwater rivers (Peters and Jones 1973, Peters and Peters 1977), but they were extremely rare in the Satilla.

Although standing stock biomass was variable through time for the major groups and seemed unrelated to discharge, there appeared to be some recognizable patterns of abundance (Figs. 7 and 8). *Parakiefferiella* was most abundant in the winter, spring, and early summer, but declined in late summer and

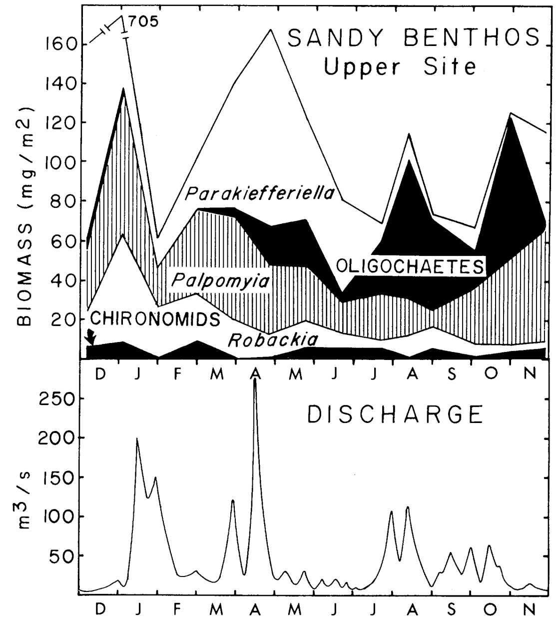

FIG. 7. Standing stock biomass (dry mass) trends for major taxa in sandy benthos at the upper site (monthly samples). Note all values on a given date are cumulative.

early autumn. Oligochaetes seemed to complement this pattern, with lowest values in the winter and maximum values in the summer and autumn. The oligochaetes consisted of *Pristina* and *Chaetogaster* (both Naididae), but part of the summer increase was due to the occurrence of the larger tubificid *Limnodrilus hoffmeisteri.* The predators *Robackia claviger* and *Palpomyia,* were rather consistent throughout the year. Other chironomids at the lower site were most abundant in the winter and autumn. The effect was a smoothing of total standing stock trends with values generally falling between 60 and 160 mg/m², considerably less temporal variation than that found on the snags. Biomass of the sandy benthos clearly was less affected by changing discharge than was biomass on the snags (Figs. 5 and 6).

For each major species and taxonomic group of sand benthos, sampling error was very high at a given site on a given date. This suggests that the distribution of organisms is more clumped than we might have expected in what appears to be a rather homogeneous habitat. The average SE/$\bar{x}$ for the biomass of each major taxon taken separately varied from 37 to 67%, and the average CV varied from 90 to 165%. However, total biomass among samples was considerably less variable. At each site, the average SE/$\bar{x}$ for total biomass was 31%, and the average CV was 75%.

Parakiefferiella reached extremely high densities at the upper site, averaging 42 726/m², but only 70.7 mg/m² standing stock (Table 12). Highest mean values were >183 000 individuals/m² and 566 mg/m², on 4 January 1975. One sample had a density equivalent to almost 800 000 larvae/m². *Parakiefferiella* was not as abundant at the lower site, but still averaged 15 666 larvae/m² and 22 mg/m² (Table 13). Mean standing stocks of predaceous midges at both sites were roughly half those of their prey.

We utilized the size-frequency production method for the sandy benthos, and as above, we used CPI's based upon Mackey's (1977*c*) development times. We assumed that on the average, oligochaetes developed at about the same rate as the larger midges. This may be conservative for the Naididae, since the maximum size was no more than 4 mm. Relatively little information actually exists on growth of the Naididae, but McElhone (1978) found that the naidid *Nais pseudobtusa* could double its numbers through asexual reproduction in 4.2 d at 20° in the laboratory. Learner et al. (1978) also discuss the rapid growth of Naididae at warm temperatures. The effect of *Limnodrilus* in biomass calculations undoubtedly would lengthen average turnover time of oligochaetes.

Production at the upper site was dominated by *Parakiefferiella* production, which reached over 21 g/m² (Table 12). This resulted in an annual $P/\bar{B}$ ratio of 306, comparable to that reported above for small midges on snags. This means that they are turning over roughly once a day, which seems high, but is consistent with our earlier discussion of high $P/\bar{B}$ values for small species in warm-water environments. Our assumptions concerning short development times are supported by collections of *Parakiefferiella* pupae from grab samples throughout the year, particularly in winter and spring.

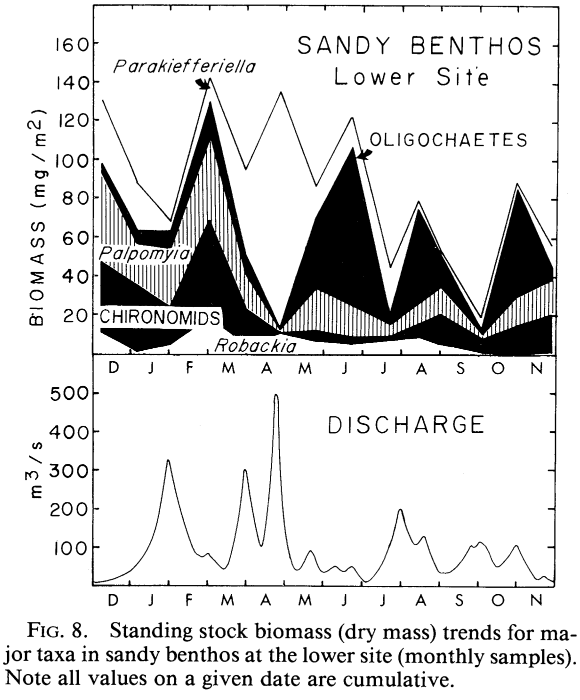

FIG. 8. Standing stock biomass (dry mass) trends for major taxa in sandy benthos at the lower site (monthly samples). Note all values on a given date are cumulative.

TABLE 12. Average cohorts and production statistics for Satilla River organisms of the sandy benthos at the upper site. Numbers in parentheses are mean individual dry mass (mg). CPI = cohort production interval.

	Total length (mm)												Uncorrected		Annual	
Taxon	1	2	3	4	5	6	7	8	9	10	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	P (mg/m^2)	$\frac{365}{\text{CPI}}$	P (mg/m^2)	Annual $P/\bar{B}$
	No. larvae/m^2 habitat surface area															
Chironomidae											46750	90.5			23768	263
Parakiefferiella	29334 (.0005)	13146 (.004)	246 (.014)								42726	70.7	470.1	46	21625	306
Corynoneura	2399 (.0008)										2399	1.9	9.5*	46	437	230
Robackia claviger (predator)		276 (.002)	144 (.008)	114 (.019)	49 (.036)	46 (.063)	28 (.100)	18 (.149)	6 (.212)		681	15.3	73.9	18	1330	87
Other Chironomidae	717 (.0005)	187 (.004)	17 (.014)	13 (.033)	8 (.066)	2 (.114)					944	2.6	23.5	16	376	145
Ceratopogonidae																
Palpomyia group (predator)		335 (.002)	202 (.008)	159 (.019)	86 (.036)	52 (.063)	36 (.100)	43 (.149)	29 (.212)	18 (.290)	960	33.1	143.4	18	2581	78
Elmidae (larvae)	75 (.01)	171 (.03)	18 (.10)	9 (.23)	1 (.44)						274	11	55*		55	5
Oligochaeta											1062	21.7	108.5*	18	1953	90
Total primary consumer											47405	107.9			24446	227
Total predator											1641	48.4			3911	81

* Assumed cohort $P/\bar{B} = 5$.

At the lower site, *Parakiefferiella* production was lower, 7411 mg/m^2 with an annual $P/\bar{B}$ of 337, but it still comprised almost three-fourths of primary consumer production (Table 13). Since the primary consumers in the sand consisted almost entirely of microinvertebrates with short development times, their combined $P/\bar{B}$ was >166 at both sites. This was considerably higher than turnover on the snags, which was strongly influenced by much larger, slower growing insects. Even the dipteran predators in the sand are turning over very rapidly, based upon our estimated development times (CPI estimated at 20 d for ceratopogonids). Actually, very little seems to be known for ceratopogonid development times, but Gray (1981) found that *Probezzia* sp. could be reared in 9 d at 22°, reasonably consistent with our assumptions. The low production and annual $P/\bar{B}$ of the elmids stands in sharp contrast to the other values presented here (Tables 12 and 13). We have assumed, as in the snags, that annual $P/\bar{B}$ is 5 for elmids (based on limited literature), but this could easily be an underestimate if elmids grow at rates of the same order of magnitude as other invertebrates in the sandy substrate.

A major group of organisms conspicuous by their absence from the sand was the molluscs, particularly mussels. Several species of filter-feeding mussels are known to occur in most Atlantic Coastal Plain rivers (Sepkoski and Rex 1974). However, for some reason, probably the very low calcium content of the water, fewer species are found in the Satilla than any other major river draining the eastern United States (Sepkoski and Rex 1974). Mussels were never collected in the Satilla with ponar sampling. On one date when the water was low, several individuals of *Elliptio crassidens* were found, but we rarely noticed their presence on other dates.

Muddy benthos production

The large freshwater oligochaete *Limnodrilus hoffmeisteri* (Tubificidae), two large Tanypodinae midges (*Coelotanypus* and *Procladius*), and the tube-dwelling caddisfly *Phylocentropus* were the most conspicuous benthic animals in the muddy backwater habitat. We believe that most, if not all, of the *Limnodrilus* were *L. hoffmeisteri,* a cosmopolitan species found in many habitats. However, it was not possible to verify the species identification for all fragmented and younger individuals. Several other species of smaller chironomids were present from time to time, and were more abundant at the lower site. These primarily included *Cryptochironomus, Harnischia* complex, and *Tanytarsus* (Appendix). *Palpomyia* group (Ceratopogonidae) were common in the mud, but not nearly as abundant as in the sand habitat. The planktonic predator *Chaoborus* was found in very high numbers on only a few dates at each site. Ostracods were sometimes very abundant, and various other invertebrates were found less frequently and in low densities (Appendix).

TABLE 13. Average cohorts and production statistics for Satilla River organisms of the sandy benthos at the lower site. Numbers in parentheses are mean individual dry mass (mg). CPI = cohort production interval.

	Total length (mm)												Uncorrected		Annual	
	1	2	3	4	5	6	7	8	9	10	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	P (mg/m^2)	$\frac{365}{\text{CPI}}$	P (mg/m^2)	Annual $P/\bar{B}$
	No. larvae/m^2 habitat surface area															
Chironomidae											18005	45.4			10101	222
Parakiefferiella	11644 (.0005)	4016 (.004)	6 (.014)								15666	22.0	161.1	46	7411	337
Corynoneura	847 (.0008)										847	0.7	3.5*	46	161	230
Robackia claviger (predator)		135 (.002)	132 (.008)	52 (.019)	37 (.036)	15 (.063)	12 (.100)	6 (.149)			389	6.8	43.0	18	774	114
Other Chironomidae	633 (.0005)	205 (.004)	121 (.014)	71 (.033)	32 (.066)	17 (.114)	11 (.181)	8 (.270)	2 (.385)	3 (.528)	1103	15.9	109.7	16	1755	110
Ceratopogonidae																
Palpomyia group (predator)		196 (.002)	153 (.008)	94 (.019)	65 (.036)	34 (.063)	31 (.100)	26 (.149)	9 (.212)	7 (.290)	615	18.7	88.8	18	1598	85
Elmidae (larvae)	39 (.01)	64 (.03)	13 (.10)	7 (.23)	5 (.44)						128	8	40*		40	5
Oligochaeta											1729	21.7	108.5*	18	1953	90
Total primary consumer											19473	68.3			11320	166
Total predator											1004	25.5			2372	93

* Assumed cohort $P/\bar{B} = 5$.

Limnodrilus is a deposit feeder, probably feeding on the rich organic mud and associated microorganisms in the backwater. *Phylocentropus* (Polycentropodidae) builds a tube in the mud with the upstream end extending above the surface, and feeds upon organic particles drawn into the tube by abdominal undulations (Wallace et al. 1976). *Procladius* and *Coelotanypus* probably feed upon ostracods and the smaller midges as well as on *Limnodrilus* (Loden 1974). Most of the remaining chironomids probably are detritivores.

As with the sandy benthos, we plotted discharge below the graph of standing stock biomass for both backwater sites (Figs. 9 and 10). At very high discharge, there was less mud in the ponar samples and a noticeable current through backwater areas which apparently carried some of the mud downstream. However, in spite of these qualitative observations, there were no noticeable influences of discharge on benthic biomass for any major group.

With only three samples taken at each site on a given date, the sampling error for each taxon was very high. For example, the average value of SE/$\bar{x}$ was 56% for *Limnodrilus* with the average CV = 97%. However, the variation for total benthic biomass was often low (SE/$\bar{x}$ ≈15%), with an overall average SE/$\bar{x}$ = 38% and CV = 66%. Interestingly, very high standing stocks for *Limnodrilus* were observed simultaneously at both sites in mid-August and early October. Total standing stock throughout the year seemed somewhat more variable in the muddy benthos than in the sandy benthos (Figs. 7 and 8 vs. Figs. 9 and 10), but this may have been due to fewer replicate samples and somewhat higher sampling error in the backwater. On the other hand, the peaks were largely due to *Limnodrilus,* and they may have represented times at which separate generations reached maturity. It was difficult to identify any definite annual trends in life history or standing stock for any taxon in the muddy benthos.

Average cohorts were determined for each major insect taxon in order to utilize the size-frequency method for estimating production (Tables 14 and 15). Development times based upon Mackey (1977*c*) were again utilized. We had no basis upon which to calculate CPI for *Coelotanypus,* which is much larger than any other chironomid in the muddy benthos. Since it is most closely related to *Procladius,* but grows to almost twice its length, we have made the assumption that CPI is twice as long for *Coelotanypus* (i.e., ≈41 d). Although this is a very crude approximation, it seems reasonable in comparison to the largest species studied by Mackey (1977*c*). We assumed that *Phylocentropus* takes a full year from hatching to pupation based upon life histories of other caddisflies.

In sorting of the muddy benthic samples, the tubificids often fragmented. Therefore, we have not attempted to estimate numerical densities. It was only possible to estimate production from the standing stock values (Figs. 9 and 10 and Tables 14 and 15), and to estimate annual $P/\bar{B}$ from the literature. Considerable variation apparently exists in the amount of time it takes for Tubificidae to grow from hatching to maximum size. For example, Aston (1973) was able to rear

Limnodrilus hoffmeisteri within 35 d at 25°, but Jonasson (1975) found that it took *Potamothrix hammoniensis* 4 yr to complete development in the cold and sometimes anaerobic Danish Lake Esrom. Potter and Learner (1974) described *Limnodrilus hoffmeisteri* as having four or five generations per year (annual $P/\bar{B} = 12.5$) in a reservoir in South Wales when the mean annual temperature was <13°. Johnson and Brinkhurst (1971) found $P/\bar{B}$ as high as 12 in a Canadian lake, and suggested that annual $P/\bar{B}$ for macroinvertebrates can be roughly calculated at $T^2/10$, where T is mean annual temperature. If applied to Satilla species ($T = 19°$), this would yield a $P/\bar{B}$ of 36. The most common finding is that *Limnodrilus* takes about a year to complete development (Kennedy 1966, Ladle 1971, Erman and Erman 1975). Unfortunately, there have apparently been no growth or production studies on *Limnodrilus* in warmer environments. In view of the available literature on life history and indications that *Limnodrilus* grows faster and has shorter generation time at higher temperatures, we are assuming that annual $P/\bar{B}$ for *Limnodrilus* is 20 in the Satilla. This seems reasonable and is probably conservative in a well-oxygenated environment where mean annual temperature is 19°.

Limnodrilus comprised a major proportion of standing stock, particularly at the lower site where it represented 71% of the total (Figs. 9 and 10 and Tables 14 and 15). The predaceous midges (*Procladius* and *Coelotanypus*) had a much higher standing stock and production at the upper site than at the lower site, but the other chironomids were more abundant at the lower site. Abundance and production of the caddisfly *Phylocentropus* was fairly low, but consistent at the two sites. Because *Chaoborus* was present in extremely high abundance on only a few dates, we estimated production as 1.5 times the maximum biomass, as has been suggested by some investigators (see Waters 1977*a*). This would have to be regarded as a minimal estimate since the procedure assumes only one generation a year.

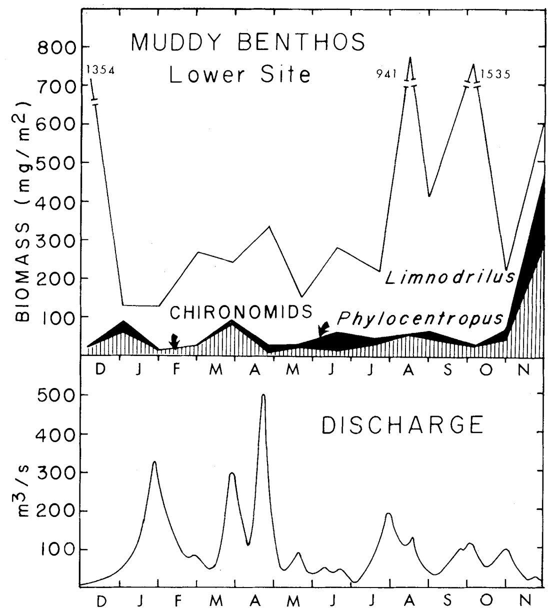

FIG. 10. Standing stock biomass (dry mass) trends for major taxa in muddy benthos at the lower site (monthly samples). Note all values on a given date are cumulative.

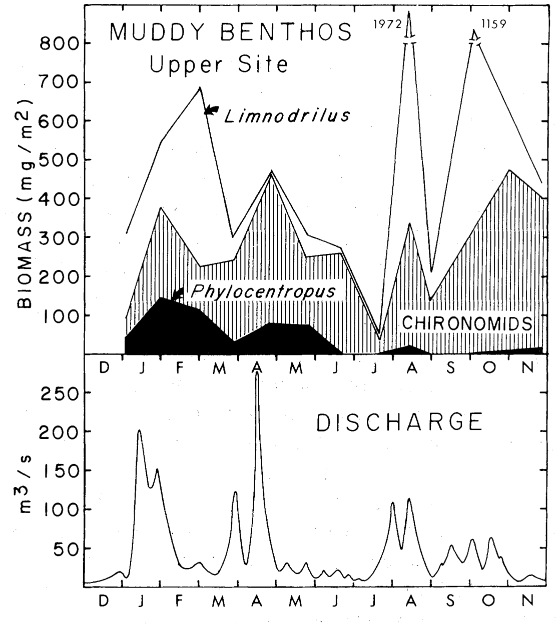

FIG. 9. Standing stock biomass (dry mass) trends for major taxa in muddy benthos at the upper site (monthly samples). Note all values on a given date are cumulative.

The relative values for production among primary consumers and predators, particularly at the upper site, seem anomalous at first glance (Table 14). Predator production seems too high in relation to primary consumers, and one is tempted to conclude that our predator turnover rates are too high. This may be true to some extent, but we feel there are better explanations. First, we undoubtedly sampled the smaller miscellaneous chironomids (and smaller oligochaetes) in the mud with less efficiency than in the sandy benthos, since we used the sugar flotation technique and a sieve with a mesh opening 2.5 times as large (0.25 mm). We doubt that the chironomids turned over much faster than we already assumed. Also, we know that microcrustaceans (especially ostracods) were sometimes present in high numbers in the backwater, and we did not sample them with high efficiency. They are known to be consumed by Tanypodinae in general, and they may turn over at a high rate. Finally, Tanypodinae are able to utilize detritus as food, although they do not grow as fast (Mackey 1977*c*). Until more efficient sampling and more detailed feeding and growth studies are done on several of these species, these questions will remain unresolved.

TABLE 14. Average cohorts and production statistics for Satilla River organisms of the muddy benthos at the upper site. Numbers in parentheses are mean individual dry mass (mg). CPI = cohort production interval.

	Total length (mm)																			
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	Uncorrected P (mg/m^2)	$\frac{365}{\text{CPI}}$	Annual P (mg/m^2)	Annual $P/\bar{B}$
	No. larvae/m^2 habitat surface area																			
Chironomidae															617	236.5			14905	63
Procladius (predator)	10 (0.001)	44 (0.01)	49 (0.04)	90 (0.08)	97 (0.16)	27 (0.27)	9 (0.45)	3 (0.67)	1 (0.95)						330	40.1	251.6	18	4529	113
Coelotanypus (predator)		1 (0.02)	6 (0.06)	13 (0.15)	3 (0.28)	6 (0.49)	15 (0.78)	24 (1.2)	24 (1.7)	19 (2.3)	4 (3.0)	4 (3.9)	2 (5.0)	2 (6.2)	123	186.5	1012.7	9	9114	49
Other Chironomidae	9 (0.001)	49 (0.007)	40 (0.02)	38 (0.05)	13 (0.11)	7 (0.18)	4 (0.29)	1 (0.43)	2 (0.61)	1 (0.84)					164	9.9	78.9	16	1262	127
Chaoboridae																				
Chaoborus (predator)		1 (0.01)	6 (0.04)	12 (0.08)	14 (0.17)	45 (0.30)	71 (0.48)	25 (0.60)	1 (1.0)						175	67.3	336.5		640*	
Ceratopogonidae																				
Palpomyia group (predator)		1 (0.002)	4 (0.01)	1 (0.02)	7 (0.04)	3 (0.06)	8 (0.10)	24 (0.15)	1 (0.21)						49	5.1	25.6	18	461	90
Trichoptera																				
Phylocentropus		4 (0.02)	4 (0.05)	3 (0.12)	1 (0.24)	3 (0.41)	4 (0.65)	8 (0.97)			11 (2.5)				38	30	150†	1	150	5
Oligochaeta																				
Limnodrilus															290				5800‡	20†
Total primary consumer															202§	299			7212	24
Predator															677	330			14744	45

* Calculated as 1.5 times maximum biomass (see text).

† Assumed cohort $P/\bar{B} = 5$.

‡ Assumed annual $P/\bar{B} = 20$ (see text).

§ This sum does not include fragmented *Limnodrilus*.

Our annual dry mass production estimates for *Limnodrilus* of 5.8–8.4 g/m^2 are comparable to those by Johnson and Brinkhurst (1971) Potter and Learner (1974), and Erman and Erman (1975), although less than estimates by Teal (1957). Our production estimates for *Coelotanypus* and *Procladius* are higher than have been reported for Tanypodinae (Waters 1977*a*), but no one has assumed similarly high turnover rates. Production of *Phylocentropus* would be considered low in comparison to most other Trichoptera (Waters 1977*a*, Benke and Wallace 1980).

Comparison of the three habitats

All of the numerical density, standing stock biomass, and production values presented above are for a unit area of habitat. For both the mud and sandy benthos, this unit is equivalent to 1 m^2 of bottom. For snags, it means 1 m^2 of snag surface. Each of these might be thought of as the "effective habitat" (Neves 1979, Resh 1979), and production calculated on each basis is the best measure of intensity of production. Standing stock biomass on the snags is much higher than that found in the benthic habitats (Table 16). Production is also highest on the snags, but because of the high overall $P/\bar{B}$ ratios in the benthic habitats, sand and mud benthos may each contribute 24–39% as much as the snag production. Studies on the Missouri River provide the most comparable results on biomass distribution. Benthic standing stocks (dry mass) were usually ≈0.01 g/m^2 (Modde and Schmulbach 1973), but colonization of invertebrates on multiple-plate samplers was roughly 1–3 g/m^2 (Nord and Schmulbach 1973).

In most studies, production is presented as amount per square metre of bottom substrate, and for some purposes it would be desirable to present data from each habitat in this common unit. Alternatively, it is sometimes desirable to compare total production in different habitats for a given stretch of river (e.g., Mackey 1977*b*). Therefore, we attempted to estimate the density of snag surfaces and thus snag productivity per length of river shoreline. On 6 December 1974, discharge at both sites was extremely low (Fig. 3), and

TABLE 15. Average cohorts and production statistics for Satilla River organisms of the muddy benthos at the lower site. Numbers in parentheses are mean individual dry mass (mg). CPI = cohort production interval.

	Total length (mm)																Uncorrected		Annual	
Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	P (mg/m^2)	$\frac{365}{\text{CPI}}$	P (mg/m^2)	Annual $P/\bar{B}$
	No. larvae/m^2 habitat surface area																			
Chironomidae															544	50.3			3748	75
Procladius (predator)	10 (0.002)	44 (0.01)	21 (0.04)	18 (0.08)	7 (0.16)	1 (0.28)		3 (0.67)							104	6.2	41.3	18	743	120
Coelotanypus (predator)		4 (0.02)	4 (0.06)	9 (0.15)	6 (0.28)	3 (0.49)	2 (0.78)	5 (1.2)	1 (1.7)	2 (2.3)		1 (3.9)		1 (6.2)	38	28.6	142.6	9	1283	45
Other Chironomidae	66 (0.001)	153 (0.007)	72 (0.02)	69 (0.05)	18 (0.11)	13 (0.18)	7 (0.29)	2 (0.43)	1 (0.61)		1 (1.1)				402	15.5	107.6	16	1722	111
Chaoboridae																				
Chaoborus (predator)				1 (0.08)	6 (0.17)	11 (0.30)	108 (0.48)	50 (0.60)	7 (1.0)						183	93.6	468		1302*	
Ceratopogonidae																				
Palpomyia group (predator)	2 (0.0003)	15 (0.002)	26 (0.01)	10 (0.02)	12 (0.04)	13 (0.06)	6 (0.10)	4 (0.15)	4 (0.21)						93	3.8	19.1	18	344	91
Trichoptera																				
Phylocentropus	1 (0.002)	4 (0.02)	2 (0.05)	1 (0.12)	5 (0.24)	3 (0.41)	5 (0.65)	4 (0.97)	1 (1.4)	1 (1.9)	4 (2.5)				31	23.9	119†	1	119	5
Oligochaeta (*Limnodrilus*)																420			8400‡	20‡
Total primary consumer															433§	459.4			10241	22
Predator															418	132.2			3672	28

* Calculated as 1.5 times maximum biomass (see text).

† Assumed cohort $P/\bar{B} = 5$.

‡ Assumed annual $P/\bar{B} = 20$ (see text).

§ This sum does not include fragmented *Limnodrilus*.

much of the snag habitat was exposed and dry. Water depth at the upper site was <1 m on the outside bend of the river where snags were usually collected. At the lower site, water depth was 1–2 m where snags were collected. We selected three representative snag areas at the upper site and four at the lower site, each set ranging from what we subjectively called "sparse" to "dense." At each snag area we delineated a 4 m stretch of shoreline. We measured the circumference of every limb, branch, twig, and root intersected by a horizontal plane along this 4 m length at three heights: (1) water level, (2) 1 m above water level, and (3) 2 m above water level. The sum of the stem circumferences (in metres) at each height provided the first (length) dimension for calculating snag surface area. This first approximation of length assumes that all snags are aligned vertically. Since snags are oriented at all angles, we assumed that the mean angle was both 45° from the vertical and 45° away from the shore. The length estimate was therefore adjusted by multplying by $\sqrt{3}$ or 1.73 (the diagonal of a unit cube). (Note: this adjustment of 1.73 was not taken into account by Benke et al. 1979). A mean length dimension was calculated from the measurements at the three heights, and this approximated the mean surface area of habitat *per 1 m of depth* along that 4 m of shoreline. Dividing this mean value by 4 yields an estimate of mean surface area of habitat per metre of depth per metre of shoreline. If this value is then multiplied by height of water (usually much higher than at the time we measured) one obtains an approximation of snag surface area submerged per metre of shoreline.

The mean surface area of habitat per metre of depth per metre of shoreline varied at the upper site from 0.317 to 2.034 m^2, and at the lower site from 0.548 to 2.566 m^2. It proved impractical to obtain estimates of the relative abundance of each snag density (sparse to dense) for a long stretch of shoreline. We therefore assumed that the measurements we made at each site were representative, and assumed that the mean of these snag measurements was a reasonable approximation for a long stretch of shoreline. This assumption alone meant that our approximation was very crude. In any case, mean values at the two sites differed by only 5%, and we therefore used a grand mean of 1.073 m^2 per metre of depth per metre of shoreline.

Since water level in the Satilla fluctuates so much and snags are rapidly recolonized after inundation (Van

TABLE 16. Annual mean density ($\bar{N}$) and standing stock biomass ($\bar{B}$), annual production (P) and annual $P/\bar{B}$ for primary consumers and predators from each habitat (on substrate surface area).

	$\bar{N}$ (no./m^2)	$\bar{B}$ (mg/m^2)	Annual P (mg/m^2)	Annual $P/\bar{B}$
		Upper site		
Snag primary consumers	33124	2450	67070	27
Predators	191	946	5166	5.5
Sand primary consumers	47405	108	24446	227
Predators	1641	48	3911	81
Mud primary consumers	202	299	7212	24
Predators	677	330	14744	45
		Lower site		
Snag primary consumers	26043	4780	51891	11
Predators	164	1045	5524	5.3
Sand primary consumers	19473	68	11320	166
Predators	1004	26	2372	93
Mud primary consumers	433	459	10241	22
Predators	418	132	3672	28

Arsdall 1977), the most practical way to account for water depth was to use an average value. We did not have sufficient data to calculate mean depth throughout the year, but since we recorded water depth at the time samples were taken, a regression was developed between discharge (Fig. 3) and water depth (Benke et al. 1979). From this regression, we estimated the water depth at mean discharge. At the upper site this depth was 3.3 m, and at the lower site 3.6 m. Thus, snag surface area was $3.3 \times 1.073 = 3.541$ m^2 per metre of shoreline at the upper site and $3.6 \times 1.073 = 3.863$ m^2 at the lower site. In other words, there was on the average roughly 3.5–4 m^2 of snag surface inundated per metre of shoreline.

When the river was at its mean discharge, the sandy channel was completely inundated, and the river began to overflow its banks and flow through the swamps. The river width at this height was roughly 50 m at the upper site and 70 m at the lower site. Thus there was roughly 14 times as much sandy substrate as snag surface at the upper site and 18 times as much at the lower site.

The relative amount of main channel sand benthos and backwater mud benthos were estimated over a river length of ≈40 km near both sites from recent topographic maps. At the upper site, the backwaters were roughly 10% of the main channel area. At the lower site, the backwaters were more common, ≈20% of the main channel. Thus, the relative amounts of snag, mud, and sand habitat areas occur in the ratio 1: 1.4:14 at the upper site, and 1:3.6:18 at the lower site.

Given the above ratios, and using Table 16, we approximated the relative standing stock and production for each habitat for a length of river (Table 17). For both sites, total standing stocks were higher in the snags than in the two benthic habitats combined. However, the sand habitat contributed 70–80% of production for all habitats, with snags contributing ≈15–16%. In short, after correcting for habitat abundance, snags still had the highest standing stock biomass, but because of the large sandy habitat area and the high turnover rates of its inhabitants, total sand benthos production was highest.

Since the snag and sandy habitat are both in the main channel, their invertebrate biomasses per effective habitat area can be added together, after taking habitat abundance into account, to provide an estimate of biomass per unit area of stream bottom. The same can be done for production (Table 18). The mean dry biomass for primary consumers of only ≈0.3 g/m^2 is quite low in comparison to many streams, and the snag organisms comprise much of this (Table 17). That such a small amount of effective habitat (snags) can contribute a significant amount to total biomass strongly implies that at least total invertebrate biomass for the river is substrate limited. Annual production for primary consumers is actually quite high in comparison to the literature (Morgan et al. 1980, Benke, *in press*). Although snag organisms make a significant contribution to total production, most of this production is contributed by the small, fast-growing organisms from the sand. The result of combining these two habitat estimates is that the annual $P/\bar{B}$ for both primary consumers and predators is quite high at both sites.

It should be emphasized that the habitat-specific approximations for a length of river are very crude. The habitats are not static, as we assume in making the calculations, but are constantly undergoing shrinking and expansion with desiccation and drift, resulting in animal losses and recolonization. Furthermore, snags sometimes occur on both sides of the river and sometimes in the middle of the river, and sometimes there are none. However, this represents the first attempt to evaluate the relative importance of these different habitats, and the relationships should be approximately correct.

Distribution of production among functional feeding groups

Nelson and Scott (1962) were the first to determine production of stream macroinvertebrates according to their feeding strategies. They found that much of the production in the Oconee River (Georgia, USA) was by filter-feeders, and this led them to suggest that the majority of food for aquatic insects was of allochthonous origin. Since that time, many investigators have stressed the importance of allochthonous detritus in streams, and increased emphasis has been placed on categorizing invertebrates into functional feeding groups (e.g., Cummins 1973, Cummins and Klug 1979). The prevailing notion is that the balance among functional groups differs according to biome and stream type (Cummins and Klug 1979), and that the invertebrate community provides a good indication of the food type and possibly its origin.

The outcome of a functional group assessment can vary considerably if different criteria of importance are used. While relative abundance of functional groups represents the simplest assessment of their importance in streams, standing stock biomass is probably considered a better measure of importance (e.g., Cummins and Klug 1979). We feel that production of functional groups provides the best measure of relative importance since it is more directly related to energy flow, but since the time of Nelson and Scott (1962), such estimates are almost nonexistent (except Neves 1979). In the following analyses, we combine our taxon-specific numerical, biomass, and production estimates into functional groups on a habitat-by-habitat basis, and then for a stretch of river.

TABLE 17. Percentages of effective habitat area, invertebrate numbers, standing stock dry biomass, and production distributed among three major habitats for a stretch of river. Note: numerical percentages for the mud do not include *Limnodrilus*, but their inclusion would make little difference in the numbers (see text).

Habitat	Distribution among habitats (%)			
	Effective habitat area	Numbers	Biomass	Production
Upper site				
Snag	6	4.6	53.7	14.5
Sand	85	95.2	32.3	79.5
Mud	9	0.2	13.9	6.0
Lower site				
Snag	4	6.6	60.4	16.2
Sand	80	92.6	17.5	69.6
Mud	16	0.7	22.1	14.2

TABLE 18. Annual mean standing stock biomass ($\bar{B}$), annual production (P), and annual $P/\bar{B}$ for a unit of stream bottom in the main channel. These values were estimated by adding snag and sand values together after adjusting for habitat abundance.

	$\bar{B}$ (mg/m^2)	P (mg/m^2)	$P/\bar{B}$
Upper site			
Primary consumers	283	29236	103
Predators	116	4280	37
Lower site			
Primary consumers	334	14203	43
Predators	84	2634	31

All taxa were first placed into one of the major functional feeding groups (i.e., shredders, filtering collectors, gathering collectors, scrapers, wood gougers, and predators; see Cummins and Klug 1979). Many of the invertebrates fall neatly into a certain group. For example, the dragonflies, stoneflies (this study), and hellgrammites are all predators. The hydropsychid caddisflies and black flies are all filtering collectors. However, the exact feeding mechanism of some animals, especially some of the midges and mayflies, was not known precisely. Some species (or genera) may be either gathering collectors or scrapers, depending on where they are found (Merritt and Cummins 1978). For the latter, we assumed that they were all gathering collectors in view of the substrate on which they were found. Some animals probably also functioned at least partly as wood gougers (e.g., *Stenochironomus*), but their numbers were so low that we have included them with the gathering collectors.

After categorizing all taxa into one of the functional groups, the relative numbers, biomass, and production contributed by each functional group in each of the three major habitats was determined (Table 19). In the snag habitat, filtering collectors were obviously the major functional group by any criterion. The two sites show remarkably similar proportions of functional groups for a given criterion. In comparison to the proportions generated using production values, it appears that using numbers underestimates the importance of predators, whereas biomass tends to overestimate their importance. The reverse appears true for gathering collectors on snags, where biomass tends to underestimate their importance. The gathering collectors predominate in both benthic habitats no matter what the criterion, with little contribution from filtering collectors. Again, the relative importance of predators seems underestimated by numbers (sand only), and overestimated by biomass. The anomalous production result in the mud habitat at the upper site was discussed above.

Fig. 11 illustrates the relative production contributions of each of the major functional groups within each habitat, as well as the relative production intensity

TABLE 19. Percentages by numbers, standing stock biomass, and production of major functional groups within the three major habitats (effective habitat area basis). Note: Numerical percentages for the mud do not include *Limnodrilus*.

Habitat	Functional group	Upper site			Lower site		
		Numbers	Biomass	Production	Numbers	Biomass	Production
		Percentage within habitat					
Snags	Filtering collectors	79.9	64.6	79.3	75.4	75.1	72.1
	Gathering collectors	16.4	6.6	9.7	21.0	6.7	15.7
	Predators	3.7	28.8	10.9	3.6	18.2	12.2
Sand	Gathering collectors	96.6	69.0	86.2	94.9	72.8	82.7
	Predators	3.4	31.0	13.8	5.1	27.2	17.3
Mud	Gathering collectors	18.7	42.7	32.1	47.2	73.6	72.7
	Filtering collectors	4.3	4.8	0.7	3.6	4.1	0.9
	Predators	77.0	52.5	67.2	49.1	22.3	26.4

(effective habitat area basis) in each of the habitats at the lower site. The figure indicates at a glance that on the snag habitat: (1) there is a much higher production than in the benthic habitats; (2) the production is primarily by filtering collectors; (3) the diversity of animals is much higher; and, (4) the average animal size is much larger. Clearly, the snag habitat imparts a biological richness to the river that would be completely undiscovered if only the benthic habitats were examined.

GENERAL DISCUSSION

Three major topics require further elaboration and discussion. The first concerns the notoriously difficult problem of estimating secondary production of an entire invertebrate community and the methodological strategy to be used. The second concerns the significance of our findings of high production in a subtropical blackwater river and the importance of snags as a general habitat in lotic systems. The third concerns the value of estimating production when addressing ecosystem-level questions of functional group feeding strategies and energy utilization along the stream continuum.

Production methods and turnover rates

Unlike primary production, in which community metabolism techniques have worked so well, estimating production of the primary consumers as a group has been especially frustrating for investigators concerned with energy flow. Populations with well-defined cohorts and long life cycles have never been much of a problem, since production can be accurately determined from quantitative field samples collected at monthly intervals (e.g., Waters 1977*a*, Gillespie and Benke 1979). The problem has been that much of the invertebrate community consists of a great number of asynchronously developing taxa, many with short life cycles, as we found in the Satilla River.

In search of a method for estimating secondary production of the entire invertebrate community, many short-cut approaches have been suggested. Originally, the size-frequency method used in the present study was a short-cut approach, applied to the entire community (Hynes and Coleman 1968), but it also proved accurate for single-species studies as well (e.g., Waters and Crawford 1973). Since it is now possible to correct size-frequency estimates for taxon-specific larval development times (Benke 1979), we feel the approach has the greatest utility of any method. Five other short-cut approaches and their limitations are discussed briefly by Benke (*in press*). One of these approaches (suggested by Waters 1979) is to assume that cohort $P/\bar{B} = 5$. This is what we have done when there were insufficient data to calculate an average cohort.

Another one of these short-cut approaches is appropriate to discuss at this point, since it bears directly on the question of the annual $P/\bar{B}$ ratio. Banse and Mosher (1980) suggested, using regression analyses on 33 invertebrates living at annual mean temperatures between 5° and 20°C, that adult body mass is a good estimator of annual $P/\bar{B}$. We urge particular caution in using such a relationship to approximate production for stream insects. We see no theoretical reason why adult body size should be related to annual $P/\bar{B}$ except that body size can be correlated with (1) development time (which is theoretically related to annual $P/\bar{B}$; see Benke 1979), and possibly (2) survivorship pattern (which is theoretically related to cohort $P/\bar{B}$; see Waters 1969). Also, we note that all the aquatic insects used by Banse and Mosher had annual $P/\bar{B}$ values <5 (i.e., almost all took at least a year to develop). While their selection of data reflected a reasonable choice of representative animals at the time of their analyses, evidence is accumulating that some multivoltine insects (particularly dipterans) have annual $P/\bar{B}$ values much higher than 10. The exclusion of such data from their regression probably results in a strong bias. Furthermore, it is our feeling that factors such as temperature and food (quality and quantity) should not be discounted as factors influencing development time (and thus annual $P/\bar{B}$) for the sake of Banse and Mosher's short-cut approach (see Morgan et al. 1980). Laboratory growth studies (and some field studies) generally support the view that growth of a given species (particularly chironomids) is very sensitive to temperature and food (e.g., Mackey 1977*c,* Ward and Cummins 1979, Menzie 1981).

While some aspects of our production analysis are still crude approximations, our overall assessment represents a finer level of resolution than most studies of entire lotic invertebrate communities. All estimates are based at least upon standing stock biomass, and most utilize an approximation of survivorship (average cohort). The major source of potential error is in the means by which we estimated the very important larval development time. Our best estimates are obviously when we had supportive field data for development time (e.g., *Hydropsyche* spp., black flies, and the large insect predators), and our crudest estimates are those in which we depended upon development times obtained from the literature (especially the chironomids). Admittedly, further resolution may show that some of our annual $P/\bar{B}$ ratios are too high (e.g., midges), but it may also reveal that some are too low (e.g., mayflies). However, we have attempted to describe a strategy for estimation of production within a consistent methodological framework and to make our assumptions clear. Taxon-specific turnover (or CPI) is clearly the major question that must be addressed in any study of secondary production, and we emphasize this point in our analyses and discussion. Investigators will rarely have the resources to document fully the CPI of all coexisting members of a benthic community. We feel the approach used here is a reasonable one, although it is by no means a short-cut. That is, collect life history data as detailed as possible for all taxa in order to estimate CPI, obtain indirect evidence of life cycle through field observation (i.e., emergence, appearance and disappearance of larvae and pupae, etc.), use laboratory growth data and well-documented literature information to fill the gaps.

An additional note regarding laboratory growth studies and the use of literature values is appropriate. Some investigators feel that laboratory growth studies under "ideal" conditions yield development times that are shorter than actually occur in nature. This is obviously true for some environments in which growth rates are limited by food quality (e.g., Ward and Cummins 1979). However, in aquatic systems where there is no obvious food limitation, we feel that in the absence of field evidence on life cycles, the best first approximation of production is one which allows growth close to that which can be achieved under laboratory conditions for a given temperature. Gray (1981) estimated short development times for several species, finding good agreement between laboratory and field methods. For many taxa (e.g., chironomids), assuming maximum growth and development times of much less than a month will mean annual $P/\bar{B}$ ratios of 100 or more. Now that several investigators have documented the short development times for several lotic species (e.g., Mackey 1977*c,* Menzie 1981), it appears that annual $P/\bar{B}$ ratios for animals such as chironomids are much higher than previously believed. The challenge for aquatic secondary production biologists is to document more accurately the length of time that it takes fast-growing species to complete their development in nature, and to determine what factors keep development rates below their physiological maximum.

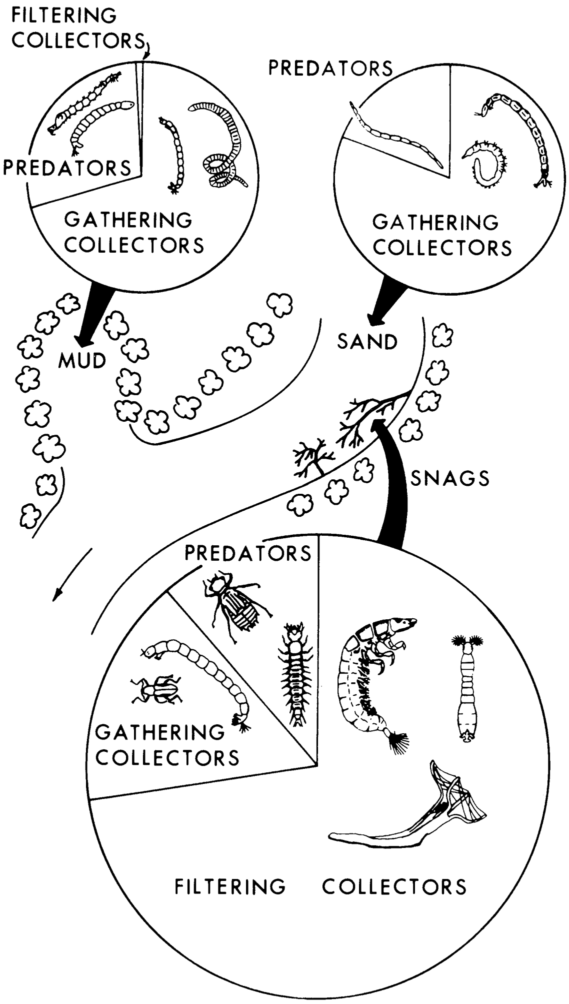

FIG. 11. Relative production of invertebrate functional feeding groups in sand, mud, and snag habitats (lower site). Size of circle indicates relative production among habitats on an effective habitat area basis.

Although the $P/\bar{B}$ ratios for some of our small species (especially dipterans) seem unusually high, in comparison to the literature in which direct production estimates have been made, our high values are entirely consistent with a growing volume of research on turnover rates of benthos required to feed fish or invertebrate predators. Allen (1951) was the first to estimate that a high turnover of invertebrates was required to feed fish predators, and the discrepancy between high

$P/\bar{B}$ values and lower values based upon direct estimates has been referred to as the "Allen paradox" (Hynes 1970). Subsequent studies on predator consumption indicate required benthic turnover times of a few days to a few weeks, and thus potential annual $P/\bar{B}$ ratios (if such rates continued through the year) of say, 15–180. There have been at least a dozen studies of this nature in the last 20 yr suggesting such short turnover times. The review by Morgan et al. (1980) summarizes much of the literature, and similar results were also found by Coffman et al. (1971) in a stream, Benke (1976) in a pond littoral zone, and Schalles (1979) in a Carolina Bay. We feel the major reason(s) for the difference between this body of literature and the literature on direct estimation of production is that either biologists using the latter approach have not adequately taken larval development time (CPI) into account, or they have tended to avoid estimating production of species with short development times.

Distribution of production in blackwater rivers

The Satilla River has been shown to be high in invertebrate production by almost any standard. Snag production estimates (on an effective habitat basis) are as high or higher than production estimates (per bottom area) from rivers (Mann 1975, Waters 1977*a*), and rivers generally have a much higher production than small shaded streams (Mann 1975, Benke and Wallace 1980). Specifically, the standing stock biomass of animals in rivers is usually higher than in small streams on an effective habitat basis if a solid substrate is available. Values (dry mass) >2 g/m^2 of solid substrate surface are commonly found in rivers as large as the Satilla, and are quite unusual in small streams, unless the stream was artificially enriched (e.g., in farming areas, or below an impoundment). In other words, food appears to be less of a limiting factor in rivers than in small streams, and where high-quality food is plentiful, substrate availability may be the major factor limiting secondary production. See Haefner and Wallace (1981) for a discussion of seston food quality vs. quantity and the potential impact of filter feeders on seston. The Speed River, actually a medium-sized stream draining an agricultural area, provides a good illustration of the influence of substrate availability on secondary production (Hynes and Coleman 1968, Coleman and Hynes 1970). Only in the Speed is benthic production much higher than on the Satilla snags, but food is probably plentiful, and there is a very high standing stock biomass distributed down at least 30 cm into the hyporheic zone. Standing stock (and thus production) is so high because the effective habitat per bottom area is extraordinarily high.

Invertebrate production is also moderately high in the sand and mud habitats of the Satilla River due to the rapid turnover of relatively low standing stock biomass. This contradicts the general notion of unstable sandy habitats being very unproductive (e.g., Hynes 1970), but little consideration has ever been given to the possibility and influence of high turnover rates. Furthermore, sampling technique is also very important, and without a sieve mesh size in the range of 0.1 mm, standing stock biomass could be grossly underestimated.

The high production of invertebrates in the Satilla River stands in sharp contrast to the presumed low secondary production of softwater (e.g., Eggislaw 1968) or blackwater (e.g., Janzen 1974) lotic systems. Janzen (1974) and others have described blackwater (particularly tropical) rivers as being low in diversity and productivity. Although there are undoubtedly more species reported from some other rivers (e.g., Bishop 1973), we have identified well over 100 invertebrate taxa, some of which (e.g., *Polypedilum spp., Stenonema spp.*) divided into a number of species. Also, Peters and Jones (1973) list well over 100 species from the Blackwater River in Florida (a river similar to the Satilla in chemical characterisitics), without even including the Diptera. Such numbers would be considered relatively high by most standards (e.g., Patrick 1975). Thus, it is possible for blackwater rivers with many of the characteristics described by Janzen (1974) to have a rather high diversity and animal productivity. Whether earlier studies on blackwater rivers overlooked smaller invertebrates and habitats such as snags, or whether there are other chemical factors (such as the secondary compounds described by Janzen) in the tropical blackwaters causing low production is not known.

We have only taken a partial view of invertebrate production in the Satilla River by considering sand, mud, and snag habitats. Other sites of production were not sampled, the most obvious being the swamp. The river is subject to extremely variable discharge, and when the river flows out into the swamps, a characteristic community develops in the temporary benthic habitat (Holder et al. 1970). How this compares with our other habitats is not known at this time. Presumably, the swamp is an important foraging area for fishes during high-water periods, as well as an important spawning area for several species.

While our snag estimates of production are based upon direct measurements and we have emphasized its importance to the river, there exists corroborating evidence suggesting that we may even be underestimating the importance of snags. First, the fact that snags are so rapidly colonized at high densities when water levels rise rapidly at any time of the year strongly supports our assumptions of rapid turnover. Second, we have estimated extremely high $P/\bar{B}$ ratios for chironomids based largely on the literature, and these organisms have a much greater influence on the overall $P/\bar{B}$ ratios of sand and mud benthos than snag fauna. If the chironomid $P/\bar{B}$ ratios prove to be too high, the snags may assume a relative importance more in line

TABLE 20. Relative numbers, standing stock biomass, and production of invertebrate functional feeding groups for a stretch of river. Values were calculated from the percentages of functional groups per habitat (Table 19), adjusting for relative habitat production statistics per stretch of river (Table 17), and summing for all habitats.

Functional group	Upper site			Lower site		
	Numbers	Biomass	Production	Numbers	Biomass	Production
	Percentages across all habitats					
Filtering collectors	3.7	35.4	11.5	5.0	46.3	11.8
Gathering collectors	92.7	31.7	71.8	89.6	33.1	70.4
Predators	3.6	32.8	16.6	5.3	20.7	17.7

with the biomass estimates for a stretch of river (Table 17). Third, drift analyses show that as much as 80% of the numbers and biomasses of drifting animals are from the snag habitat (Hunter 1980). While we interpret this as an indication that snag animals drift more than those from the other habitats, it may also indicate that we have underestimated the importance of snags from the production analyses. Finally, several major fish species obtain the overwhelming number of their prey from the snag habitat (Henry 1979).

Our production analyses from two widely separated sites on the Satilla River are consistent in documenting the importance of the snag habitat as one of intense invertebrate production. Our values (on an effective habitat basis) agree well with the caddisfly production estimates by Cudney and Wallace (1980) on snags from the Coastal Plain portion of the Savannah River. However, we feel that the importance of snags is by no means limited to just blackwater rivers or even Coastal Plain rivers. We suspect that snags may be similarly important in any river lacking a solid, semipermanent rocky benthic habitat, and that investigators should pay particular attention to them in future studies.

Production of functional feeding groups

In an attempt to provide a unifying theory of stream ecosystems, Vannote et al. (1980) have developed the "river continuum concept," which relates changes in various ecosystem properties to the continuum of drainage basin influences from headwaters to mouth. The concept predicts, among other things, that the relative dominance (as biomass) of the various invertebrate functional feeding groups will change from shredders and collectors in headwaters (order 1–3), to grazers (scrapers) and collectors in medium-sized streams (4–6), to primarily collectors in large rivers (>6). The identification of stream order in Coastal Plain streams like the Satilla, where the poorly defined headwater channels originate primarily in swamps, may not be as meaningful as in other watersheds. Nevertheless, our upper site would be a 5th order stream and our lower site a 6th order stream. For comparison, the mean discharge at our lower site is comparable to the 7th order McKenzie River in Oregon (Naiman and Sedell 1980), but the McKenzie drains a watershed area of 1024 km^2 and the Satilla drains an area of 7300 km^2.

In order to compare our analyses with that predicted by the continuum concept, we have approximated relative numbers, biomass and production of invertebrate functional feeding groups for a stretch of river (Table 20). This was done by combining information on the proportion of functional groups in each habitat (Table 19) with the relative habitat production statistics per stretch of river (Table 17). Unlike the continuum concept, in which grazers are of major importance in medium-sized streams, only collectors are found in the Satilla. The Satilla, with its unstable sandy bottom and greatly fluctuating discharge, does not appear to provide sufficient habitat for much primary production (i.e., periphyton). The resulting community primarily consists of filtering and gathering collectors. The use of numbers, biomass, and production obviously provides very different results when considering the importance of functional groups across all habitats (Table 20). The numerical analysis indicates that gathering collectors (mostly from the sandy habitat) are of overriding importance, whereas the biomass analysis indicates filtering collectors are of somewhat greater importance than gathering collectors. The distribution of production among functional groups clearly indicates that the importance of gathering collectors is underestimated by the biomass analysis and overestimated by the numerical analysis. While this comparison may provide encouragement to those who might use relative numbers as an approximation of relative production, such an assumption could be dangerous if small animals are not sampled efficiently (see below).

In view of the predominance of collectors in the Satilla River, it is tempting to suggest that the Satilla more closely resembles a high-order stream based upon the continuum concept, except that at least the snag inhabitants (i.e., net-spinning caddisflies, black flies, etc.) were obviously not the lentic-like collectors envisioned for high-order streams according to the continuum concept (Cummins 1979, Vannote et al. 1980). Based upon this initial analysis, we predict that the continuum for low-gradient rivers found in the southeastern Coastal Plain will deviate considerably from the continuum concept suggested by Vannote et al (1980). Unlike the streams described by Vannote et al., streams like the Satilla meander within a broad swampy floodplain for most of their length. We doubt that autochthonous primary production is ever of much significance. Although we have not yet studied lower order streams of the Satilla, we suspect that allochthonous materials are of overriding importance as a food source along the entire continuum, and that the limitations imposed by an unstable benthic habitat (sand) and availability of snags determine the composition of the invertebrate community.

Although there were some differences in relative abundance of species between the two study sites, our final comparison shows that the distribution of production among functional feeding groups is almost identical (Table 20). At least in terms of invertebrate functional feeding groups, there was no obvious shift along a 160 km stretch of river continuum in which the size of the drainage basin more than doubled.

While we have continually emphasized the importance of habitat-specific sampling and taxon-specific production analysis, there is one other methodological aspect worth emphasizing as we discuss functional groups. It is the aspect of sorting. Investigators tend to use a rather wide range of sieve sizes in sorting freshwater invertebrates, and sieve size can make a large difference in the outcome of functional group analysis. Consider that much of our production, no matter which habitat, was attributed to very small organisms with fast turnover rates. If a sieve opening as large as that used in many water quality studies (0.6 mm) were used to separate invertebrates, we would have overlooked the contribution (numbers, biomass, and production) of virtually the entire sand community, and a major portion of the mud and snag communities. Clearly these small animals should not be overlooked if one wants an accurate assessment of their contribution to relative numbers or production. On the other hand, even if these small animals are adequately sampled and sorted, their relative importance may be underestimated if biomass is the criterion for functional group analysis (see Table 19).

We feel that assessing absolute or relative production of invertebrates within specific habitats is the most meaningful way to analyze functional feeding groups in natural ecosystems. This does not mean that numerical and biomass analysis are not useful for certain purposes, and in some cases they might be preferable, since they require considerably less sampling effort and no life history information. For example, Hawkins and Sedell (1981) have shown dramatic longitudinal shifts in relative numbers of functional feeding groups that closely fit predictions of the River Continuum model. However, production, more than numbers or biomass, is the most direct reflection of utilization of organic resources by the invertebrate community.

While functional group analysis suggests the means of food acquisition, it is only an indirect reflection of the type and source of food actually utilized by invertebrates at a given time and place. Clearly, knowledge of the distribution of invertebrate production among functional groups and habitats provides a significant degree of insight into stream function, but detailed analysis of food consumption by the invertebrates is necessary before the type and source of food actually supporting the production can be determined. Since the snag community primarily consists of filter-feeders, it would appear that the food source for these animals is sestonic, but the composition and source of the seston can only be guessed at this time. The sandy benthic habitat covers a large area, and because of the rapid turnover of its small inhabitants, it seems of considerable importance to the over-all organic energy budget of the river. Yet the types and source of food for animals in this habitat is a major unanswered question. The ultimate energy source for all consumers appears to be allochthonous organic matter from the broad river swamps, but this has not been demonstrated. If the availability of food types and its utilization by invertebrates is assessed in the various habitats, it should be possible to determine the biological basis of invertebrate production, as well as determine the total amount consumed per unit time (Benke and Wallace 1980). When this can be achieved, a more accurate evaluation of the role of invertebrates in organic energy budgets of lotic systems is possible.

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LITERATURE CITED

Allen, K. R. 1951. The Horokiwi Stream. Fisheries Bulletin Number 10, New Zealand Marine Department, Wellington, New Zealand.

Anderson, N. H., and K. W. Cummins. 1979. Influences of diet on the life histories of aquatic insects. Journal of the Fisheries Research Board of Canada **36**:335–342.

Anderson, N. H., J. R. Sedell, L. M. Roberts, and F. J. Triska. 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. American Midland Naturalist **100**:64–82.

Anderson, R. O. 1959. A modified flotation technique for sorting bottom fauna samples. Limnology and Oceanography **4**:223–225.

Aston, R. J. 1973. Field and experimental studies on the effects of a power station effluent on Tubificidae (Oligochaeta, Annelida). Hydrobiologia **42**:225–242.

Banse, K., and S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. Ecological Monographs **50**:355–379.

Beck, K. C., J. H. Reuter, and E. M. Perdue. 1974. Organic and inorganic geochemistry of some coastal plain rivers of the southeastern United States. Geochimica et Cosmochimica Acta **38**:341–364.

Beck, W. M., Jr. 1967. Comparative limnology of the streams of Florida and the upper Amazon Basin. Atas do simpasio sobre a Biota Amazonica. Limnologia **3**:51–62.

Becker, C. D. 1973. Development of *Simulium (Psilozia) vittatum* Zett. (Diptera: Simuliidae) from larvae to adults at thermal increments from 17.0° to 27.0° C. American Midland Naturalist **89**:246–251.

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. Limnology and Oceanography **24**:168–171.

———. *In press.* Secondary production of aquatic insects. *In* V. H. Resh and D. M. Rosenberg, editors. Ecology of aquatic insects: a life history and habitat approach. Praeger, New York, New York, USA.

Benke, A. C., D. M. Gillespie, F. K. Parrish, T. C. Van Arsdall, Jr., R. J. Hunter, and R. L. Henry, III. 1979. Biological basis for assessing impacts of channel modifications: invertebrate production, drift, and fish feeding in a southeastern blackwater river. Environmental Resources Center Publication Number ERC 06-79, Georgia Institute of Technology, Atlanta, Georgia, USA.

Benke, A. C., and J. B. Waide. 1977. In defence of average cohorts. Freshwater Biology **7**:61–63.

Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Ecology **61**:108–118.

Berner, L. M. 1951. Limnology of the lower Missouri River. Ecology **32**:1–12.

Bishop, J. E. 1973. Limnology of a small Malayan River, Sungai Gombak. W. Junk, The Hague, The Netherlands.

Boling, R. H., Jr., E. D. Goodman, J. A. Van Sickle, J. O. Zimmer, K. W. Cummins, R. C. Peterson, and S. R. Reice. 1975. Toward a model of detritus processing in a woodland stream. Ecology **56**:141–151.

Brenner, R. J., E. W. Cupp, and M. J. Bernardo. 1981. Growth and development of geographic and crossbred strains of colonized *Simulium decorum* (Diptera: Simuliidae). Canadian Journal of Zoology **59**:2072–2079.

Brittain, J. E. 1982. Biology of mayflies. Annual Review of Entomology **27**:119–147.

Brown, A. V., and L. C. Fitzpatrick. 1978. Life history and population energetics of the dobson fly, *Corydalus cornutus*. Ecology **59**:1091–1108.

Brown, H. P. 1972. Aquatic dryopoid beetles (Coleoptera) of the United States. Biota of Freshwater Ecosystems, Identification Manual Number 6, Environmental Protection Agency, Washington, D.C., USA.

Butler, M. G. 1982. Production dynamics of some arctic *Chironomus* larvae. Limnology and Oceanography **27**:728–736.

Carlsson, M., L. M. Nilsson, Bj. Svensson, S. Ulfstrand, and R. S. Wotton. 1977. Lacustrine seston and other factors influencing the blackflies (Diptera: Simuliidae) inhabiting lake outlets in Swedish Lapland. Oikos **29**:229–238.

Chutter, F. M. 1968. On the ecology of the fauna of stones in the current in a south African River supporting a very large *Simulium* (Diptera) population. Journal of Applied Ecology **5**:531–561.

Clifford, H. F. 1978. Descriptive phenology and seasonality of a Canadian brownwater stream. Hydrobiologia **58**:213–231.

———. 1982. Life cycles of mayflies (Ephemeroptera) with special reference to voltinism. Quaestiones Entomologicae **18**:15–90.

Coffman, W. P. 1978. Chironomidae. Pages 345–376 *in* R. W. Merritt and K. W. Cummins, editors. An introduction to the aquatic insects. Kendall/Hunt, Dubuque, Iowa, USA.

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. Archiv für Hydrobiologie **68**:232–276.

Colbo, M. H., and B. H. Thompson. 1978. An efficient technique for laboratory rearing of *Simulium verecundum* S. & J. (Diptera: Simuliidae). Canadian Journal of Zoology **56**:507–510.

Coleman, M. J., and H. B. N. Hynes. 1970. The vertical distribution of the invertebrate fauna in the bed of a stream. Limnology and Oceanography **15**:31–40.

Cudney, M. D., and J. B. Wallace. 1980. Life cycles, microdistribution and production dynamics of six species of net-spinning caddisflies in a large southeastern (U.S.A.) river. Holarctic Ecology **3**:169–182.

Cummins, K. W. 1973. Trophic relations of aquatic insects. Annual Review of Entomology **18**:183–206.

———. 1979. The natural stream ecosystem. Pages 7–24 *in* J. V. Ward and J. A. Stanford, editors. The ecology of regulated streams. Plenum, New York, New York, USA.

Cummins, K. W., and M. J. Klug. 1979. Feeding ecology of stream invertebrates. Annual Review of Ecology and Systematics **10**:147–172.

Cushing, C. E. 1963. Filter-feeding insect distribution and planktonic food in the Montreal River. Transactions of the American Fisheries Society **92**:216–219.

Cushman, R. M., J. W. Elwood, and S. G. Hildebrand. 1977. Life history and production dynamics of *Alloperla mediana* and *Diplectrona modesta* in Walker Branch, Tennessee. American Midland Naturalist **98**:354–364.

Dahlberg, M. D., and D. C. Scott. 1971. The freshwater fishes of Georgia. Bulletin of the Georgia Academy of Science **29**:1–64.

Driver, E. A. 1981. Calorific values of pond invertebrates eaten by ducks. Freshwater Biology **11**:579–581.

Edmunds, G. F., Jr. 1978. Ephemeroptera. Pages 57–80 *in* R. W. Merritt and K. W. Cummins, editors. An introduction to the aquatic insects. Kendall/Hunt, Dubuque, Iowa, USA.

Egglishaw, H. J. 1968. The quantitative relationship between bottom fauna and plant detritus in streams of different calcium concentrations. Journal of Applied Ecology **5**:731–740.

Erman, D. C., and N. A. Erman. 1975. Macroinvertebrate composition and production in some Sierra Nevada minerotrophic peatlands. Ecology **56**:591–603.

Fisher, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. Internationale Revue der gesamten Hydrobiologie und Hydrographie **62**:701–727.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs **43**:421–439.

Fittkau, E. J., U. Irmler, W. J. Junk, F. Reiss, and G. W. Schmidt. 1975. Productivity, biomass, and population dynamics in Amazonian water bodies. Pages 289–311 *in* F. B. Golley, editor. Ecological studies II. Tropical ecological systems. Springer-Verlag, New York, New York, USA.

Flint, O. S., J. R. Voshell, and C. R. Parker. 1979. The *Hydropsyche scalaris* group in Virginia, with description of two new species (Trichoptera: Hydropsychidae). Proceedings of the Biological Society of Washington **92**:837–862.

Flössner, D. 1976. Biomasse und Produktion des Makrobenthos der mittleren Saale. Limnologica (Berlin) **10**:123–153.

Flowers, R. W., and W. L. Hilsenhoff. 1978. Life cycles and habitats of Wisconsin Heptageniidae (Ephemeroptera). Hydrobiologia **60**:159–171.

Fredeen, F. J. H. 1959. Rearing blackflies in the laboratory (Diptera: Simuliidae). Canadian Entomologist **41**:78–83.

———. 1964. Bacteria as food for blackfly larvae (Diptera: Simuliidae) in laboratory cultures and in natural streams. Canadian Journal of Zoology **42**:527–548.

Fremling, C. R. 1960. Biology and possible control of nuisance caddisflies of the upper Mississippi River. Research Bulletin 483, Iowa Agricultural Experiment Station, Ames, Iowa, USA.

Georgia Department of Natural Resources, Environmental Protection Division. 1975. Water quality monitoring data for Georgia streams 1974. Atlanta, Georgia, USA.

Georgia Department of Natural Resources, Environmental Protection Division. 1977. Water quality monitoring data for Georgia streams 1976. Atlanta, Georgia, USA.

Georgian, T. J., and J. B. Wallace. 1981. A model of seston capture by net-spinning caddisflies. Oikos **36**:147–157.

Giani, N., and H. Laville. 1973. Cycle biologique et production de *Sialis lutaria* L. (Megaloptera) dans le Lac de Port-Bielh (Pyrenees Centrales). Annales de Limnologie **9**: 45–61.

Gillespie, D. M., and A. C. Benke. 1979. Methods of calculating cohort production from field data—some relationships. Limnology and Oceanography **24**:171–176.

Gordon, A. E., and J. B. Wallace. 1975. Distribution of the family Hydropsychidae (Trichoptera) in the Savannah River Basin of North Carolina, South Carolina and Georgia, U.S.A. Hydrobiologia **46**:405–424.

Gray, L. J. 1981. Species composition and life histories of aquatic insects in a lowland Sonoran desert stream. American Midland Naturalist **106**:229–242.

Haefner, J. D., and J. B. Wallace. 1981. Production and potential seston utilization by *Parapsyche cardis* and *Diplectrona modesta* (Trichoptera: Hydropsychidae) in two streams draining contrasting southern Appalachian watersheds. Environmental Entomology **10**:433–441.

Hall, R. J., T. F. Waters, and E. F. Cook. 1980. The role of drift dispersal in production ecology of a stream mayfly. Ecology **61**:37–43.

Hamilton, A. L. 1969. On estimating annual production. Limnology and Oceanography **14**:771–782.

Hawkins, C. P., and J. R. Sedell. 1981. Longitudinal and seasonal changes in functional organization of macroinvertebrate communities in four Oregon streams. Ecology **62**:387–397.

Henry, R. L., III. 1979. Food habits and feeding relationships of Satilla River fishes. Thesis. Georgia Institute of Technology, Atlanta, Georgia, USA.

Holder, D. R., W. D. Hill, Jr., W. King, and C. Sweat. 1970. Invertebrate studies in warmwater streams: survey and inventory. Annual Progress Report, Statewide Fisheries Investigation, State Game and Fish Commission, Atlanta, Georgia, USA.

Hopkins, C. L. 1976. Estimate of biological production in some stream invertebrates. New Zealand Journal of Marine and Freshwater Research **10**:629–640.

Hunter, R. J. 1980. Drift dynamics of a southeastern blackwater river. Thesis. Georgia Institute of Technology, Atlanta, Georgia, USA.

Hynes, H. B. N. 1961. The invertebrate fauna of a Welsh mountain stream. Archiv für Hydrobiologie **57**:344–388.

———. 1970. The ecology of running waters. University of Toronto Press, Toronto, Ontario, Canada.

———. 1976. The biology of Plecoptera. Annual Review of Entomology **21**:135–153.

———. 1980. A name change in the secondary production business. Limnology and Oceanography **25**:778.

Hynes, H. B. N., and M. J. Coleman. 1968. A simple method of assessing the annual production of stream benthos. Limnology and Oceanography **13**:569–573.

Iverson, T. M. 1980. Densities and energetics of two stream-living larval populations of *Sericostoma personatum* (Trichoptera). Holarctic Ecology **3**:65–73.

Janzen, D. H. 1974. Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. Biotropica **6**: 69–103.

Johnson, M. G., and R. O. Brinkhurst. 1971. Production of benthic macroinvertebrates of Bay of Quinte and Lake Ontario. Journal of the Fisheries Research Board of Canada **28**:1699–1714.

Jonasson, P. M. 1972. Ecology and production of the profundal benthos in relation to phytoplankton in Lake Esrom. Oikos (Supplement) **14**:1–148.

———. 1975. Population ecology and production of benthic detritivores. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen **19**:1066–1072.

Kajak, Z., and J. I. Rybak. 1966. Production and some trophic dependencies in benthos against primary production and zooplankton production of several Masurian lakes. Internationale Vereinigung für theoretische und angewandte Limnologie, Verhandlungen **16**:441–451.

Kamlyuk, L. V. 1973. Energy balance of the larval association in the Naroch Lake littoral. Trudy Belorusskogo Nauchno-Issledovatel 'skogo Instituta Rhybnogo Khozyaistva 135 (in Russian). English summary in Odonatologica **4**(1975):194.

Kennedy, C. R. 1966. The life history of *Limnodrilus hoffmeisteri* Clap. (Oligochaeta: Tubificidae) and its adaptive significance. Oikos **17**:158–168.

Kimerle, R. A., and N. H. Anderson. 1971. Production and bioenergetic role of the midge *Glyptotendipes barbipes* (Staeger) in a waste stabilization lagoon. Limnology and Oceanography **16**:646–659.

Kondratieff, B. C., and J. R. Voshell, Jr. 1980. Life history and ecology of *Stenonema modestum* (Banks) (Ephemeroptera: Heptageniidae) in Virginia, USA. Aquatic Insects **2**:177–189.

Konstantinov, A. S. 1958. The influence of temperature on rate of growth and development of chironomid larvae. Doklady Akademii Nauk S.S.S.R. **120**:1362–1365.

Kovalak, W. P. 1978. Effects of a pool on stream invertebrate drift. American Midland Naturalist **99**:119–127.

Krueger, C. C., and F. B. Martin. 1980. Computation of confidence intervals for the size-frequency (Hynes) method of estimating secondary production. Limnology and Oceanography **25**:773–777.

Ladle, M. 1971. The biology of Oligochaeta from Dorset chalk streams. Freshwater Biology **1**:83–97.

LaForge, L., W. Cooke, A. Keith, and M. R. Campbell. 1925. Physical geography of Georgia. Bulletin Number 42, Geological Survey of Georgia, Atlanta, Georgia, USA.

Lapchin, L., and A. Neveu. 1979. Ecology of the principal filter-feeding invertebrates from the lower Nivelle (Atlantic Pyrenees). II. Hydropsychidae (Trichoptera). Annales de Limnologie **15**:139–153.

Lawton, J. H. 1971. Ecological energetics studies on larvae of the damselfly *Pyrrhosoma nymphula* (Sulzer) (Odonata: Zygoptera). Journal of Animal Ecology **40**:385–423.

Learner, M. A., G. Lochhead, and B. D. Hughes. 1978. A review of the biology of British Naididae (Oligochaeta) with emphasis on the lotic environment. Freshwater Biology **8**: 357–375.

Liaw, W. K., and H. R. MacCrimmon. 1977. Assessment of particulate organic matter in river water. Internationale Revue der gesamten Hydrobiologie und Hydrographie **62**: 445–463.

Loden, M. S. 1974. Predation by chironomid (Diptera) larvae on oligochaetes. Limnology and Oceanography **19**:156–159.

Mackay, R. J. 1979. Life history patterns of some species of *Hydropsyche* (Trichoptera: Hydropsychidae) in southern Ontario. Canadian Journal of Zoology **57**:963–975.

Mackey, A. P. 1976*a*. Quantitative studies on the Chironomidae (Diptera) of the Rivers Thames and Kennet. I. The Acorus zone. Archiv für Hydrobiologie **78**:240–267.

———. 1976*b*. Quantitative studies of the Chironomidae (Diptera) of the Rivers Thames and Kennet. II. The flint zone. Archiv für Hydrobiologie **78**:310–318.

———. 1977*a*. Quantitative studies on the Chironomidae (Diptera) of the Rivers Thames and Kennet. III. The Nuphar zone. Archiv für Hydrobiologie **79**:62–102.

———. 1977*b*. Quantitative studies on the Chironomidae (Diptera) of the Rivers Thames and Kennet. IV. Production. Archiv für Hydrobiologie **80**:327–348.

———. 1977*c*. The growth and development of larval Chironomidae (Diptera). Oikos **28**:270–275.

Mann, K. H. 1975. Patterns of energy flow. Pages 248–263 *in* B. A. Whitton, editor. River ecology. University of California Press, Berkeley, California, USA.

Mann, K. H., R. H. Britton, A. Kowalczewski, T. J. Lack, C. P. Mathews, and I. McDonald. 1972. Productivity and energy flow at all trophic levels in the River Thames, England. Pages 579–596 *in* Z. Kajak and A. Hillbricht-Ilkowska, editors. Productivity problems of freshwaters. International Biological Program, UNESCO, Polish Scientific Publishers, Warsaw, Poland.

Marzolf, G. R. 1978. The potential effects of clearing and snagging on stream ecosystems. Fish and Wildlife Service, United States Department of the Interior, Washington, D.C., USA.

McElhone, M. J. 1978. A population study of littoral dwelling Naididae (Oligochaeta) in a shallow mesotrophic lake in North Wales. Journal of Animal Ecology **47**:615–626.

Menzie, C. A. 1981. Production ecology of *Cricotopus sylvestris* (Fabricius) (Diptera: Chironomidae) in a shallow estuarine cove. Limnology and Oceanography **26**:467–481.

Merritt, R. W., and K. W. Cummins. 1978. An introduction to the aquatic insects of North America. Kendall/Hunt, Dubuque, Iowa, USA.

Modde, T. C., and J. C. Schmulbach. 1973. Seasonal changes in the drift and benthic macroinvertebrates in the unchannelized Missouri River in South Dakota. Proceedings of the South Dakota Academy of Science **52**:118–126.

Morgan, N. C., T. Backiel, G. Bretschko, A. Duncan, A. Hillbricht-Ilkowska, Z. Kajak, J. F. Kitchell, P. Larsson, C. Leveque, A. Nauwerck, F. Schiemer, and J. E. Thorpe. 1980. Secondary production. Pages 247–340 *in* E. D. Le Cren and R. H. Lowe-McConnell, editors. The functioning of freshwater ecosystems. Cambridge University Press, Cambridge, England.

Morris, L. A., R. N. Langemeier, T. R. Russell, and A. Witt, Jr. 1968. Effects of main stem impoundments and channelization upon the limnology of the Missouri River, Nebraska. Transactions of the American Fisheries Society **97**: 380–388.

Naiman, R. J., and J. R. Sedell. 1980. Relationships between metabolic parameters and stream order in Oregon. Canadian Journal of Fisheries and Aquatic Sciences **37**:834–847.

Nelson, D. J., and D. C. Scott. 1962. Role of detritus in the productivity of a rock-outcrop community in a Piedmont stream. Limnology and Oceanography **7**:396–413.

Neves, R. J. 1979. Secondary production of epilithic fauna in a woodland stream. American Midland Naturalist **102**: 209–224.

Nilson, H. C., and R. W. Larimore. 1973. Establishment of invertebrate communities on log substrates in the Kaskaskia River, Illinois. Ecology **54**:366–374.

Nord, A. E., and J. C. Schmulbach. 1973. A comparison of the macroinvertebrate aufwuchs in the unstabilized and stabilized Missouri River. Proceedings of the South Dakota Academy of Science **52**:127–139.

Odum, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs **27**:55–112.

Oswood, M. W. 1976. Comparative life histories of the Hydropsychidae (Trichoptera) in a Montana lake outlet. American Midland Naturalist **96**:493–497.

Otto, C. 1975. Energetic relationships of the larval population of *Potamophylax cingulatus* (Trichoptera) in a south Swedish stream. Oikos **26**:159–169.

Patrick, R. 1975. Structure of stream communities. Pages 445–459 *in* M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.

Pearson, W. D., and D. R. Franklin. 1968. Some factors affecting drift rates of *Baetis* and Simuliidae in a large river. Ecology **49**:75–81.

Peters, W. L., and J. Jones. 1973. Historical and biological aspects of the Blackwater River in northwestern Florida. Pages 242–253 *in* W. L. Peters and J. C. Peters, editors. Proceedings of the First International Conference on Ephemeroptera. E. J. Brill, Leiden, The Netherlands.

Peters, W. L., and J. G. Peters. 1977. Adult life and emergence of *Dolania americana* in northwestern Florida (Ephemeroptera: Behningiidae). Internationale Revue der gesamten Hydrobiologie und Hydrographie **62**:409–438.

Potter, D. W. B., and M. A. Learner. 1974. A study of the benthic macroinvertebrates of a shallow eutrophic reservoir in South Wales with emphasis on the Chironomidae (Diptera); their life histories and production. Archiv für Hydrobiologie **74**:186–226.

Pritchard, G. 1964. The prey of dragonfly larvae (Odonata: Anisoptera) in ponds in Northern Alberta. Canadian Journal of Zoology **42**:785–800.

Reisen, W. K. 1975. Quanitative aspects of *Simulium virgatum* Coq. and *S.* species life history in a southern Oklahoma stream. Annals of the Entomological Society of America **68**:949–954.

———. 1977. The ecology of Honey Creek, Oklahoma: the downstream drift of three species of aquatic dryopoid beetles (Coleoptera: Dryopoidea). Entomological News **88**:185–191.

Resh, V. H. 1977. Habitat and substrate influences on population and production dynamics of a stream caddisfly, *Ceraclea ancylus* (Leptoceridae). Freshwater Biology **7**:261–277.

———. 1979. Sampling variability and life history features: basic considerations in the design of aquatic insect studies. Journal of the Fisheries Research Board of Canada **36**:290–311.

Rhame, R. E., and K. W. Stewart. 1976. Life cycles and food habits of three Hydropsychidae (Trichoptera) species in the Brazos River, Texas. Transactions of the American Entomological Society **102**:65–99.

Richardson, M. Y., and D. C. Tarter. 1976. Life histories of *Stenonema vicarium* (Walker) and *S. tripunctatum* (Banks) in a West Virginia stream (Ephemeroptera: Heptageniidae). American Midland Naturalist **95**:1–9.

Rosenberg, D. M., A. P. Wiens and O. A. Saether. 1977. Life histories of *Cricotopus (Cricotopus) bicinctus* and *C. (C.) mackenziensis* (Diptera: Chironomidae) in the Fort Simpson area, Northwest Territories. Journal of the Fisheries Research Board of Canada **34**:247–253.

Ross, D. H., and D. A. Craig. 1980. Mechanisms of fine particle capture by larval black flies (Diptera: Simuliidae). Canadian Journal of Zoology **58**:1186–1192.

Ross, D. H., and R. W. Merritt. 1978. The larval instars and population dynamics of five species of black flies (Diptera: Simuliidae) and their responses to selected environmental factors. Canadian Journal of Zoology **56**:1633–1642.

Ross, D. H., and J. B. Wallace. 1981. Production of *Brachycentrus spinae* Ross (Trichoptera: Brachycentridae) and its role in seston dynamics of a southern Appalachian stream (USA). Environmental Entomology **10**:240–246.

Schalles, J. F. 1979. Comparative limnology and ecosystem analysis of Carolina Bay ponds on the upper Coastal Plain of South Carolina. Dissertation. Emory University, Atlanta, Georgia, USA.

Sepkoski, J. J., and M. A. Rex. 1974. Distribution of freshwater mussels; coastal rivers as biogeographic islands. Systematic Zoology **23**:165–188.

Shapas, T. J., and W. L. Hilsenhoff. 1976. Feeding habits of Wisconsin's predominant lotic Plecoptera, Ephemeroptera, and Trichoptera. Great Lakes Entomologist **9**:175–188.

Sheldon, A. L. 1969. Size relationships of *Acroneuria californica* (Perlidae, Plecoptera) and its prey. Hydrobiologia **34**:85–94.

Sheldon, A. L., and M. W. Oswood. 1977. Blackfly (Diptera: Simuliidae) abundance in a lake outlet: test of a predictive model. Hydrobiologia **56**:113–120.

Siegfried, C. A., and A. W. Knight. 1976. Trophic relations of *Acroneuria (Calineuria) californica* (Plecoptera: Perlidae) in a Sierra foothill stream. Environmental Entomology **5**: 575–581.

Siegfried, C. A., and A. W. Knight. 1978. Aspects of the life history and growth of *Acroneuria (Calineuria) californica* in a Sierra foothill stream. Annals of the Entomological Society of America **71**:149–154.

Snellen, R. K., and K. W. Stewart. 1979. The life cycle of *Perlesta placida* (Plecoptera: Perlidae) in an intermittent stream in northern Texas. Annals of the Entomological Society of America **72**:659–666.

Stewart, K. W., G. P. Friday, and R. E. Rhame. 1973. Food habits of hellgrammite larvae, *Corydalus cornutus* (Megaloptera: Corydalidae), in the Brazos River, Texas. Annals of the Entomological Society of America **66**:959–963.

Stone, A. S., and E. L. Snoddy. 1969. The blackflies of Alabama (Diptera: Simuliidae). Auburn University Experiment Station Bulletin 390, Auburn, Alabama, USA.

Tarshis, I. B. 1968. Collecting and rearing blackflies. Annals of the Entomological Society of America **61**:1072–1083.

Teal, J. M. 1957. Community metabolism in a temperate cold spring. Ecological Monographs **27**:283–302.

Tilly, L. J. 1968. The structure and dynamics of Cone Spring. Ecological Monographs **38**:169–197.

Ulfstrand, S. 1968. Benthic animal communities in Lapland streams. Oikos Supplement **10**:1–20.

United States Geological Survey. 1976. Water Resources Data for Georgia—Water Year 1975, Doraville, Georgia, USA.

———. 1977. Water Resources Data for Georgia—Water Year 1976, Doraville, Georgia, USA.

United States Study Commission on the Savannah, Altamaha, Saint Marys, Appalachicola-Chattahoochee, and Perdido-Escambia River Basins and Intervening Areas. 1963. Plan for development of the land and water resources of the Southeast river basins; report of the U.S. Study Commission, Southeast River Basins. Appendix 4, Satilla-St. Marys Basins. Atlanta, Georgia, USA.

Van Arsdall, T. C., Jr. 1977. Production and colonization of the snag habitat in a southeastern blackwater river. Thesis. Georgia Institute of Technology, Atlanta, Georgia, USA.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**: 130–137.

Wallace, J. B. 1975. The larval retreat and food of *Arctopsyche*; with phylogenetic notes on feeding adaptations in Hydropsychidae larvae (Trichoptera). Annals of the Entomological Society of America **68**:167–173.

Wallace, J. B., and D. M. Malas. 1976. The fine structure of capture nets of larval Philopotamidae, with special emphasis on *Dolophilodes distinctus*. Canadian Journal of Zoology **54**:1788–1802.

Wallace, J. B., and R. W. Merritt. 1980. Filter-feeding ecology of aquatic insects. Annual Review of Entomology **25**: 103–132.

Wallace, J. B., D. H. Ross, and J. L. Meyer. 1982. Seston and dissolved organic carbon dynamics in a southern Appalachian stream. Ecology **63**:824–838.

Wallace, J. B., and F. F. Sherberger. 1974. The larval retreat and feeding net of *Macronema carolina* Banks (Trichoptera: Hydropsychidae). Hydrobiologia **45**:177–184.

Wallace, J. B., J. R. Webster, and W. R. Woodall. 1977. The role of filter-feeders in flowing waters. Archiv für Hydrobiologie **79**:506–532.

Wallace, J. B., W. R. Woodall, and A. A. Staats. 1976. The larval dwelling-tube, capture net and food of *Phylocentropus placidus* (Trichoptera: Polycentropodidae). Annals of the Entolomological Society of America **69**:149–154.

Ward, G. M., and K. W. Cummins. 1979. Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). Ecology **60**: 57–64.

Waters, T. F. 1969. The turnover ratio in production ecology of freshwater invertebrates. American Naturalist **103**:173–185.

———. 1977*a*. Secondary production in inland waters. Advances in Ecological Research **10**:91–164.

———. 1977*b*. The streams and rivers of Minnesota. University of Minnesota Press, Minneapolis, Minnesota, USA.

———. 1979. Influence of benthos life history upon the estimation of secondary production. Journal of the Fisheries Research Board of Canada **36**:1425–1430.

Waters, T. F., and G. W. Crawford. 1973. Annual production of a stream mayfly population: a comparison of methods. Limnology and Oceanography **18**:286–296.

Waters, T. F., and J. C. Hokenstrom. 1980. Annual production and drift of the stream amphipod *Gammarus pseudolimnaeus* in Valley Creek, Minnesota. Limnology and Oceanography **25**:700–710.

Welton, J. S., M. Ladle, and J. A. B. Bass. 1982. Growth and production of five species of Ephemeroptera larvae from an experimental recirculating stream. Freshwater Biology **12**:103–122.

Wetzel, R. G. 1983. Limnology. Saunders, Philadelphia, Pennsylvania, USA.

White, D. S. 1978. Life cycle of the riffle beetle, *Stenelmis sexlineata* (Elmidae). Annals of the Entomological Society of America **71**:121–125.

Wiggins, G. B. 1977. Larvae of the North American caddisfly genera (Trichoptera). University of Toronto Press, Toronto, Ontario, Canada.

Winterbourn, M. J. 1974. The life histories, trophic relations and production of *Stenoperla prasina* (Plecoptera) and *Deleatidium* sp. (Ephemeroptera) in a New Zealand river. Freshwater Biology **4**:507–524.

Wotton, R. S. 1976. Evidence that blackfly larvae can feed on particles of colloidal size. Nature **261**:697.

———. 1977. The size of particles ingested by moorland stream blackfly larvae (Simuliidae). Oikos **29**:332–335.

———. 1978. Life histories and production of blackflies (Diptera: Simuliidae) in moorland streams in Upper Teesdale, Northern England. Archiv für Hydrobiologie **83**:232–250.

Wu, Y. F. 1930. A contribution to the biology of *Simulium* (Diptera). Papers of the Michigan Academy of Science, Arts and Letters **13**:543–599.

Yamamoto, G. 1972. Trophic structure in Lake Tatsu-Numa, an acidotrophic lake in Japan, with special reference to the importance of the terrestrial community. Pages 404–419 *in* Z. Kajak and A. Hillbricht-Ilkowska, editors. Productivity problems of freshwaters. International Biological Program, UNESCO, Polish Scientific Publishers, Warsaw, Poland.

Zelinka, M. 1977. The production of Ephemeroptera in running waters. Hydrobiologia **56**:121–125.

Zieba, J. 1971. Production of macrobenthos in fingerling ponds. Polski Archiwum Hydrobiologii **18**:235–246.

APPENDIX

Invertebrates found in the Satilla River and the habitats in which they are found (*** very common, ** frequent, * rare).

Higher taxa	Species	Snag	Sand	Mud
Insecta				
Diptera				
Chironomidae	Chironominae			
	Chironomini sp. A	**		*
	Chironomini sp. B		**	
	Cladotanytarsus		**	**
	Cryptochironomus		**	***
	Demicryptochironomus		**	*
	Dicrotendipes			*
	Harnischia complex	*	**	***
	Micropsectra	*		*
	Nilothauma	*		
	Paracladopelma			*
	Paralauterborniella		*	
	Paratendipes		*	
	Polypedilum spp.	***	**	**
	Rheotanytarsus	***	**	**
	Robackia claviger	*	***	
	Stempellina			*
	Stenochironomus	***		*
	Stictochironomus			*
	Tanytarsus	***	**	***
	Tribelos	**		*
	Xenochironomus	**		
	Orthocladiinae			
	Corynoneura	***	***	
	Cricotopus	***		
	Eukiefferiella		*	
	Parakiefferiella		***	
	Rheocricotopus	***		
	Thienemanniella	?	**	
	Tanypodinae			
	Ablabesmyia	***	*	**
	Coelotanypus			***
	Procladius			***
	Thienemannimyia group	***	*	*
Ceratopogonidae	*Atrichopogon*	**		
	Palpomyia group	**	***	***
Chaoboridae	*Chaoborus*			***
Empididae	*Hemerodromia*	***		
Athericidae	*Atherix lantha*	**		
Simuliidae	*Simulium* sp.	***	*	
	Simulium taxodium	***	*	
Tipulidae	*Hexatoma*		**	
	Ulomorpha		**	
Trichoptera				
Hydropsychidae	*Cheumatopsyche*	***		
	Hydropsyche elissoma	***		
	Hydropsyche incommoda	***		
	Macronema carolina	***		
Hydroptilidae		*		

APPENDIX

Continued.

Higher taxa	Species	Snag	Sand	Mud
Leptoceridae	*Ceraclea*	***		
	Nectopsyche	*		
	Oecetis	***		**
	Triaenodes	**		
	Mystacides	*		
Philopotamidae	*Chimarra*	***		
Phryganeidae				*
Polycentropodidae	*Cyrnellus fraternus*	***		
	Neureclipsis	***		
	Phylocentropus			***
	Polycentropus			**
Ephemeroptera				
Baetidae	*Baetis*	**		*
Baetiscidae	*Baetisca*	*	*	*
Behningiidae	*Dolania americana*		*	
Ephemerellidae	*Eurylophella*	**		
Ephemeridae	*Hexagenia*			*
Heptageniidae	*Stenonema integrum*	***		
	Stenonena exiguum	***		
	Stenonema spp.	***		
Leptophlebiidae	*Habrophlebiodes*	**		
Metretopodidae	*Siphloplecton*			
Caenidae	*Caenis*	**		
Polymitarcyidae	*Ephoron*			*
Coleoptera				
Curculionidae				
Dytiscidae	*Hydroporus*	*		*
Elmidae	*Ancyronyx variegatus*	**		
	Dubiraphia	*		*
	Stenelmis	***	**	**
Gyrinidae	*Dineutus*	**		
	Gyrinus			
Plecoptera				
Perlidae	*Perlinella*		*	
	Acroneuria mela	**		
	Perlesta placida	***		
Perlodidae	*Isoperla*	*		
Taeniopterygidae	*Taeniopteryx*	*		
Leuctridae	*Leuctra*			
Megaloptera				
Corydalidae	*Corydalus cornutus*	***		
Sialidae	*Sialis*			*
Odonata				
Calopterygidae	*Calopteryx(=Agrion) maculata*			
Coenagrionidae	*Argia*	**		
	Ischnura			
Aeshnidae	*Aeshna*			
	Boyeria vinosa	***		
Corduliidae	*Neurocordulia molesta*	***		
Gomphidae	*Dromogomphus*			*
	Gomphus			
	Hagenius			
	Progomphus obscurus		*	

APPENDIX
Continued.

Higher taxa	Species	Snag	Sand	Mud
Libellulidae				*
Macromiidae	*Didymops*	*		
	Macromia	*		
Crustacea				
Copepoda				**
Cladocera		*		*
Isopoda	*Asellus*			**
Amphipoda				
Ostracoda				***
Decapoda	*Procambarus*			
Oligochaeta	*Chaetogaster*	*	**	
	Pristina	**	***	**
	Limnodrilus	*	**	***
Bivalvia	*Elliptio crassidens*		*	