Production Dynamics and Resource Utilization of Snag-Dwelling Mayflies in a Blackwater River

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PRODUCTION DYNAMICS AND RESOURCE UTILIZATION OF SNAG-DWELLING MAYFLIES IN A BLACKWATER RIVER[1]

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Abstract. We quantified production dynamics, determined the trophic basis of production, and assessed the overlap in resource utilization within a diverse assemblage of mayfly larvae from the submerged woody (snag) habitat of a Coastal Plain blackwater river (Ogeechee River). Total annual production (as dry mass) was among the highest reported for mayflies, ranging from 20.8 to 42.2 g/m² of snag surface (7.4 to 12.3 g/m² of channel bottom) in two consecutive years. Relatively little change occurred between years for four out of six families. Biomass turnover rates (annual production/biomass) were generally high, ranging from 8 (single generation per year) to 96 (multiple generations per year) for individual taxa. Distinct types of temporal production patterns occurred: (1) concentration in winter (*Ephemerella argo, E. dorothea, Eurylophella* sp., and *Isonychia*), (2) concentration in summer (*Baetis ephippiatus, Tricorythodes* sp., *Caenis* spp.), or (3) spread throughout the year and peaking in summer (*Baetis intercalaris, Stenonema modestum, S. integrum, S. exiguum,* and *Hexagenia* sp.). Temporal overlap of production, using the proportional similarity index, was highest among closely related taxa (>0.60), with the least overlap (<0.15) among taxa in different families. Overlap based upon the amount that various food types contribute to production was high among all species, suggesting even less resource partitioning for food than for time. Of the annual food consumption (as dry mass) by mayflies per unit snag surface area (423 g·m⁻²·yr⁻¹), ≈87% consisted of amorphous detritus that is rapidly replenished on snags from floodplain-derived seston. This food source accounted for ≈70% of total mayfly production. We suggest that a fluctuating habitat (snags), a continuously replenished food supply, high biomass turnover, and high drift densities help perpetuate a persistent, resilient, and diverse mayfly assemblage with little resource partitioning.

Key words: energy flow; Ephemeroptera; mayflies; resource partitioning; secondary production; snag habitat; stream ecology; stream insects; trophic relations.

INTRODUCTION

Invertebrates are the major metazoans in most ecosystems, and this is readily apparent in communities of running waters (Hynes 1970, Ward 1992). Densities of lotic macroinvertebrates often exceed 10 000 individuals/m² (e.g., Benke et al. 1984, Corkum 1992) and richness is frequently well over 100 species (e.g., Smock and Gilinsky 1992, Zwick 1992). Such abundance and diversity of stream invertebrates has prompted numerous ecological questions and approaches, including: (1) comparisons of life history and population dynamics among closely related species, (2) community analysis according to functional feeding roles, (3) quantification of the flow of energy and matter within an ecosystem context, (4) assessment of vertical interactions with both food resources (e.g., algae) and natural enemies (e.g., predators), (5) assessment of horizontal interactions among potential competitors, and (6) analysis of biotic vs. abiotic controls of community struc-

ture. Most studies of stream invertebrates have dealt with no more than two of these approaches at a time, and as a consequence, our understanding of consumer dynamics in streams is often fragmentary. In this study, we simultaneously address most of these issues for the mayfly (Ephemeroptera) component of a riverine community using secondary production analyses as the common currency for integration and focusing on their utilization of resources.

The utilization distribution along a resource dimension commonly has been used to define a species niche and to measure the degree of resource partitioning among similar species (e.g., Schoener 1986, 1989). Habitat (or space), food type, and time have been widely considered to be the three primary resource dimensions (Pianka 1969, Schoener 1986, 1989). Although time has often been described as the least important dimension, an early analysis of the literature suggested that time was much more important for invertebrates than for vertebrates (Schoener 1974). Life history studies of aquatic insects in small streams have tended to support the importance of the time dimension, since temporal separation among closely related coexisting

species has been observed often. This separation appears to minimize the time when resources are used by similar species, and thus reduces the likelihood of competition (e.g., Hynes 1970, Vannote and Sweeney 1980, Hart 1983). Such observations have been incorporated into the River Continuum Concept (Vannote et al. 1980) in suggesting that species occupying the same functional feeding group (or guild, see Hawkins and MacMahon 1989), with high overlap along the food dimension, form a continuous sequence of species replacement that distributes the utilization of food resources over time. Quantification of the temporal distribution of resource utilization rarely has been attempted, but a few studies of stream insects have demonstrated that a logical means to do this is through time-specific secondary production measurements (Georgian and Wallace 1983, Rader and Ward 1987, 1989a).

Secondary production is the most comprehensive measure of success for a population because it is a composite of several other components of success: density, biomass, individual growth rate, reproduction, survivorship, and development time (Benke 1993). Also, since production is directly related to consumption, it represents a quantification of a population's resource utilization (food and space) in a given time interval. Thus, secondary production is a response variable that may prove appropriate for many ecological questions, including temporal partitioning of resources by coexisting species, consumption rates of food resources by primary consumers, and even quantification of predator–prey relationships (Benke 1993). Furthermore, time-specific, trophic-based production analysis of coexisting species, such as we describe here, provides a natural linkage between population and ecosystem-level understanding of macroconsumers. Unfortunately, secondary production is rarely used for addressing many ecological questions, as investigators often settle for what may be less meaningful but more easily obtained surrogates, density or biomass.

Over 2000 estimates of invertebrate production in streams have now been made, and >300 are on mayflies (Benke 1993). Most analyses include only a single annual estimate of production, but there are notable exceptions in which the production patterns or resource utilization have been determined over the course of a year (e.g., Elliott 1981, Georgian and Wallace 1983, Rader and Ward 1989a, Benke and Parsons 1990). While most approaches have considered no more than a few species at a time, several recent investigations have attempted to place population estimates within the context of production for a larger taxonomic or functional feeding group, or the entire macroinvertebrate community (Benke 1993). In one such study, we documented relatively high invertebrate production estimates and their distribution among functional groups on the snag habitat (submerged wood) in the Satilla River, a Georgia Coastal Plain river (Benke et

al. 1984). Snags are a specialized mesoscale habitat type of importance in many lotic ecosystems (e.g., Sedell and Froggatt 1984, O'Connor 1992), but they are especially characteristic of unaltered low-gradient rivers in the southeastern USA (e.g., Cudney and Wallace 1980, Benke et al. 1984, Smock et al. 1985).

Subsequent to our work on the Satilla River, we conducted extensive ecological studies on snag-dwelling invertebrates from the Ogeechee River, just two river basins to the north. In contrast to the Satilla, mayflies represented a diverse and abundant component of the snag community in the Ogeechee River and provided an opportunity to address various ecological questions, including assessment of feeding habits (Wallace et al. 1987), estimation of natural growth rates and the influence of temperature and food (Benke and Jacobi 1986, Benke et al. 1992), analysis of life histories and patterns of abundance (Jacobi and Benke 1991), and quantification of drift dynamics (Benke et al. 1991).

In the present paper, which incorporates much of this previous work, our primary objectives were to: (1) quantify the production dynamics of an assemblage of coexisting consumers using temperature-specific growth rates and a model of habitat availability, (2) determine the trophic basis of production for each taxon and the magnitude of food resources consumed, (3) assess the degree of temporal overlap in production patterns and resource utilization of taxa, and (4) attempt to explain the within- and between-year production dynamics of these consumers with regard to the emerging ecosystem properties of Coastal Plain rivers (Benke and Meyer 1988, Meyer 1990, 1992). Although our analyses address a single taxonomic group (the order Ephemeroptera), all but one of the genera belong to the functional feeding group described as gathering collectors (Merritt and Cummins 1984), a group to which the mayflies are one of the major contributors in the Ogeechee River. Furthermore, since this study addresses temporal patterns of production and quantification of resource utilization, it represents a significant increase in understanding beyond what was possible in the Satilla River study where only single annual estimates of production and turnover were presented (Benke et al. 1984).

STUDY SITE

The Ogeechee River is a sixth-order blackwater river in the Coastal Plain of Georgia, USA. As in other Coastal Plain rivers that have not received major anthropogenic disturbances, snags represent a major habitat type for aquatic invertebrates (Wallace and Benke 1984). True benthic habitats in the Ogeechee River are represented by a shifting sandy bottom in the main channel and organic sediments in backwater areas. This low-gradient river drains extensive floodplain swamps along most of its length.

Discharge typically fluctuates between 10 m³/s in the summer and several hundred m³/s in winter–spring

with a long-term mean of 66.8 m³/s (Benke and Parsons 1990). Mean discharge during our study years was 50.7 (1982) and 79.1 m³/s (1983). Temperatures usually fluctuate between 8° and 16°C in the winter and between 24° and 30° in the summer (Benke and Parsons 1990). Mean temperature was 19.5° in 1982 and 19.2° in 1983. An extensive summary of physical and chemical characteristics is in Meyer (1992).

In addition to the mayflies described in this paper, the snag community from the Ogeechee River also contains a diversity of other primary consumers, including midges (Chironomidae: Diptera), black flies (Simuliidae: Diptera), caddisflies (Trichoptera), stoneflies (Pteronarcyidae: Plecoptera), and beetles (Elmidae: Coleoptera). Invertebrate predators include stoneflies (Perlidae: Plecoptera), hellgrammites (Megaloptera), and dragonflies (Odonata).

METHODS

Snag samples were collected every 2 wk from April through September and monthly during colder months in 1982. Monthly samples were collected in 1983. Twenty samples were collected on each sampling date in 1982 and 10 samples in 1983. Our first year (1982) was defined from December 1981 to November 1982, and the second (1983) from December 1982 to November 1983. Details of the sampling and quantification procedure are described in Benke and Parsons (1990) and Jacobi and Benke (1991). All animals were identified, counted, and measured (head widths and body lengths) using an ocular micrometer in a dissecting microscope.

Length/mass regressions were usually determined at the generic level using fresh (nonpreserved) animals. Head width and body length were measured before animals were placed in a drying oven for 24 h at 60°C. Animals were weighed on a Mettler 5-place balance after spending ≈1 h in a desiccator. Using the length/mass regressions (Appendix), size-specific densities were converted to population biomass values (dry mass per unit area).

Production calculations were done in two ways, depending on life history type. For those species in which a cohort could be followed from field data (Ephemerellidae and *Isonychia* spp., Jacobi and Benke 1991), we used the increment–summation method in which production during a time interval is calculated as the increase in mean individual mass times the mean density (Benke 1984). For the remaining species, all of which had mixed size distributions throughout most dates (Jacobi and Benke 1991), we used the instantaneous growth method to calculate production between sampling periods.

Growth rates used with the instantaneous growth method were measured independently in growth chambers simulating natural conditions (Benke and Jacobi 1986, Benke et al. 1992). A single summer growth rate of 0.162/d was measured for *Tricorythodes* sp. (Benke

and Jacobi 1986), a species found only during warm months (Jacobi and Benke 1991). The same growth rate was assumed for *Caenis* spp., a less abundant taxon with very similar ecological and life history characteristics (Corkum 1989, Jacobi and Benke 1991). Growth rates for *Baetis* and Heptageniidae (*Stenonema*) were based on temperature-specific growth equations (Benke et al. 1992):

$$\log g = 0.0481T - 2.421 \text{ (}Stenonema\text{)}$$

$$g = 0.012T - 0.050 \text{ (}Baetis\text{)},$$

where g is the mean daily growth rate and T is mean daily temperature. Thus, mean daily production between two sampling dates for these taxa was estimated as:

$$P_d = gB,$$

where B is the mean biomass of the two sampling dates (Benke 1993). When using the temperature-specific equations, daily g was calculated first from daily temperature in order to estimate mean g for the interval. Thus, each of these procedures enabled us to determine production between sampling dates as well as annual production. Standard errors for interval biomass values were calculated using the formula presented by Newman and Martin (1983).

In order to determine the consistency of year-to-year production dynamics, a somewhat reduced sampling and analysis procedure was used in the second year. Production calculations were made at the family level, greatly reducing analysis time, and only 10 instead of 20 samples were used, greatly reducing sorting time. The production analysis was basically the same as in the first year for Heptageniidae (*Stenonema* spp. and *Heptagenia* sp.), Baetidae (all *Baetis* spp.), Caenidae (all *Caenis* spp.), and Tricorythidae (*Tricorythodes* sp.) with the instantaneous growth method, except that the biomass for all species within a family was summed before growth rates were applied in calculating production. The increment–summation method was again used for Oligoneuriidae (all *Isonychia*) and Ephemerellidae (*Ephemerella* spp. and *Eurylophella*), except that the three ephemerellids were combined. Since there was a high degree of correspondence in size-frequency distributions (especially the two *Ephemerella* species, Jacobi and Benke 1991), these calculations produced reasonably good estimates of growth increments (as required by the increment–summation method).

Production values are presented using two kinds of units: production per surface area of snag and production per area of river bottom. The former was calculated by measuring surface areas of each snag (from stem lengths and diameters) immediately after invertebrates were removed (Benke et al. 1984). The latter was calculated from snag quantification and equations that estimate snag surface area as a function of water level (Wallace and Benke 1984). The utilization of these

TABLE 1. Mean annual biomass, annual production and annual P/B (all as dry mass) for mayfly species per unit of snag surface area and per unit area of channel bottom for 1982.

	Snag surface			Channel bottom		
	Biomass (mg/m²)	Production (mg·m⁻²·yr⁻¹)	P/B	Biomass (mg/m²)	Production (mg·m⁻²·yr⁻¹)	P/B
Baetidae						
Baetis ephippiatus	17.0	1611.2	94.6	5.4	514.0	95.7
Baetis intercalaris	121.0	8137.3	67.2	40.0	2735.3	68.4
Baetis spp.*	25.2	1536.6	60.9	9.0	38.4	59.7
Total	163.3	11285.1	69.1	54.4	3787.6	69.6
Caenidae						
Caenis spp.†	4.0	239.0	59.1	1.4	82.1	59.1
Tricorythidae						
Tricorythodes sp.‡	23.7	1400.0	59.1	7.7	457.0	59.1
Oligoneuriidae						
Isonychia spp.§	203.8	3033.0	14.9	91.0	1308.7	14.4
Ephemerellidae						
Ephemerella argo	53.1	633.7	11.9	23.5	275.9	11.7
Ephemerella dorothea	95.0	762.6	8.0	42.9	325.5	7.6
Eurylophella sp.‖	8.9	68.8	7.8	2.5	21.9	8.7
Total	156.9	1465.1	9.3	68.9	623.3	9.0
Heptageniidae						
Stenonema exiguum	29.2	508.0	17.4	9.5	165.4	17.4
Stenonema integrum	22.6	389.1	17.3	7.5	133.9	17.8
Stenonema modestum	88.1	1520.4	17.3	29.0	502.8	17.4
Stenonema spp.¶	7.3	111.7	15.3	2.5	39.9	15.8
Heptagenia sp.#	52.4	858.2	16.4	19.1	310.9	14.8
Total	200.0	3398.1	17.0	67.8	1156.0	17.0
All mayflies	751.7	20820.3	27.7	291.3	7414.7	25.5

  * Primarily a single unidentified species, but also includes the indistinguishable early instars of all *Baetis* species.
  † Constituted three species (*C. diminuta, C. hilaris, C. macafferti*), indistinguishable as larvae.
  ‡ Unknown species, possibly *T. allectus.*
  § Constituted two or three species (*I. georgiae, I. sayi*), appearing to grow as a cohort in winter.
  ‖ Unknown species, possibly *E. doris.*
  ¶ Indistinguishable early instars of the three known *Stenonema* species.
  # Unknown species, possibly *H. julia.*

equations was described by Benke and Parsons (1990) in estimating black fly production on these same snag samples. Production per snag surface area represents concentration of production per unit of habitat surface and permits comparisons among habitats within a system (e.g., snag vs. benthic) and comparisons of the same habitat (e.g., snags) between systems. Production per unit area of river bottom accounts for relative abundance of habitats and provides a means to compare total production among different systems.

Since the increment–summation and instantaneous growth methods permit estimation of the temporal patterns of production, it is possible to determine the proportion of a taxon's production during each sampling interval. These values were then used to calculate temporal overlap among taxa with the proportional similarity index (Whittaker 1975):

$$PS_{ab} = \sum_{i=1}^{n} \min(P_{ai}, P_{bi})$$

where PS_{ab} is the proportional similarity between species a and b, n is the number of sampling intervals

during the year, P_{ai} is the fraction of species a production in time interval i, and P_{bi} is the fraction of species b production in the interval. Thus, when $PS_{ab} = 1$, it indicates perfect overlap for two species.

In order to help understand how this assemblage of mayflies fits in the trophic dynamics of the snag habitat and the river as a whole, we have combined feeding (gut) analyses with production analysis. Benke and Wallace (1980) demonstrated a procedure for estimating the relative contribution of various food types to production, total amount of each food type consumed, and the amount of fecal material released. Wallace et al. (1987) estimated relative contributions of various food types to production of several mayflies from the Ogeechee River by assuming literature-derived values for ecological efficiencies (Benke and Wallace 1980). Assimilation efficiencies (assimilation/ingestion) were assumed to be 10% for vascular plant and amorphous detritus, 30% for diatoms, 70% for animals, and 50% for fungi. Net production efficiency (production/assimilation) was assumed to be 40%. We applied these ecological efficiencies to our production analyses to estimate the contribution of each food type to production
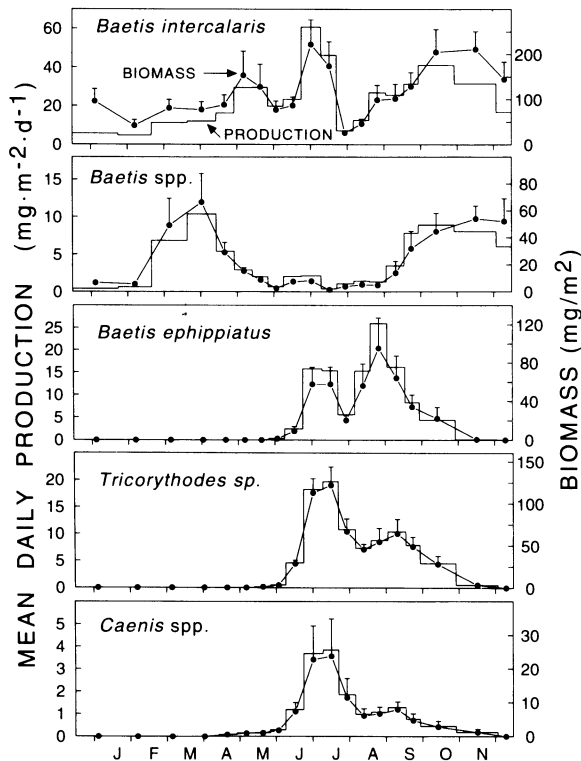
FIG. 1. Mean daily production (histograms) and biomass (●, means ± 1 SE) between 2–4 wk sampling dates, for Baetidae, *Tricorythodes* sp., and *Caenis* spp. on the snag surfaces of the Ogeechee River for 1982. *Baetis* spp. included a separate, but unnamed, species and early instars of other *Baetis* not separated to species. All values as dry mass.

Annual production divided by mean annual biomass (P/B) represents a measure of annual biomass turnover rate. P/B values were quite variable, ranging from 8–12 for Ephemerellidae to 14–18 for Heptageniidae and *Isonychia* to the very high values of 59–96 for *Baetis, Tricorythodes,* and *Caenis* (Table 1). Slight differences in P/B values could be found for snag surface and channel bottom due to time-specific differences in the biomass conversions with the latter (Benke and Parsons 1990).

Mean daily production through time showed distinctive patterns for species, genera, and families (Figs. 1–3). *Baetis intercalaris* had relatively high production throughout the year, whereas *Baetis ephippiatus, Tricorythodes* sp. and *Caenis* spp. all concentrated their production in the summer (Fig. 1). *Baetis* spp., which primarily included an unidentified species, had its highest production in winter–spring and fall.

The two *Ephemerella* species had relatively high daily production (i.e., >10 mg/m² of snag surface), but it was concentrated within only a few months in the winter–spring (Fig. 2). *Eurylophella* production was much lower and occurred somewhat earlier in the winter. *Isonychia* daily production was very high (>70 mg·m⁻²·d⁻¹) and also was concentrated in the winter–spring, even though animals were found well into the summer. Production of all Heptageniidae (*Stenonema* and *Heptagenia*) occurred throughout the year, but daily values for all species were highest during the warmer months (Fig. 3).

Production patterns tended to follow biomass patterns for each taxon (Figs. 1–3). However, for taxa in

for each major mayfly taxon, the total amount of food ingested by each mayfly taxon, and the total amount of each food type ingested by the entire mayfly assemblage.

RESULTS

Production dynamics for 1982—species level

Out of a total of at least 20 mayfly species found on the snag habitat (Jacobi and Benke 1991), 13 taxa (at either the species or genus level) were sufficiently abundant for production analyses. Mean annual biomass, annual production, and annual P/B were estimated on both a snag surface and a channel bottom basis (Table 1). The *Baetis* species, particularly *B. intercalaris,* were by far the most productive mayflies, with >11 g/m² of snag surface per year and almost 4 g/m² when converted to channel bottom area. *Baetis ephippiatus, Tricorythodes* sp., *Isonychia* spp., and *Stenonema modestum* all had relatively high production values of >1 g/m² of snag surface, and several other species were >0.5 g/m². Thus, although the three *Baetis* species contributed more than half of total mayfly production, the remaining production was spread across a wide spectrum of species.
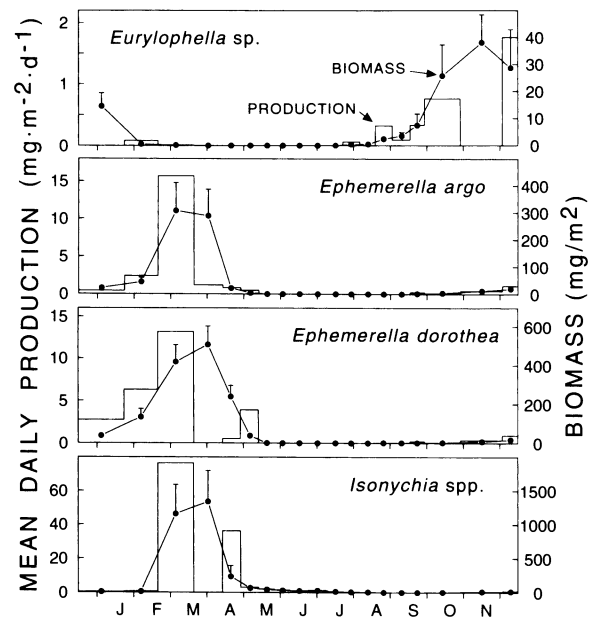

FIG. 2. Mean daily production (histograms) and biomass (●, means ± 1 SE) between 2–4 wk sampling dates, for Ephemerellidae and *Isonychia* spp. on the snag surfaces of the Ogeechee River for 1982. All values as dry mass.

TABLE 2. Mean annual biomass, annual production, and annual P/B (all as dry mass) for mayfly families per unit of snag surface area for consecutive years.

	1982			1983		
	Biomass (mg/m²)	Production (mg·m⁻²·yr⁻¹)	P/B	Biomass (mg/m²)	Production (mg·m⁻²·yr⁻¹)	P/B
Baetidae	163.3	11285.1	69.1	320.0	26669.0	83.4
Caenidae	4.0	239.0	59.1	6.0	349.5	58.7
Tricorythidae	23.7	1400.0	59.1	148.0	8793.7	59.4
Oligoneuriidae	203.8	3033.0	14.9	70.0	1660.1	23.7
Ephemerellidae	156.9	1465.1	9.3	110.9	1842.6	16.6
Heptageniidae	200.0	3398.1	17.0	188.8	2948.9	15.5
Total mayflies	751.7	20820.3	27.7	843.6	42263.7	50.1

which temperature-dependent growth equations were used and which were found throughout the year, temperature also had an influence on daily production (e.g., *Baetis intercalaris,* Fig. 1). Production was relatively high in the warm months in relation to biomass (i.e., higher daily P/B), in comparison to cold months in which production was relatively lower. One standard error for biomass was typically ≈25% of the mean for the most abundant species (e.g., *B. intercalaris*), but was higher for rarer taxa (e.g., *Caenis* spp.), indicating a very clumped distribution.

Production dynamics for 1982–1983 — family level

Total mayfly production was roughly twice as high in 1983 as in 1982, whether viewed on a snag surface (Table 2) or channel bottom basis (Table 3). The increase in production was associated with a similar increase in total mayfly density from 4758 to 10 725 individuals/m² of snag surface and from 1505 to 3120 individuals/m² of channel bottom (Jacobi and Benke 1991). In contrast, total biomass increased only a modest amount (12%) when viewed on a snag surface basis (Table 2) and actually decreased slightly on a channel bottom basis (Table 3). Mayfly production was represented by the same six families in roughly the same relative order, with the exception of the Tricorythidae. The difference in total production was largely due to increases of Baetidae (more than twofold) and Tricorythidae (more than fourfold). Production of the other families was more consistent (<50% change) between years, with Oligoneuriidae (*Isonychia* spp.) and Heptageniidae declining, and Caenidae and Ephemerellidae increasing. Thus, the shift in biomass to the fast-growing Baetidae and Tricorythidae, rather than an overall increase in biomass, resulted in an increase in annual P/B for total Ephemeroptera from 1982 (25–28) to 1983 (44–50) and a subsequent increase in production.

Although the magnitude of family-level production changed between years, particularly for the Baetidae and Tricorythidae, temporal patterns were quite consistent (Fig. 4). The Baetidae and Heptageniidae were

productive during all months, with peaks in the summer of each year, and the other families maintained their seasonal patterns of production. These patterns clearly show that temporal trends in production among mayflies on Ogeechee River snags are reasonably predictable at the family level. The complementary nature of production patterns among families in both years resulted in a consistently high level of mayfly activity throughout the 2-yr period, but with the major peaks during summer. A substantial fraction of the winter/
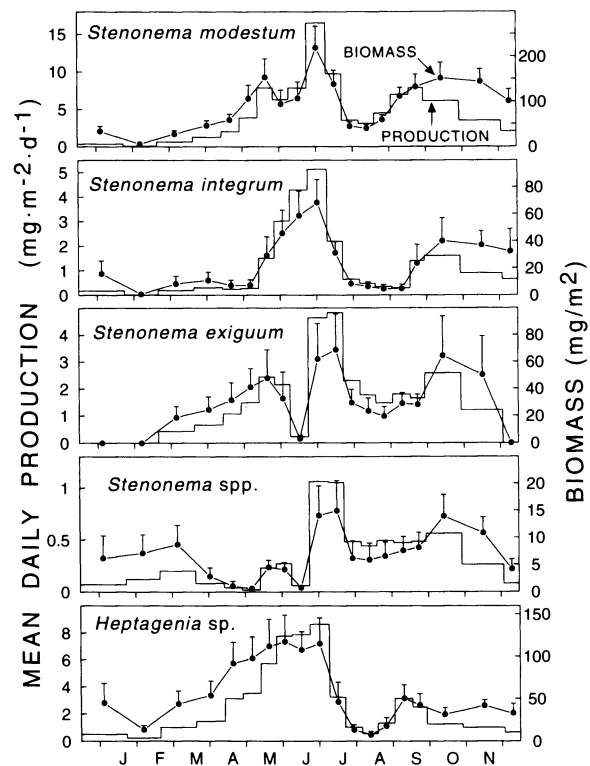

FIG. 3. Mean daily production (histograms) and biomass (●, means ± 1 SE) between 2–4 wk sampling dates, for Heptageniidae on the snag surfaces of the Ogeechee River for 1982. *Stenonema* spp. included early instars that could not be placed with one of the three known species. All values as dry mass.

TABLE 3. Mean annual biomass, annual production, and annual P/B (all as dry mass) for mayfly families per unit area of channel bottom for consecutive years.

	1982			1983		
	Biomass (mg/m^2)	Production (mg·m^{-2}·yr^{-1})	P/B	Biomass (mg/m^2)	Production (mg·m^{-2}·yr^{-1})	P/B
Baetidae	54.4	3787.6	69.6	95.7	7474.3	78.1
Caenidae	1.4	82.1	59.1	1.5	85.8	58.8
Tricorythidae	7.7	457.0	59.1	35.9	2134.5	59.5
Oligoneuriidae	91.0	1308.7	14.4	27.7	817.0	29.5
Ephemerellidae	68.9	623.3	9.0	53.1	880.5	16.6
Heptageniidae	67.8	1156.0	17.0	65.8	941.6	14.3
Total mayflies	291.3	7414.7	25.5	279.6	12333.7	44.1

spring production was contributed by filtering collectors (i.e., *Isonychia* spp.), whereas production during the rest of the year was almost entirely by gathering collectors.

Temporal overlap of production among species—1982

Overlap in temporal distribution of production in 1982, as expressed by the index of proportional similarity, was usually very high (i.e., >0.6) among species within the same family (Table 4). This was especially so for the Heptageniidae (*Stenonema exiguum, S. modestum, S. integrum,* and *Heptagenia* sp.) and the two most abundant Ephemerellidae (*Ephemerella argo* and *E. dorothea*). High overlap was also found for those species that concentrated their production only in summer (*Tricorythodes, Caenis, Baetis ephippiatus*) or only in winter (*Isonychia* and *Ephemerella* spp.). The lowest similarity (i.e., <0.15) was found primarily among species that concentrated their production in opposite seasons (e.g., *Ephemerella dorothea* vs. *Tricorythodes*).

Trophic basis of mayfly production

Detailed gut analyses and the relative contributions of various food types to production were presented by Wallace et al. (1987) for *Baetis, Heptagenia, Stenonema, Ephemerella, Eurylophella,* and *Isonychia* from the Ogeechee River. Extensive gut content data were not available for *Tricorythodes* and *Caenis,* but since there was a high degree of overlap among other gathering collectors, a mean value was assumed for these two taxa. Multiplying the fraction of production attributed to each food type by total production for each mayfly genus provided an estimate of actual production attributed to each food type (Table 5).

For the gathering collectors, the amount of production attributed to eating amorphous detritus was 66% (11 739 mg·m^{-2}·yr^{-1}) and to diatoms 21% (3802 mg·m^{-2}·yr^{-1}, Table 5). Production of filtering collectors (i.e., *Isonychia* spp.) was almost entirely (96%) attributed to consumption of amorphous detritus. For those species whose production was concentrated in winter (ephemerellids and *Isonychia*), diatoms contributed relatively little to production. For all mayflies, 70% of
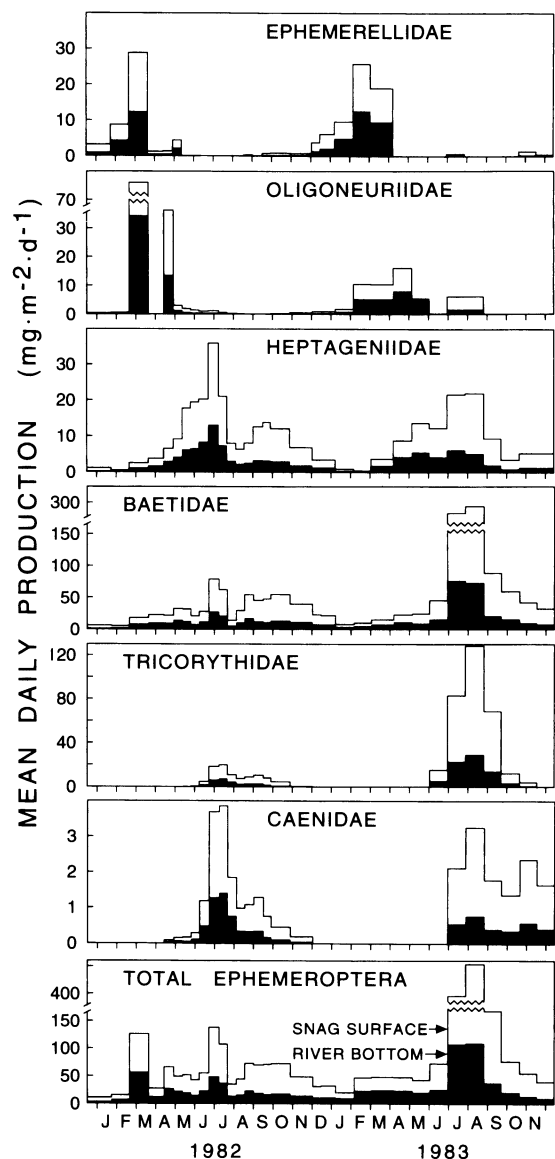

FIG. 4. Two-year patterns of mean daily production for the major mayfly families on the snag habitat of the Ogeechee River for 1982–1983. All values are dry mass per unit area of snag surface (open) or river bottom (shaded).

TABLE 4. Proportional similarity (PS_{ab}) of temporal distribution of production for 12 mayfly taxa from the snag habitat of the Ogeechee River.* All relatively high values (>0.50) are underlined.

	Species number										
	1	2	3	4	5	6	7	8	9	10	11
1. *Isonychia* spp.	···										
2. *Ephemerella argo*	0.79	···									
3. *Ephemerella dorothea*	0.55	0.69	···								
4. *Eurylophella* sp.	0.02	0.10	0.08	···							
5. *Baetis intercalaris*	0.15	0.22	0.21	0.33	···						
6. *Baetis ephippiatus*	0.05	0.01	0.00	0.20	0.44	···					
7. *Tricorythodes* sp.	0.03	0.02	0.01	0.22	0.48	0.75	···				
8. *Caenis* spp.	0.05	0.04	0.03	0.18	0.50	0.64	0.87	···			
9. *Stenonema exiguum*	0.12	0.13	0.11	0.28	0.78	0.57	0.61	0.63	···		
10. *Stenonema modestum*	0.10	0.13	0.11	0.29	0.79	0.55	0.62	0.65	0.81	···	
11. *Stenonema integrum*	0.08	0.12	0.09	0.24	0.67	0.42	0.53	0.58	0.64	0.79	···
12. *Heptagenia* sp.	0.17	0.18	0.18	0.16	0.71	0.38	0.43	0.51	0.67	0.74	0.75

* $PS_{ab} = \Sigma \min (P_{ai}, P_{bi})$ where P_{ai} is the fraction of species a production in time interval i, and P_{bi} is the fraction of species b production in the interval.

production was due to amorphous detritus and 18% to diatoms.

Using our production calculations and assuming the bioenergetic efficiencies indicated above (Wallace et al. 1987), we approximated annual ingestion of each food type for both gathering and filtering collectors, as well as total ingestion of each mayfly genus (Table 5). *Baetis* was responsible for more than half of total production and ingestion. Out of 423 g/m² of organic matter consumed by all mayflies, detritus represented ≈91% (367 g/m² for amorphous detritus and 18 g/m² for vascular plant detritus). Almost 300 g/m² of this amorphous detritus was consumed by gathering collectors and the rest by filterers (Oligoneuriidae). Gathering collectors also consumed ≈32 g/m² of diatoms.

DISCUSSION

Magnitude and stability of mayfly production and turnover

Annual production of snag-dwelling mayflies from the Ogeechee River, whether considered on a snag surface area basis (21–42 g·m⁻²·yr⁻¹) or a channel bottom basis (7.4–12.3 g·m⁻²·yr⁻¹), was among the highest estimates reported from lotic systems for either Ephemeroptera (e.g., Fisher and Gray 1983, Jackson and Fisher 1986, Rader and Ward 1989b) or gathering collectors (Benke 1993). Unlike most mayfly assemblages, production on Ogeechee snags was distributed among many taxa. Five out of six major families had production values >1 g·m⁻²·yr⁻¹ (snag surface area),

TABLE 5. Annual production and ingestion (as dry mass) of mayfly genera (P, in mg·m⁻²·yr⁻¹) attributed to various food types. Percentage of production attributed to each food type for six genera was obtained from Wallace et al. (1987).

	Food type							
	Amorphous detritus		Fungi		Vascular plant detritus		Diatom	
	P	%	P	%	P	%	P	%
Baetis spp.	7886	69.7	327	2.9	147	1.3	2945	26.1
Heptagenia sp.	672	78.3	15	1.8	20	2.3	61	7.1
Stenonema spp.	356	53.4	155	6.1	13	0.5	594	23.4
Ephemerella spp.	714	51.1	92	6.6	397	28.4	13	0.9
Eurylophella sp.	53	76.9	5	7.9	5	7.9	0	0
Caenis spp.*	157	65.9	12	5.1	20	8.2	28	11.5
Tricorythodes sp.*	922	65.9	71	5.1	115	8.2	161	11.5
Isonychia spp.	2921	96.3	79	2.6	0	0	30	1.0
Production (gatherer)	11739		678		715		3802	
Production (total)	14660		757		715		3832	
Ingestion (gatherer)	293495		3390		17878		31681	
Ingestion (filterer)	73020		395		0		253	
Ingestion (total)	366515		3785		17878		31933	

* Percentages for *Caenis* and *Tricorythodes* were assumed to be equal to the mean for other gatherers (i.e., excluding *Isonychia*, a filterer).

developed from 13 individual estimates of taxa (genus or species level) representing up to 20 species. Mayfly production on snags in the Satilla River was substantially lower ($1.2 \ g \cdot m^{-2} \cdot yr^{-1}$, snag surface area) and less diverse (mostly *Stenonema*) than found in the Ogeechee (Benke et al. 1984). Mayfly production on snags in a second-order blackwater stream was similar to that found in the Satilla River (Smock et al. 1985).

Baetis production has been estimated more often than any other mayfly genus. Our estimates (3.8–7.5 $g \cdot m^{-2} \cdot yr^{-1}$, channel bottom area) were among the highest reported, which include populations with high P/B values from desert streams (Fisher and Gray 1983, Jackson and Fisher 1986, Gaines et al. 1992) and those with high biomass downstream of a dam, where habitat is stabilized and algal food is plentiful (Rader and Ward 1989b). Relatively few estimates of *Caenis* production exist, but our low estimates ($\approx 85 \ mg \cdot m^{-2} \cdot yr^{-1}$) were not much lower than the highest values from other streams (e.g., MacFarlane and Waters 1982). Our production estimates for ephemerellids (0.6–0.9 $g \cdot m^{-2} \cdot yr^{-1}$) were similar to many previous estimates, but are lower than has been found in some productive coldwater streams (4–16 $g \cdot m^{-2} \cdot yr^{-1}$, Waters and Crawford 1973, Rader and Ward 1987, 1989b). Production of Heptageniidae has been widely estimated and our values ($\approx 1 \ g \cdot m^{-2} \cdot yr^{-1}$) are among the highest (e.g., Zelinka et al. 1977, MacFarlane and Waters 1982). Relatively few production estimates exist for *Isonychia*, but our values (0.8–1.3 $g \cdot m^{-2} \cdot yr^{-1}$) are about half those of Sullivan and Topping (1984) for *Isonychia bicolor* and substantially less than found for a related genus (7–10 g/m^2, *Coloburiscus*) in an enriched New Zealand stream (Hopkins 1976). Relatively few estimates of *Tricorythodes* production have been made, but high values (9–19 $g \cdot m^{-2} \cdot yr^{-1}$) have been found in a desert

stream (Fisher and Gray 1983, Jackson and Fisher 1986) and in the upper Mississippi River (Hall et al. 1980). Although lower than these, our values (0.5–2.1 $g \cdot m^{-2} \cdot yr^{-1}$) should still be considered quite high.

Annual production values and temporal patterns at the family level were reasonably consistent for two consecutive years, with relatively little change between years (i.e., <50%) for four out of six families. We believe that even the twofold increase in total mayfly production in the 2nd yr should be considered a modest degree of inter-year variation since the difference was largely due to a shift in family-level composition and turnover rates, rather than any substantial change in biomass (Tables 2 and 3). The change also seems relatively small when viewed in the context of production of gathering collectors in different streams, which ranges over five orders of magnitude, and total invertebrate production, which ranges over more than two orders of magnitude (Benke 1993). Irrespective of the change in magnitude of production, the temporal patterns are clearly consistent between years. This stability in biomass, production, and temporal patterns on the snag habitat occurred in spite of quite different flood regimes for the 2 yr, which affects not only snag surface area, but potentially the timing, quality, and quantity of food resources (Benke and Parsons 1990). An even higher degree of persistence in invertebrate dynamics was found in drift analysis where mean annual drift biomass (nocturnal) for mayflies varied from only 72.4 to 75.0 $mg/100 \ m^3$ during these same 2 yr (Benke et al. 1991).

Annual P/B values (or biomass turnover rates) for mayflies typically have varied from ≈ 5 for univoltine species to 10 for bivoltine species (Waters 1977, Benke 1984). In the snag mayfly assemblage, P/B values for several multivoltine taxa were substantially higher than has been found in most previous studies (but see Fisher and Gray 1983, Jackson and Fisher 1986). The high P/B values of Baetidae (60–96) and Tricorythidae (59) reflected their high daily growth rates and short larval life spans (Benke and Jacobi 1986, Benke et al. 1992) and are comparable to those of black flies inhabiting the same snags (Benke and Parsons 1990). Intermediate P/B values (14–30) for Heptageniidae and Oligoneuriidae reflected 2–3 generations per year. Even the univoltine Ephemerellidae had P/B values (8–17) higher than typical univoltine species (3–8), since their larval life span and production only covered about a 6-mo period or less. When P/B values within a group such as the Ephemeroptera vary by an order of magnitude (i.e., 8–96), the relative production among the various taxa strongly affects the order-level P/B, as shown in our 2-yr study. Total mayfly biomass changed little between years, but P/B, and thus total production, roughly doubled (Tables 2 and 3). Obviously, the use of an order-level P/B value to estimate production from biomass, without consideration of taxonomic composition, could lead to substantial errors.

TABLE 5. Continued.

Food type			
Animal		Total production	Total ingestion
P	%		
0	0	11285	226492
90	10.5	858	18199
422	16.6	2540	41458
182	13.0	1396	28964
5	7.3	69	1502
23	9.5	239	4796
133	9.5	1400	28082
3	0.1	3033	73678
854		17787	
857		20820	
3049			349493
11			73678
3059			423170

Snags as a productive mesoscale habitat

Snags previously have been shown to be a major site of invertebrate production in two other major rivers in the southeastern Coastal Plain, the Savannah and Satilla Rivers (Cudney and Wallace 1980, Benke et al. 1984). In the Satilla, snags were estimated to be far more productive than the sandy benthic habitat on a unit area basis. However, since snags only contributed ≈5% to total habitat surface area, their contribution to total river production was only ≈15%. In contrast, the Ogeechee River has ≈5 times more snag habitat than the Satilla (Wallace and Benke 1984). Our calculation of mayfly production per unit area of river bottom as being 29–36% of values per snag surface area provides a first indication of an even greater significance of snags in the Ogeechee River than in the Satilla River. Drift biomass in the Ogeechee was also ≈5 times higher than in the Satilla, apparently due to a greater amount of submerged wood as habitat (Benke et al. 1991).

Snags are very stable habitats, persisting in the same location for much longer periods of time than the life cycles of most river invertebrates (Benke and Wallace 1990). While the snags themselves are stable, their utility as a habitat for aquatic invertebrates is variable. As water levels rise and fall, upper portions of the habitat are continuously inundated and desiccated, and total snag surface area varies by ≈2× from low to high discharge (Wallace and Benke 1984, Benke and Parsons 1990). This variation in inundated surface area can certainly have some degree of influence on monthly production estimates, but total mayfly production is simultaneously influenced strongly by biomass, time of year (and thus species composition), and temperature. In order for discharge to affect total annual production through its effect on snag surface area by as much as 2×, one year would have to be extremely dry with discharge always <20 m³/s, and another year would have to be extremely wet, with discharge always >200 m³/s. Such a scenario is highly unlikely, since even relatively dry years (such as 1982) have high-water periods, and wet years have low-water periods. Thus, discharge differences between years rarely cause mean snag surface area to vary >20%, and surface area is unlikely to be the most important variable controlling temporal variability in production within or between years.

Although high discharge, or flooding, is usually perceived as a disturbance to community structure in many streams (e.g., Power et al. 1988, Resh et al. 1988), the interaction between snags and water level suggests a beneficial effect in Coastal Plain streams. At least in warmwater environments, the high growth rates, extensive periods of reproduction, and high drift rates of invertebrate consumers enable them to rapidly colonize newly inundated surfaces. These characteristics provide a high degree of resiliency to these populations in adjusting to natural variations in water level and habitat availability.

Production as a means of assessing resource utilization and overlap

Production analysis provides an objective, comprehensive, and quantitative means of measuring resource overlap since it directly reflects a species success and usage of its resources. Under ideal circumstances, production analysis might be used to measure overlap along each of the three major niche dimensions (food, space, and time). Although we have focused our efforts on the distribution of production along the time dimension, the contribution of each food type to production of individual mayfly taxa can also be used to estimate resource overlap. Similarly, production can be estimated along the spatial dimension using stratified sampling across mesoscale habitats. Since all animals in our study were collected from the same mesoscale habitat (snags), possibilities for separation along this dimension appear somewhat restricted. Although there may be species-specific preferences on snag micro-habitats, the opportunities for spatial separation appear to be considerably less than those found in a typical benthic environment. Even in a more heterogeneous rubble–riffle stream habitat, Rader and Ward (1987) found little indication of spatial separation among six mayfly species.

The temporal distribution of production was first used with aquatic insects to assess resource overlap by Georgian and Wallace (1983). They found very low overlap (proportional similarity = 0.0–0.30) among six grazing insects in a southeastern US mountain stream, and suggested a high degree of temporal partitioning. Production was also used to assess temporal overlap among mayflies in a reach of the Cache la Poudre River (Rader and Ward 1987) and in the upper Colorado River (Rader and Ward 1989a). Both studies by Rader and Ward showed a high degree of temporal overlap (0.39–0.76) and little resource partitioning among 5–6 species that were primarily univoltine.

In contrast, mayfly species on Ogeechee River snags had much higher temporal overlap than found by Georgian and Wallace (1983), and both higher and lower overlap than found by Rader and Ward (1987) (Table 4). The range in overlap values of snag mayflies from the Ogeechee River is not surprising considering the relatively high number of species and the multivoltine life histories of most. Of particular significance is that the highest overlap was often between the most closely related species, which would presumably have the closest food and space requirements as well. While high overlap also existed between members of some families (e.g., *Isonychia*-Ephemerellidae, and *Caenis*-*Tricorythodes*-*B. ephippiatus*), low overlap was mostly a family-level phenomenon (e.g., Ephemerellidae vs. Caenidae). These family-level patterns were quite con-

TABLE 6. Proportional similarity (PS_{ab}) of selected mayfly taxa from the snag habitat of the Ogeechee River, based upon gut-content analysis (from Wallace et al. 1987).* Numbers in parentheses are recalculations of overlap based upon the fraction of production attributable to each food source.

Taxon	Taxon number					
	1	2	3	4	5	6
1. *Baetis* spp.	...					
2. *Heptagenia* sp.	0.92 (0.80)	...				
3. *Stenonema* spp.	0.94 (0.80)	0.88 (0.83)	...			
4. *Ephemerella* spp.	0.64 (0.56)	0.67 (0.67)	0.66 (0.72)	...		
5. *Eurylophella* sp.	0.89 (0.74)	0.92 (0.88)	0.86 (0.67)	0.73 (0.73)	...	
6. *Isonychia* spp.	0.88 (0.74)	0.93 (0.81)	0.83 (0.57)	0.63 (0.55)	0.89 (0.80)	...

* $PS_{ab} = \Sigma \min(P_{ai}, P_{bi})$, where P_{ai} is the fraction of food type i used by species a, and P_{bi} is the fraction used by species b. Food categories were amorphous detritus, fungi, vascular plant detritus, diatoms, and animals.

sistent in two consecutive years, and regardless of the inter-familial interactions, they are most likely associated with thermal constraints.

Regardless of the degree of overlap among individual species or families, the complementary pattern of production among families resulted in total mayfly production that was relatively high throughout the year, but with consistent peaks during summer and consistent declines in early winter (Fig. 4). Although these gathering collectors did not form a continuous sequence of species replacements as suggested by the River Continuum Concept (Vannote et al. 1980), their production patterns did function to distribute the utilization of resources over time, as predicted. These temporal patterns are somewhat different than those found from drift analysis, in which drift biomass peaked during the winter, reflecting the relatively high fraction of drifting *Isonychia* and ephemerellids and their high biomass (>2 g/m^2) during this short span of time (Benke et al. 1991).

Using the fraction of food types found in guts, showing extensive utilization of amorphous detritus (Table 5), Wallace et al. (1987) estimated high overlap among all taxa along the food dimension (Table 6). We have recalculated overlap based upon the amount each food type contributes to a mayfly's production and found only slightly lower overlap than when using the food fraction alone (Table 6). With overlap >0.7 in 10 out of 15 cases, there is even less partitioning along the food dimension than the temporal dimension. Ideally, one could multiply the trophic-based overlap of production by the time-based overlap of production to obtain a two-dimensional measure of resource overlap. Unfortunately, since the feeding analyses were only done at the genus level, it was not possible to combine these two resource dimensions. Nonetheless, the high trophic-based values in Table 6 suggest that such a

two-dimensional assessment would likely produce high values.

High resource overlap among closely related and trophically similar species, as we have found for snag-dwelling mayflies, has often seemed enigmatic when attempting to explain coexistence. Competition theory suggests that such high overlap is not possible in a resource-limited environment. The simplest rationale in such cases is that physical components are more important than biological ones, as Rader and Ward (1987) suggested in interpreting their high overlap values for mayflies in Rocky Mountain streams. However, in the Ogeechee River, high production of mayflies, as well as high production of other coexisting insect groups (*unpublished data,* but see Wallace and Benke [1984] for preliminary biomass values) is suggestive that biological interactions, such as competition, may be intense on snag habitats. While high production in itself certainly does not demonstrate the importance of biological interactions, it is a function of several variables that do imply interactions: high densities, high biomass, and high resource use.

Several characteristics of the snag environment and its community might permit both high richness and overlap in resource use, even if strong competitive interactions were present. Since snag surface area is a function of water height, variable discharge generates continuous fluctuations in carrying capacity for snag invertebrates (Benke and Parsons 1990). Invertebrate drift densities are high in the Ogeechee and snags inundated by rising water are rapidly colonized. Benke et al. (1991) estimated that on the average, $\approx 1.5\%$ of mayfly biomass is in the drift at any time during darkness. This means that the average net displacement of mayfly biomass downstream is 270 m/d (see Benke et al. 1991 for rationale). Such high drift densities, coupled with rapid growth and short development times

for many species, should enable them to quickly utilize newly inundated surfaces before superior competitors arrive. The aerial adult stage is independent of interactions at the larval stage, and with reproduction throughout most of the year, is capable of resetting the balance between species. High replacement rates of the food resource (mostly amorphous detritus) from seston prevent its depletion from snag surfaces, and thus reduces the likelihood of competitive exclusion through resource exploitation. Thus, if competition occurs on snags, it is most likely due to interference on a limited substrate space. Such an interpretation is supported by the small differences in total mayfly biomass between years (Tables 2 and 3). Finally, the snag community also includes several large invertebrate predators (hellgrammites, perlid stoneflies, and dragonflies) which, together with insectivorous fishes (Benke et al. 1985), might exert sufficient predation pressures on gathering collectors to facilitate coexistence.

Trophic basis of mayfly production on snags

In contrast to many streams in which mayflies are most likely to be considered as scrapers (or grazers), this group clearly falls in the category of gathering collectors (except for the filtering *Isonychia* spp.) in the Ogeechee River. Here, >70% of the mayfly production on Ogeechee River snags was attributed to feeding on amorphous detritus and only ≈18% was based upon eating diatoms. Gathering and filtering collectors typically represent half or considerably more than half of total invertebrate production across all stream sizes (Benke 1993), and it is important to account for their food resources. Unfortunately, the origin and composition of amorphous detritus as a food for collectors is probably the least understood of all trophic pathways in streams, particularly in comparison to scrapers and shredders.

In the case of the Ogeechee River, and probably other similar Coastal Plain streams, much of the amorphous organic material (primarily in the form of dissolved organic matter [DOM] and bacteria) appears to originate from the broad floodplain swamps that adjoin it throughout most of its length (Edwards and Meyer 1986, Carlough 1990, Edwards et al. 1990). Wainright et al. (1992) have shown that in addition to floodplain soils, a significant input of DOM and bacteria also originates from channel sediments. The conversion of DOM to particles through flocculation and the utilization of DOM by bacteria is now widely accepted as a significant trophic pathway to invertebrate consumers in many aquatic ecosystems (e.g., Wotton 1990, Maltby 1992), and it seems particularly important in DOM-rich Coastal Plain rivers. Couch and Meyer (1992) have demonstrated the rapid development of biofilm on snags from the Ogeechee River and that it arises from sestonic deposition. Their biofilm accumulation measurements (as ash-free dry mass) of ≈1 $g \cdot m^{-2} \cdot d^{-1}$ in low current velocities (10 cm/s) are almost identical to consumption of amorphous detritus by the mayflies (Table 5). Although these two independent estimates are based on many assumptions, their correspondence suggests that sufficient food is likely to be supplied from sestonic sources and that mayflies consume a substantial portion of it. It is quite possible that sestonic accumulation rates are greater on snags in higher current velocities where most mayflies are found (i.e., 20–50 cm/s), than Couch and Meyer (1992) found at 10 cm/s.

Feeding experiments using mayflies from the Ogeechee River have helped substantiate the importance and nutritional value of amorphous organic matter and their associated microbes. *Stenonema* were found to incorporate enough bacteria from seston into their tissues to meet at least 47% of their total carbon requirement (Edwards and Meyer 1990). Furthermore, *Stenonema* grown in complete darkness (with negligible algae) grew at natural rates, and river seston passed through an ultra-fine filter (<1 μm) had relatively little effect on the rapid accumulation of amorphous material on substrata or on *Stenonema* growth rates (Benke et al. 1992). Thus, interception of seston by woody substrata through flocculation and aggregation of particles <1 μm in size, including bacteria, appears to be the major source of nourishment for these mayfly collectors.

In summary, the continuous delivery of a nutritious food source from the seston, coupled with a fluctuating habitat space, appears to create an environment that allows high mayfly production and high overlap in resource utilization among one of the most diverse mayfly assemblages described to date. The temporal pattern of production for mayflies as a group, both within and between years, shows a consistent pattern of resource consumption by primary consumers and availability of consumer production to predators. Thus, secondary production analysis provides a means to assess resource overlap among closely related coexisting species and represents a linkage from population dynamics to ecosystem-level processes.

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APPENDIX

Length/mass regressions for mayflies from the Ogeechee River. DM = dry mass, HW = head width, BL = body length. *Eurylophella* biomass was estimated using the *Ephemerella* regression.

Taxon	Equation	Source	r^2	n
Baetis spp.	ln DM = 3.33 ln HW + 0.236	This study	0.96	49
Ephemerella spp.	ln DM = 2.51 ln BL − 4.39	This study	0.86	32
Heptagenia sp.	ln DM = 2.94 ln HW − 1.68	This study	0.98	11
Stenonema spp.	ln DM = 3.04 ln HW − 1.69	This study	0.83	67
Isonychia spp.	ln DM = 2.92 ln BL − 5.79	This study	0.97	123
Caenis spp.	ln DM = 1.54 ln BL − 3.48	Rogers 1982	0.84	
Tricorythodes	ln DM = 3.22 ln BL − 4.69	McCullough et al. 1979		