

Production of benthic macroinvertebrate communities along a southern Appalachian river continuum

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SUMMARY

1. Annual production was estimated for macroinvertebrate communities of principle habitats along a first- to seventh-order river continuum in the southern Appalachian Mountains (U.S.A.). Annual production was relatively low in depositional habitats, pebble/gravel substrata, and on cobble devoid of plant biomass (mosses and hydrophytes). Production was greater in bedrock habitats and greatest on hydrophyte-covered cobble, with estimates reaching 364 g AFDM (ash-free dry mass) $m^{-2} yr^{-1}$ in a sixth-order river reach. Annual production in depositional habitats was correlated to standing crops of benthic organic material (BOM) in low-order stream reaches but not in higher-order reaches, indicating differences in BOM availability with stream size. In cobble, pebble/gravel and bedrock habitats production was significantly correlated to standing crops of aquatic plants, which can stabilize substrata and enhance access of collector-filtering invertebrates to entrained food resources.

2. By accounting for proportional availability of habitats along the continuum, estimates of total production ranged from 5 to 154 g AFDM $m^{-2} yr^{-1}$, and increased significantly with stream size. Annual production estimated for sixth- and seventh-order reaches of the continuum were amongst the highest reported thus far for lotic systems.

Organization of the benthic community along the continuum, based on production estimates for individual functional feeding-groups, generally supported predictions of the River Continuum Concept (RCC): shredder contributions were greatest in low-order reaches and declined downstream; scraper percentages were greatest in the middle of the continuum; collector-filterer contributions increased with increasing stream size. Longitudinal trends for collector-gatherers and predators did not support RCC predictions; these groups appeared to be influenced by localized changes in habitat availability and occurrence of vertebrate predators along the continuum.

Introduction

Estimates of secondary production have been used to characterize taxonomic and functional organization of benthic macroinvertebrate communities in stream ecosystems. In contrast to estimates of abundance or biomass, secondary production accounts for growth rates and turnover times of macroinvertebrate populations and can provide insight into the energy base and interactions between functional components of the benthic community (Benke *et al.*, 1984; Smock & Roeding, 1986).

A number of procedures have been published over the past 30 years to estimate secondary production (Hynes & Coleman, 1968; Hamilton, 1969; Waters, 1977; Benke, 1979; Benke, 1984). The most recent review and synthesis of current knowledge (Benke, 1993), defines theory and outlines protocols pertinent to the study of secondary production in lotic systems. It also suggests that secondary production analysis is a useful approach to provide insight into specific areas of lotic ecology, including: (i) the relationships of

benthic community composition to stream habitat heterogeneity; and (ii) longitudinal trends in the functional organization of benthic communities along stream-size continua.

Production analyses have often been used to assess relationships between the benthic community and stream habitat, and these studies underscore the importance of considering habitat availability when characterizing community composition. Mackey (1977) found that much of the chironomid production in the River Thames (U.K.) was associated with habitats containing water lilies (*Nuphar* sp.). Benke *et al.* (1984) and Smock, Gilinsky & Stoneburner (1985) showed that submersed wood (snag habitat) in Coastal Plain rivers (U.S.A.) supported higher secondary production than surrounding sand substratum. Huryn & Wallace (1987a), Lughart & Wallace (1992), and Wohl, Wallace & Meyer (1995) found benthic production of functional feeding-groups differed greatly between various habitats in Appalachian (U.S.A.) headwater streams. Similarly, Kirk & Perry (1994) found production estimates for selected taxa differed in the sixth-order Kanawha River (U.S.A.) between gravel and large-cobble substrata.

The River Continuum Concept (RCC; Vannote *et al.*, 1980) suggests that predictable shifts in functional organization of the benthic community occur with changing stream size along a continuum. Benke (1993) noted that since production is a direct, quantitative measure of functional performance, it is an appropriate means to test this RCC prediction. However, most studies to date which examine community composition along stream continua are based primarily on macroinvertebrate abundance data, or, to a much lesser degree, relative biomass. In his review, Benke (1993) was unaware of any studies that examined secondary production of functional feeding-groups along stream continua. Since then, Wohl *et al.* (1995) used production estimates to characterize functional organization along the Wine Spring stream gradient in the southern Appalachian mountains. This continuum was relatively short in length (≈ 5 km), with reach sizes no greater than third-order. Similarly, Benke (1993) pointed out that the majority ($> 85\%$) of production estimates in general are from small-stream systems (discharge $< 10 \text{ m}^3 \text{ s}^{-1}$); little is known about benthic production in larger stream and river systems and whether patterns of functional organization

exhibited in low-order systems persist along more extensive river continua.

The approach of this study was to examine secondary production of the benthic macroinvertebrate community along a first- to seventh-order river continuum in the southern Appalachian Mountains. Our objectives were to: (i) assess the influence of habitat heterogeneity on functional organization of the benthic community; (ii) compare production estimates from specific habitats and stream reaches to estimates from other lotic ecosystems; (iii) examine changes in dominant taxa along the continuum; and (iv) employ secondary production estimates to compare functional organization along this continuum to predictions of the RCC.

Study area

The study was conducted in Ball Creek, Coweeta Creek and the Little Tennessee River, a first- to seventh-order stream continuum in the Blue Ridge province of the southern Appalachian Mountains (North Carolina, U.S.A.). The continuum is situated between $35^{\circ}00'$ and $35^{\circ}20'N$; summer temperatures are generally cool and winters are relatively mild (Wallace, Webster & Lowe, 1992). Crystalline rock is the primary geological feature of this area and ionic concentrations in streamwater are low (Swank & Waide, 1988; Swank & Bolstad, 1994). Ball Creek, which drains one of three primary catchments of the Coweeta Hydrologic Laboratory (CHL), is about 5 km in length and flows to the north-east. Ball Creek joins with other CHL streams to form Coweeta Creek, which, in turn, joins the Little Tennessee River about 5 km downstream. The Little Tennessee River flows north and north-west for ≈ 55 km before entering Fontana Reservoir (Fig. 1).

Eleven stream reaches, each about 100–200 m in length, were identified along the continuum as sampling stations (Fig. 1). The upper three stations, S-1 to S-3, were located in small-stream reaches (stream orders 1 and 2) of Ball Creek. The forest canopy of Ball Creek consists of mixed hardwoods and rosebay rhododendron (*Rhododendron maximum* L.), effectively shading the stream year-round. Streambed slope is relatively steep with an elevation change of more than 500 m over the length of Ball Creek (Fig. 1). Primary benthic habitats at stations S-1 to S-3 include bryophyte-covered bedrock

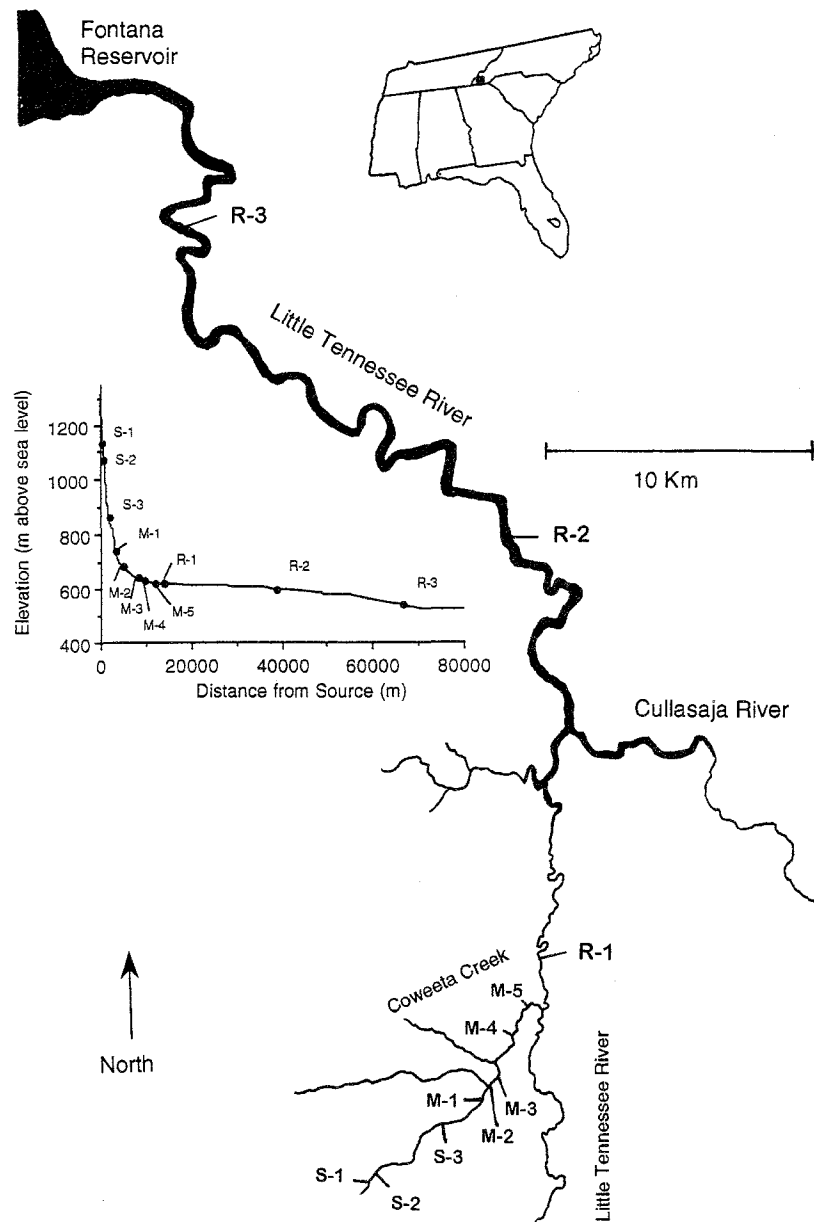


Fig. 1 Locations of the eleven sampling stations along the Ball Creek-Coweeta Creek-Little Tennessee River continuum. S-1 to S-3 are first- and second-order stream reaches in upper Ball Creek; M-1 to M-5 are fourth- and fifth-order reaches in lower Ball Creek and Coweeta Creek; R-1 to R-3 are in sixth- and seventh-order reaches of the Little Tennessee River.

outcrops, cobble riffles and depositional areas formed behind natural channel obstructions such as debris dams (Table 1).

The middle five stations (M-1 to M-5) include a fourth-order reach of Ball Creek and fifth-order locations along the 5-km length of Coweeta Creek (Fig. 1). Over 91% of the Coweeta basin is in deciduous forest, and Coweeta Creek is flanked by a wooded riparian zone (Swank & Bolstad, 1994). Stream width varies between 5 and 15 m, and stream canopy cover is often open. Lush growths of a submersed hydrophyte, *Podostemum ceratophyllum* Michaux, occur on larger

cobble substrata. Benthic habitat availability is variable among the middle stations; bedrock outcrops occur only at M-1 and M-2 while M-3 and M-4 support *P. ceratophyllum*-covered cobble riffles (Table 1). M-5 has no riffle areas and pebble/gravel run habitat prevails. Depositional areas, which occur at all five stations, form behind channel obstructions (snags or logs) or in pooled reaches. Mean discharge at stations M-1 to M-5 is less than $2.0 \text{ m}^3 \text{ s}^{-1}$, but occasional spates increase discharge about five to ten times above mean flow for short durations.

The lower three stations (R-1 to R-3) lie within the

Table 1 Physical characteristics of sampling stations along the Ball Creek–Coweeta Creek–Little Tennessee River continuum

Station code	S-1	S-2	S-3	M-1	M-2	M-3	M-4	M-5	R-1	R-2	R-3
<i>Geomorphic features</i>											
Stream order	1	2	2	4	5	5	5	5	6	7	7
Distance from headwater (km)	0.5	0.8	2.0	4.5	5.3	9	10	14	15	38	67
Catchment area (ha)	12	39	119	690	1548	3052	4163	4456	36 260	83 660	112 900
Elevation (m.a.s.l.)	1356	1159	847	690	671	642	633	622	620	597	540
Water-surface slope (%)	38.6	21.2	9.4	7.0	2.9	0.43	0.53	0.43	0.05	0.14	0.35
Mean annual discharge (m ³ s ⁻¹)	< 0.01	0.02	0.10	0.27	0.58	1.06	1.35	1.43	10.85	22.18	29.54
Average bankful width (m)	0.5	3.8	5.1	5.5	7.2	13	15	13	25	60	70
Average bankful depth (cm)	4	8	12	18	25	25	25	30	50	50	50
<i>Habitat proportions (%)</i>											
Depositional area	8	14	22	8	16	16	38	19	42	35	28
Pebble/gravel run	-	-	-	-	-	-	-	81	-	-	-
Bare cobble riffle	33	69	57	74	79	75	-	-	44	-	-
Plant-covered cobble riffle	-	-	-	-	-	9	62	-	14	27	-
Plant-covered bedrock outcrop*	59	17	21	18	5	-	-	-	-	38	72
<i>Temperature (°C)</i>											
Daily average	9.5	10.0	10.4	10.8	11.2	11.9	12.0	12.1	13.0	13.5	13.8
Annual degree-days	3454	3568	3794	3937	4078	4322	4389	4401	4763	4922	5064

*Includes bryophytes and *Podostemum ceratophyllum*.

m.a.s.l. = metres above sea level.

55-km length of the Little Tennessee River between the Coweeta Creek confluence and Fontana reservoir (Fig. 1). River width ranges between 20 and 100 m with minimal canopy cover. The river is sixth-order at the upper station; middle and lower stations lie within a seventh-order reach below the Cullasaja River confluence (Fig. 1). River geomorphology varies between sampling stations; streambed slope is shallow at R-1 and the river meanders through an alluvial floodplain valley. The floodplain in this reach is utilized for row-crop agriculture and pasturage, therefore, R-1 was established in an area flanked by wooded riparian buffer strips to minimize anthropogenic impacts. Further downstream the Little Tennessee River passes through the municipality of Franklin, North Carolina, after which streambed slope increases and floodplain areas become narrow. Below Franklin, agricultural and residential land use influences are minimal as the river enters Nanthahala National Forest. Benthic habitat availability changes with geomorphology; cobble riffles occur upstream and bedrock outcrops downstream as streambed slope increases (Table 1). Bedrock outcrops and most cobble riffles are *P. ceratophyllum*-covered, with bare cobble found only at R-1. Depositional areas occur at all stations behind channel obstructions (bedrock shelves)

or in pooled areas. The Little Tennessee River is subject to spates which can increase discharge over five times the mean daily flow for brief periods.

Materials and methods

Relative availability of various habitats was determined at each of the lower nine sampling stations from about 300 measurements of substratum particle size (Wolman, 1954) and presence/absence of *P. ceratophyllum*. Occurrence frequencies of predetermined particle size classes were used as indicators of relative availability of habitats. Specifically, particle sizes represented: < 2 mm depositional areas; > 2 mm < 64 mm pebble/gravel runs; > 64 mm < 256 mm cobble riffles; and > 256 mm boulder/bedrock outcrops (Wolman, 1954). In general, two to three principle habitats were present at each station (Table 1). Habitat availability at the upper two sampling stations (S-1 and S-2) was based on estimations derived from random samples and reported by Huryn & Wallace (1987a).

From July 1991 to May 1992 macroinvertebrate collections were conducted seasonally, except for summer when monthly samples were taken. During sampling, three replicates were collected in principle

habitats at each station; specific collection methods employed depended upon habitat sampled and station location along the continuum. Depositional areas in Ball Creek were sampled to a depth of ≈ 10 cm using a 400-cm² stovepipe corer; in Coweeta Creek and the Little Tennessee River a 232-cm² Eckman dredge was used. Following collection, all depositional samples were repeatedly elutriated through a 250- μ m mesh sieve. Cobble riffles and the pebble/gravel run habitats in Ball Creek and Coweeta Creek were sampled with a 930-cm² Surber sampler fitted with a 250- μ m mesh catchnet. All stones within the sampling frame to a depth of about 10 cm were thoroughly scrubbed clean and attached bryophytes or *P. ceratophyllum* were scraped into the catchnet using a putty knife. Water depths in the Little Tennessee River were too great for Surber sampling; to sample these cobble areas a 250- μ m mesh catchnet was held on the bottom and an upstream stone was dislodged into the catchnet. Substratum immediately under the stone was agitated to a depth of ≈ 10 cm and into the net before bringing stone and net to the surface. *P. ceratophyllum* was scraped into the catchnet and stone dimensions were measured to determine upper surface area. On bedrock outcrops in Ball Creek and Coweeta Creek, collections were made by scraping and brushing material from 100-cm² rockface areas into a 250- μ m mesh catchnet. In the Little Tennessee River, rockface samples were taken with a modified T-sampler (English, 1987) with a sampling area of 103 cm² and fitted with a 250- μ m mesh catchnet. The sampler was firmly pressed against the bedrock such that the *P. ceratophyllum* mat formed an effective seal around the sampler. *P. ceratophyllum* and associated invertebrates inside the sampler were scraped from the bedrock with a putty knife. Material collected from all habitats was preserved with 5–10% formalin containing Phloxine-B dye to aid in sample processing.

In the laboratory, samples were washed through nested 1-mm and 250- μ m mesh testing sieves. Samples containing bryophytes or *P. ceratophyllum* (plant material) were repeatedly agitated in a bucket of water to dislodge invertebrates, and bucket contents were poured through sieves. Plant material was examined at 15 \times magnification to recover any attached invertebrates which were added to sieved material. Material retained on the 1-mm sieve was sorted under 15 \times magnification and all macroinvertebrates removed. Material retained on the

250- μ m sieve was subsampled using a sample splitter (Waters, 1969) and organisms removed under 30 \times magnification.

Plant material from bedrock and cobble samples was washed clean of attached material, dried at 60 °C for 5–7 days to constant weight, ashed at 550 °C for 12 h, and reweighed to determine ash-free dry mass (AFDM). Organic material associated with depositional, pebble/gravel, and bare cobble habitats was treated similarly to determine AFDM of benthic organic matter (BOM).

Identifications of insect and molluscan taxa were generally made to genus (Brigham, Brigham & Gnilka, 1982; Merritt & Cummins, 1984); exceptions were the dipterans Ceratopogonidae, Simuliidae and Chironomidae (identified as Tanypodinae and non-Tanypodinae), and the bivalve Sphaeriidae. In summer and winter chironomids were identified to genus or species for all stations. Because total number of chironomid taxa are based only on two dates, our estimates are undoubtedly conservative. Identifications of other macroinvertebrates were made to class or order. During identification, organisms were counted and total body length was measured to the nearest mm (carapace length was used for decapods). Using predetermined regressions of length-to-weight relationships for collected taxa (Smock, 1980; Huryn, 1986; A. D. Huryn and J. B. Wallace, unpublished data), length measurements were converted to estimates of individual biomass expressed as mg AFDM. To account for differences in area sampled by various collection methods, biomass estimates were standardized to m⁻² basis. Annual standing-stock biomass for each taxon (mg AFDM m⁻²) was computed as the mean of all samples collected in a given habitat-type at each sampling station.

Functional feeding-group designations were generally based on Merritt & Cummins (1984) or Huryn & Wallace (1987b). Exception was the brachycentrid trichopteran *Micrasema* sp.; 50% of its annual standing-stock biomass was ascribed to shredders and 50% to collector-filterers (Brigham *et al.*, 1982; Merritt & Cummins, 1984).

Annual secondary production was estimated using the size frequency method for most taxa collected (Hamilton, 1969) and corrected for cohort production interval (CPI; Benke, 1979). CPIs were estimated by examining relative abundances of size classes for individual taxa across sampling dates. Non-

Tanypodinae chironomid production was estimated using the community-level method (Huryn, 1990), which incorporates thermal regimen into calculations of daily growth rates. To estimate production for Hydracarina, Nematoda, Oligochaeta and Turbellaria, a P/B ratio of 5 was assumed (Benke, 1984). For Cladocera and Ostracoda, a P/B of 10 was used and P/Bs of 0.58 and 18 were assumed, respectively, for Decapoda (Huryn & Wallace, 1987b) and Copepoda (O'Doherty, 1985).

Annual secondary production of the macroinvertebrate community was estimated for individual habitats at each sampling station. For comparisons of habitat-specific production along the continuum, habitats were grouped into three general classes: depositional areas, pebble/gravel and cobble substrata (with or without *P. ceratophyllum*), and bedrock outcrops, all of which supported bryophytes or *P. ceratophyllum*. To determine habitat-weighted production, habitat-specific production estimates were multiplied by the habitat proportions (Table 1) and the products were summed for each sampling station.

To assess longitudinal trends in functional organization along the Ball Creek–Coweeta Creek–Little Tennessee River continuum, optimum-fit regression models were computed for habitat-specific and habitat-weighted production estimates, using \log_{10} of catchment area (km^2 of basin upstream of each sampling station) as the independent variable. Because sampling stations are along a continuum, basin area is an indicator of relative stream size. Trends are reported by the type of optimum-fit regression model (linear, exponential, logarithmic, or quadratic) and coefficient of determination (r^2). Analysis of variance was used to test significance of regression models (Zar, 1984); all regressions were significant ($P < 0.05$) unless otherwise stated. Percent contributions of functional feeding-groups to total production were arcsine-transformed prior to calculating regression models (Zar, 1984). The Pearson product-moment correlation coefficient (r) was used to compare relationships of BOM and plant biomass standing crops to stream size and secondary production estimates (Zar, 1984). Correlations were considered significant at $P < 0.05$.

Results

Organic matter

Standing crops of BOM in depositional habitats ranged from 89 to 1369 g AFDM m^{-2} (Table 2) and

Table 2 Mean standing crops (g AFDM $\text{m}^{-2} \pm 1$ SD) of benthic organic material (BOM) in depositional habitats, and plant biomass (bryophytes and *Podostemum ceratophyllum*) in cobble, pebble/gravel, and bedrock habitats along the Ball Creek–Coweeta Creek–Little Tennessee River continuum. – indicates habitat was not found at that station

Station code	BOM in depositional habitats	Plant material in cobble and pebble/gravel habitats	Plant material in bedrock habitats
S-1	1369 \pm 968	1 \pm 1	64 \pm 38
S-2	446 \pm 472	1 \pm 1	46 \pm 47
S-3	155 \pm 204	< 1	38 \pm 56
M-1	165 \pm 207	< 1	23 \pm 49
M-2	136 \pm 256	0	24 \pm 40
M-3	150 \pm 51	38 \pm 32	–
M-4	132 \pm 35	75 \pm 13	–
M-5	89 \pm 19	0	–
R-1	105 \pm 44	180 \pm 230	–
R-2	230 \pm 106	582 \pm 111	212 \pm 30
R-3	172 \pm 89	–	122 \pm 15

were significantly and negatively correlated to stream size ($r = -0.64$, $n = 11$). Standing crops of plant material on cobble and bedrock substrata were low in the upper stream reaches and significantly increased with increasing stream size (cobble: $r = 0.72$, $n = 9$; bedrock: $r = 0.71$, $n = 7$). No plant biomass was found on pebble/gravel substratum at station M-5 (Table 2). Plant standing crops consisted entirely of bryophytes at stations S-1 to M-2; below M-2 *P. ceratophyllum* accounted entirely for plant standing crop.

Habitat-specific production

Secondary production estimates for depositional habitats ranged from 1 to 7 g AFDM $\text{m}^{-2} \text{yr}^{-1}$ and decreased exponentially with stream size along the continuum ($r^2 = 0.94$). Collector-gatherers were a major component of production in all depositional areas sampled, and shredders provided substantial contributions in the small and middle stream reaches (Table 3). Collector-filterers, scrapers and predators generally contributed little to benthic production in depositional habitats. BOM standing crop was significantly correlated to production at upstream stations S-1 to M-2 ($r = 0.94$, $n = 5$, $P < 0.01$), but no significant correlation was detected for downstream stations M-3 to R-3 ($r = -0.03$, $n = 6$, $P > 0.50$).

Secondary production in cobble and pebble/gravel habitats ranged from 3 to 364 g AFDM $\text{m}^{-2} \text{yr}^{-1}$, with highest production occurring on *P. ceratophyllum*-

Table 3 Secondary production estimates (g AFDM m⁻² yr⁻¹) for benthic macroinvertebrate functional feeding groups associated with depositional habitat along the Ball Creek–Coweeta Creek–Little Tennessee River continuum. Relationship of catchment area (x) to total production best fits the exponential equation: $y = 4.850 \cdot 10^{-0.004x}$ ($r^2 = 0.94$, $n = 11$)

Station code	Scrapers	Shredders	Collector-gatherers	Collector-filterers	Predators	Total
S-1	0.6	2.9	2.0	0.1	1.9	7
S-2	0.2	0.8	2.2	0.2	1.7	5
S-3	0.1	0.4	2.0	0.4	1.1	4
M-1	0.1	1.1	1.4	0.6	1.0	4
M-2	< 0.1	1.2	2.2	0.7	0.6	5
M-3	0.5	3.4	2.6	0.1	0.7	7
M-4	0.2	3.1	1.3	0.1	0.5	5
M-5	0.7	0.1	1.6	0.1	1.3	4
R-1	< 0.1	< 0.1	1.3	0.2	0.1	2
R-2	0.2	0.4	2.0	0.5	0.1	3
R-3	0.1	< 0.1	1.2	0.2	< 0.1	1

Table 4 Secondary production estimates (g AFDM m⁻² yr⁻¹) for benthic macroinvertebrate functional feeding groups associated with pebble/gravel and cobble habitats along the Ball Creek–Coweeta Creek–Little Tennessee River continuum. Estimates for *Podostemum ceratophyllum*-covered and bare cobble at stations M-3 and R-1 are averaged. Relationship of catchment area (x) to total production best fits the linear equation: $y = 4.025x - 3.23$ ($r^2 = 0.94$, $n = 10$)

Station code	Scrapers	Shredders	Collector-gatherers	Collector-filterers	Predators	Total
S-1	0.4	0.9	0.6	0.4	1.0	3
S-2	0.6	0.9	0.7	0.6	0.8	3
S-3	0.6	0.4	0.4	1.1	0.8	3
M-1	0.6	2.1	0.5	0.7	0.6	4
M-2	1.0	1.3	0.7	1.0	0.4	4
M-3	4.5	1.9	2.2	5.7	1.2	15
M-4	5.6	1.2	6.9	15.9	1.1	31
M-5	1.5	0.1	3.8	0.9	0.9	7
R-1	3.3	6.7	12.4	48.0	0.6	71
R-2	18.7	13.8	29.5	280.7	21.1	364

covered cobble at station R-2 (Table 4). Total production per unit area increased linearly with stream size ($r^2 = 0.94$). Contributions of individual functional groups varied along the continuum; shredders and predators provided the greatest proportions upstream, scrapers in the mid-order reaches, and collector-filterers downstream. Collector-gatherers contributed modestly to production on cobble substratum, but accounted for over half of production on pebble/gravel substratum at station M-5.

Production in bedrock habitats ranged from 10 to 168 g AFDM m⁻² yr⁻¹ and increased linearly with stream size ($r^2 = 0.99$). Collector-filterers contributed substantially in both the small-order and river reaches, and collector-gatherers dominated production in the mid-order reach (Table 5). Scrapers, shredders and

predators accounted for little of total production in bedrock outcrop habitats.

Total habitat-specific secondary production was significantly correlated to plant standing-crop biomass in cobble, pebble/gravel and bedrock habitats ($r = 0.96$, $n = 17$, $P < 0.001$). Production estimates for all five functional feeding-groups were also significantly correlated ($n = 17$, $P < 0.001$) to plant biomass (scrapers, $r = 0.84$; shredders, $r = 0.93$; collector-gatherers, $r = 0.91$; collector-filterers: $r = 0.94$; predators: $r = 0.90$).

Habitat-weighted production

Estimates of total habitat-weighted production ranged from 5 to 154 g AFDM m⁻² yr⁻¹ and increased linearly

Table 5 Secondary production estimates (g AFDM m⁻² yr⁻¹) for benthic macroinvertebrate functional feeding groups associated with bedrock habitat along the Ball Creek–Coweeta Creek–Little Tennessee River continuum. Relationship of catchment area (x) to total production best fits the linear equation: $y = 1.4x + 17.0$ ($r^2 = 0.99$, $n = 7$)

Station code	Scrapers	Shredders	Collector-gatherers	Collector-filterers	Predators	Total
S-1	0.2	1.2	4.1	7.4	1.5	14
S-2	0.5	2.6	3.1	21.4	1.6	29
S-3	1.1	0.5	4.0	3.8	1.0	10
M-1	1.3	0.6	6.8	0.9	1.3	11
M-2	0.8	1.3	13.4	4.3	1.4	21
R-2	4.1	3.7	10.8	123.5	1.1	143
R-3	13.3	0.1	12.8	139.7	2.0	168

Table 6 Habitat-weighted, secondary production estimates (g AFDM m⁻² yr⁻¹) for benthic macroinvertebrate functional feeding groups along the Ball Creek–Coweeta Creek–Little Tennessee River continuum. Relationship of catchment area (x) to total production best fits the linear equation: $y = 1.23x + 6.23$ ($r^2 = 0.87$, $n = 11$)

Station code	Scrapers	Shredders	Collector-gatherers	Collector-filterers	Predators	Total
S-1	0.3	1.2	2.8	4.5	1.3	10
S-2	0.5	1.2	1.3	4.1	1.0	8
S-3	0.6	0.4	1.5	1.5	0.9	5
M-1	0.7	1.7	1.7	0.7	0.7	6
M-2	0.9	1.3	1.6	1.1	0.5	5
M-3	4.3	2.0	1.5	3.9	1.3	13
M-4	3.5	1.9	4.8	9.9	0.8	21
M-5	1.4	0.1	3.4	0.8	1.0	7
R-1	1.1	2.4	4.6	13.8	0.2	22
R-2	6.7	5.3	12.8	122.9	6.2	154
R-3	9.6	0.1	9.6	100.6	1.4	121

with stream size along the continuum ($r^2 = 0.86$; Table 6). Habitat-weighted production of scrapers ($r^2 = 0.77$), collector-gatherers ($r^2 = 0.81$) and collector-filterers ($r^2 = 0.89$) also increased linearly down the continuum; however, no significant trends were detected for habitat-weighted shredder ($r^2 = 0.08$, $P > 0.25$) or predator ($r^2 = 0.29$, $P > 0.05$) production.

Contributions of individual taxonomic groups to habitat-weighted production varied along the continuum (Table 7). In upstream reaches scraper production was dominated by ephemeropterans, while both ephemeropterans and coleopterans (Elmidae) accounted for most of scraper production in downstream reaches. Plecopterans were responsible for much of the shredder production along the continuum, with *Tallaperla* generally dominant upstream and *Pteronarcys* downstream. The trichopteran *Micrasema* also contributed substantially to shredder production at several downstream stations (Table 7). Collector-gatherer production was less variable along the

continuum; Chironomidae (Diptera) and the ephemeropterans *Ephemerella* and *Serratella* were primary contributors to gatherer production at all stations. Hydropsychid trichopterans accounted for most of the collector-filterer production at all stations, with *Parapsyche* dominant in upper and *Hydropsyche* in lower portions of the continuum (Table 7). Simuliid dipterans also became a major component of filterer production in mid-order and river reaches. Trends in taxonomic composition were not as evident for predators. Upstream and middle reaches were generally dominated by various genera of Plecoptera, Trichoptera and Diptera, while noninsect taxa contributed to predator production in the downstream reaches (Table 7).

Richness without and with chironomid taxa displayed similar trends along the continuum, with greatest diversity in the mid-order reaches and lower diversity at both the upstream and downstream reaches (Table 8). No positive correlation was detected

Table 7 Contributions of the three dominant taxa in each functional feeding-group to habitat-weighted production at sampling stations along the Ball Creek–Coweeta Creek–Little Tennessee River continuum. Numbers in parentheses indicate percentage contribution of taxa to total production

Sampling station	S-1	S-2	S-3	M-1	M-2	M-3
Scrapers	<i>Stenonema</i> ^a (1) <i>Goerita</i> ^e (1) <i>Neophylax</i> ^e (< 1)	<i>Stenonema</i> ^a (3) <i>Baetis</i> ^a (1) <i>Ectopria</i> ^f (< 1)	<i>Epeorus</i> ^a (4) <i>Baetis</i> ^a (3) <i>Stenonema</i> ^a (3)	<i>Baetis</i> ^a (5) <i>Stenonema</i> ^a (2) <i>Epeorus</i> ^a (2)	<i>Baetis</i> ^a (7) <i>Stenonema</i> ^a (5) <i>Epeorus</i> ^a (2)	<i>Baetis</i> ^a (21) <i>Epeorus</i> ^a (8) <i>Blepharicera</i> ^g (1)
Shredders	<i>Tallaperla</i> ^c (8) <i>Leuctra</i> ^c (1) <i>Pycnopsyche</i> ^e (1)	<i>Tallaperla</i> ^c (11) Decapoda (2) <i>Leuctra</i> ^c (1)	<i>Tallaperla</i> ^c (4) Decapoda (1) <i>Allocapnia</i> ^c (1)	<i>Pteronarcys</i> ^c (23) <i>Tallaperla</i> ^c (6) <i>Allocapnia</i> ^c (1)	<i>Pteronarcys</i> ^c (16) <i>Allocapnia</i> ^c (3) <i>Tallaperla</i> ^c (2)	<i>Pteronarcys</i> ^c (8) <i>Pycnopsyche</i> ^e (4) <i>Tallaperla</i> ^c (1)
Collector-gatherers	<i>Amphinemura</i> ^c (10) <i>Serratella</i> ^a (8) Chironomidae ^g (7)	Chironomidae ^g (5) <i>Serratella</i> ^a (5) Decapoda (2)	Chironomidae ^g (28) <i>Serratella</i> ^a (5) Oligochaeta (3)	Chironomidae ^g (16) <i>Serratella</i> ^a (9) <i>Lype</i> ^e (1)	Chironomidae ^g (13) <i>Antocha</i> ^g (5) <i>Serratella</i> ^a (4)	Chironomidae ^g (7) <i>Eurylophella</i> ^a (2) <i>Serratella</i> ^a (1)
Collector-filterers	<i>Parapsyche</i> ^e (40) <i>Wormaldia</i> ^e (2) <i>Dolophiolodes</i> ^e (1)	<i>Parapsyche</i> ^e (47) <i>Diplectrona</i> ^e (2) <i>Dolophiolodes</i> ^e (2)	<i>Parapsyche</i> ^e (17) <i>Diplectrona</i> ^e (5) Simuliidae ^g (1)	<i>Brachycentrus</i> ^e (3) <i>Dolophiolodes</i> ^e (3) <i>Diplectrona</i> ^e (2)	<i>Hydropsyche</i> ^e (10) Simuliidae ^g (2) <i>Diplectrona</i> ^e (2)	<i>Hydropsyche</i> ^e (18) Simuliidae ^g (4) <i>Dolophiolodes</i> ^e (3)
Predators	<i>Rhyacophila</i> ^a (3) <i>Isoperla</i> ^c (3) <i>Beloneuria</i> ^c (2)	<i>Malirekus</i> ^c (2) <i>Rhyacophila</i> ^a (2) Decapoda (2)	<i>Rhyacophila</i> ^a (3) <i>Isoperla</i> ^c (2) Ceratopogonidae ^g (2)	Ceratopogonidae ^g (3) <i>Malirekus</i> ^c (2) <i>Rhyacophila</i> ^a (2)	<i>Isoperla</i> ^c (2) Ceratopogonidae ^g (1) <i>Maltrekus</i> ^c (1)	<i>Paragnetina</i> ^c (4) <i>Rhyacophila</i> ^a (2) <i>Atherix</i> ^g (1)

^aEphemeroptera, ^bOdonata, ^cPlecoptera, ^dMegaloptera, ^eTrichoptera, ^fColeoptera, ^gDiptera, ^hGastropoda.

Table 7 Continued

Sampling station	M-4	M-5	R-1	R-2	R-3
Scrapers	<i>Promoresia</i> ^f (3) <i>Optioservus</i> ^f (< 1) <i>Elimia</i> ^h (< 1)	<i>Baetis</i> ^a (8) <i>Goera</i> ^e (4) <i>Elimia</i> ^h (2)	<i>Baetis</i> ^a (4) <i>Promoresia</i> ^f (< 1) <i>Stenonema</i> ^a (< 1)	<i>Promoresia</i> ^f (1) <i>Stenonema</i> ^a (< 1) <i>Hydroptila</i> ^e (< 1)	<i>Baetis</i> ^a (7) <i>Promoresia</i> ^f (1) <i>Strophopteryx</i> ^c (< 1)
Shredders	<i>Pteronarcys</i> ^c (6) <i>Micrasema</i> ^e (2) <i>Tipula</i> ^g (< 1)	<i>Taeniopteryx</i> ^c (< 1) <i>Micrasema</i> ^e (< 1) <i>Shipsa</i> ^c (< 1)	<i>Pteronarcys</i> ^c (6) <i>Taeniopteryx</i> ^c (2) <i>Tipula</i> ^g (1)	<i>Pteronarcys</i> ^c (2) <i>Micrasema</i> ^e (1) <i>Tipula</i> ^g (< 1)	<i>Micrasema</i> ^e (< 1) <i>Nectopsyche</i> ^e (< 1) <i>Lepidostoma</i> ^e (< 1)
Collector-gatherers	Chironomidae ^g (12) <i>Ephemerella</i> ^a (10) <i>Serratella</i> ^a (2)	<i>Ephemerella</i> ^a (20) Oligochaeta (15) Chironomidae ^g (7)	Chironomidae ^g (10) <i>Ephemerella</i> ^a (7) <i>Antocha</i> ^g (1)	Chironomidae ^g (4) <i>Ephemerella</i> ^a (1) Oligochaeta (1)	<i>Ephemerella</i> ^a (4) <i>Serratella</i> ^a (2) Chironomidae ^g (1)
Collector-filterers	<i>Hydropsyche</i> ^e (34) <i>Brachycentrus</i> ^e (7) Simuliidae ^g (6)	<i>Hydropsyche</i> ^e (7) Simuliidae ^g (2) <i>Cheumatopsyche</i> ^e (2)	<i>Hydropsyche</i> ^e (31) <i>Cheumatopsyche</i> ^e (19) Simuliidae ^g (10)	<i>Hydropsyche</i> ^e (57) <i>Cheumatopsyche</i> ^e (17) Simuliidae ^g (4)	<i>Hydropsyche</i> ^e (70) <i>Cheumatopsyche</i> ^e (9) Simuliidae ^g (4)
Predators	<i>Isoperla</i> ^c (1) Ceratopogonidae ^g (1) <i>Rhyacophila</i> ^a (1)	Hydracarina (7) <i>Cordulegaster</i> ^b (3) Turbellaria (2)	<i>Atherix</i> ^g (< 1) <i>Hemerodromia</i> ^g (< 1) Ceratopogonidae ^g (< 1)	<i>Corydalus</i> ^d (2) Turbellaria (1) <i>Perlesta</i> ^c (< 1)	<i>Paragnetina</i> ^c (1) <i>Perlesta</i> ^c (< 1) Turbellaria (< 1)

^aEphemeroptera, ^bOdonata, ^cPlecoptera, ^dMegaloptera, ^eTrichoptera, ^fColeoptera, ^gDiptera, ^hGastropoda.

between taxonomic diversity and secondary production; rather, weak negative relationships between habitat-weighted secondary production and richness without ($r = -0.40$, $n = 11$, $P < 0.10$) and with

chironomid taxa ($r = -0.52$, $n = 11$, $P < 0.10$) were noted.

Significant longitudinal trends were detected in percentage contributions of all five functional

Table 8 Number of taxa collected at each site along the Ball Creek–Coweeta Creek–Little Tennessee River continuum and habitat-weighted production at each site

Site	Number of taxa without Chironomidae	Number of taxa with Chironomidae	Habitat-weighted production (g AFDM m ⁻² yr ⁻¹)
S-1	55	83	6
S-2	56	84	8
S-3	73	104	5
M-1	77	110	6
M-2	78	111	5
M-3	106	141	13
M-4	86	114	21
M-5	70	95	7
R-1	72	97	22
R-2	66	86	154
R-3	43	63	121

feeding-groups to total secondary production along the Ball Creek–Coweeta Creek–Little Tennessee River continuum (Fig. 2). Scraper contributions were best represented by a quadratic regression model, with greater percentages in the middle-order reaches than either small-stream or river reaches. Scraper contributions were generally low throughout the continuum, and usually accounted for less than one-quarter of total production, except at station M-5 (Fig. 2). Shredder contributions were also generally low along the continuum, with highest proportions occurring in small-stream and upper middle-order reaches and decreasing exponentially downstream. Proportions of collector-gatherer production also decreased exponentially with increasing stream size, but contributions were generally greater than those of scrapers and shredders. Gatherer percentage of total production was especially high at station M-5 (Fig. 2). Collector-filterers usually accounted for a substantial proportion of secondary production throughout the continuum with contributions increasing linearly with stream size. Conversely, predator contributions were relatively low throughout the continuum and decreased logarithmically as stream size increased (Fig. 2).

Discussion

Habitat-specific production

Secondary production estimates for depositional habitats were negatively correlated to stream size

(Table 3), and significantly correlated to BOM in upstream, but not downstream, reaches of the continuum. This indicates relative differences in availability and stability of BOM in upstream vs. downstream depositional habitats. In the Ball Creek headwaters, depositional areas are generally formed behind structures such as large woody debris and logs (Huryn & Wallace, 1987a). BOM, which is primarily allochthonous, coarse-particulate organic material, is efficiently retained in these habitats (Webster *et al.*, 1994). Thus, headwater depositional areas provide a stable resource base for benthic community production, including much of the shredder production in these systems (Huryn & Wallace, 1987a; Wohl *et al.*, 1995). In contrast to upstream stability, depositional habitats in the lower reaches of Coweeta Creek and the Little Tennessee River occur primarily as pooled areas with fine sand and silt substrata which are susceptible to scouring during spates. BOM, which consists of highly fragmented wood and leaf material distributed within the sand/silt substratum, is more readily entrained than deposited in larger streams (Young, Kovalak & del Signore, 1978). Thus, depositional BOM is neither a stable nor predictable resource for secondary production. Collector-gatherers, represented by non-Tanypodinae chironomids, oligochaetes and small ephemeropterans, dominate production in downstream depositional areas (Table 7). Multivoltine life-cycles and small body sizes enable these taxa to utilize ephemeral BOM resources in fine-grained substrata of these habitats (*sensu* Lugthart & Wallace, 1992).

Cobble and pebble/gravel habitats at the five upper stations and M-5 supported very little plant biomass (Table 2); secondary production estimates in these areas were relatively low and did not exceed 7 g AFDM m⁻² yr⁻¹ (Table 4). Cobble habitats at the other four stations (M-3, M-4, R-1 and R-2) supported large standing crops of *P. ceratophyllum*, and secondary production estimates were much greater, ranging from 15 to 364 g AFDM m⁻² yr⁻¹. Production estimates from bedrock habitats with *P. ceratophyllum* were also greater than for bryophyte-covered bedrock (Table 4).

The presence of *P. ceratophyllum* increases stability of cobble habitats. Plant runners and holdfast structures form a connective matrix which inhibits substratum scouring, and vegetative mats provide refugia and catchnet attachment sites for filter-feeding hydro-psychids (Parker & Voshell, 1983) which dominate

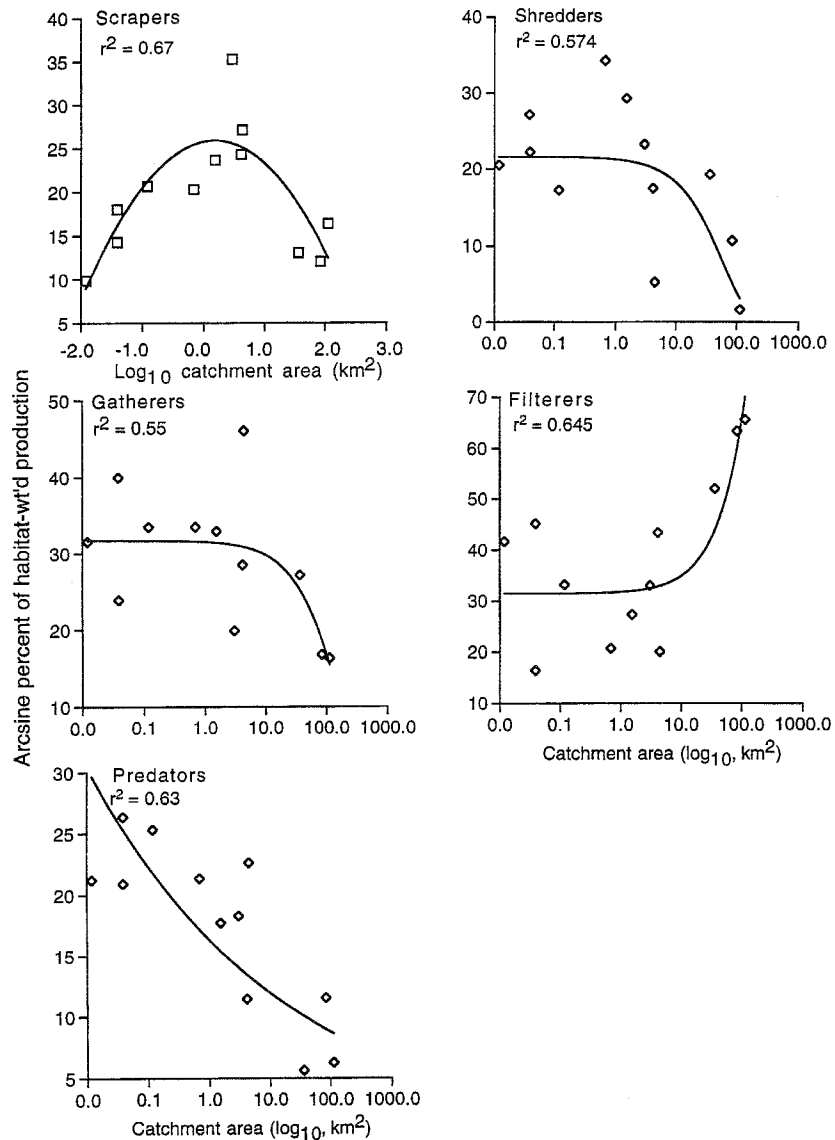


Fig. 2 Relative contributions of functional feeding-groups to habitat-weighted, secondary production of the benthic macroinvertebrate community along the Ball Creek–Coweeta Creek–Little Tennessee River continuum. Contributions are expressed as percentages of total habitat-weighted production at each sampling station, arcsine transformed prior to plotting to obtain a nearly normal distribution (Zar, 1984). Relationships of catchment area (x) to functional feeding-group contributions to total production best fit the following equations: shredders, $y = 21.62 \cdot 10^{-0.007x}$ ($r^2 = 0.57$); collector-gatherers, $y = 31.71 \cdot 10^{-0.003x}$ ($r^2 = 0.55$); collector-filterers, $y = 0.34x + 31.46$ ($r^2 = 0.64$); predators, $y = 16.34x^{-0.123}$ ($r^2 = 0.63$).

production on both plant-covered cobble and bedrock habitats (Table 6). The third dimension to habitat availability provided by *P. ceratophyllum* results in greater standing-stock abundances and biomass of benthic macroinvertebrates per unit area (Grubaugh, Wallace & Houston, 1996), which, in turn, is reflected by greater secondary production. Annual production on cobble at station R-2 was greater than for bedrock habitats which also supported *P. ceratophyllum* (Table 5). This is perhaps due to greater microhabitat heterogeneity of cobble vs. bedrock (Minshall, 1984),

and absence of a hyporheic component to bedrock habitat.

Production for all functional feeding-groups, including scrapers, was positively correlated to plant standing-crop biomass. This contrasts with findings of McAuliffe (1983) for Owl Creek in Montana, where hydrophyte biomass was inversely correlated with scraper colonization. Scrapers in Owl Creek, such as *Leucotrichia pictipes* (Hydroptila: Trichoptera), are sessile in nature and require bare-stone surface areas to support epilithic food resources (McAuliffe, 1983).

In Coweeta Creek and the Little Tennessee River the dominant scraper, *Baetis*, is mobile (McAuliffe, 1983) and better able to utilize patchy distributions of epiphyton and epilithon found on *P. ceratophyllum*-covered substrata.

Intersite comparisons of secondary production

Habitat-weighted secondary production at small-stream and middle stations ranged from 5 to 21 g AFDM m⁻² yr⁻¹ (Table 6) and were similar to other estimates made for southern Appalachian streams by Hury & Wallace (1987a; 8 g AFDM m⁻² yr⁻¹), Lugthart & Wallace (1992; 9–17 g AFDM m⁻² yr⁻¹) and Wohl *et al.* (1995; 7–11 g AFDM m⁻² yr⁻¹). These estimates are also similar to other streams of comparable discharge, as compiled by Benke (1993).

In contrast, habitat-weighted production at Little Tennessee River stations was very high; the estimate at R-2 (154 g AFDM m⁻² yr⁻¹) exceeded all but two studies cited by Benke (1993; the exceptions were Voshell, 1985 and Lazim & Learner, 1986). Most studies reported thus far which estimate community-level benthic production have been conducted in relatively small lotic systems with discharge less than 10 m³ s⁻¹ (Benke, 1993). Production estimates for the Little Tennessee may be more representative of larger-stream and river systems with discharge about 10–30 m³ s⁻¹; additional production studies in other large-stream and river systems are important to test this premise. Also, the presence of *P. ceratophyllum* in this and other systems appears greatly to enhance benthic community production. Grubaugh & Wallace (1995) estimated secondary production on *P. ceratophyllum*-covered bedrock in a Piedmont (U.S.A.) stream to be 182 g AFDM m⁻² yr⁻¹. The highest estimate of benthic production reported to date, 612 g m⁻² yr⁻¹ (Voshell, 1985), was from *P. ceratophyllum*-covered habitat in the New River of West Virginia (U.S.A.).

There is no apparent positive relationship between taxonomic diversity and secondary production among our study sites. High benthic production has been associated with either: (i) organically enriched habitats where a few species dominate production (Lazim & Learner, 1986); or, (ii) habitats where a few collector-filtering taxa contribute most to secondary production (Benke, 1993). This phenomenon appears to be associated with high quantity and quality of food, favour-

able physical conditions, and animals capable of exploiting the resource. High production of collector-filterers and/or collector-gatherers is often associated with lake outflows (Wotton, 1988; Parker & Voshell, 1983; and Voshell, 1985), or shallow, swift-water bedrock habitats with dense plant cover (Grubaugh & Wallace, 1995) similar to that found at downstream sites in the Little Tennessee River. Thus, the absence of a significant positive relationship between total taxa present and secondary production as found among our study sites is not surprising.

Functional organization along a river continuum

According to RCC predictions (Vannote *et al.*, 1980; Minshall *et al.*, 1985), functional organization of the benthic community changes as follows along a river continuum: (i) in the headwaters, the community is dominated by shredders and collector-gatherers, which diminish in importance in middle-order reaches; (ii) in middle reaches, scrapers (grazers) are the dominant component and, in turn, diminish further downstream; and (iii) in higher-order reaches, benthic community composition consists primarily of collector-filterers and sediment burrowers.

Production-based functional organization of the benthic macroinvertebrate community along the Ball Creek–Coweeta Creek–Little Tennessee River continuum generally supported these predictions of the RCC (Fig. 2). Relative contributions to total production made by shredders and collector-gatherers are high in the upper reach of the continuum, and both groups decrease as stream size increases. Scraper contributions, which are highest in the middle reach, decline further downstream. Collector-filterer percentages are relatively low in Ball Creek and upper Coweeta Creek relative to contributions made by the group in lower Coweeta Creek and the Little Tennessee River (Fig. 2).

When comparing functional organization along the Ball Creek–Coweeta Creek–Little Tennessee River continuum to predictions of the RCC, it is important to note that this system is in a temperate climate, with a catchment dominated by deciduous forests, and has steep-gradient headwater reaches. Similar physical conditions occur in the rivers upon which the RCC was originally based (Minshall *et al.*, 1983). Since these physical factors can substantially influence benthic community organization (Brussock, Brown & Dixon, 1985), it follows that systems with similar conditions

will demonstrate similar trends in benthic functional organization. Stream continua in different climates or with different geomorphic structures may not therefore exhibit these predictions of the RCC.

Some aspects of functional organization along the Ball Creek–Coweeta Creek–Little Tennessee River continuum departed from RCC predictions as localized conditions influenced community composition. The greatest contribution of collector–gatherers to total production occurred in the middle of the continuum (station M-5) rather than further upstream (Fig. 2). This stream segment was dominated by pebble/gravel and depositional habitats with no cobble or bedrock to support *P. ceratophyllum* (Table 1). Thus, habitat availability in this segment favoured production of smaller-bodied collector–gatherers such as non-Tanytopodinae chironomids and oligochaetes, while limiting contributions by collector–filterers associated with plant-covered substrata. Also, although some sediment burrowers were present in the Little Tennessee River (bivalves, gastropods and ephemeropterans), they contributed very little to total production in the downstream portion of the continuum. Bedrock outcrop habitat is a dominant feature of the seventh-order Little Tennessee (Table 1), and depositional habitat which supports sediment-burrower production is limited. In other river systems of similar size but with more suitable habitat, such as sediment-covered cobble of the Kanawha River (Kirk & Perry, 1994), sediment burrowers such as *Hexagenia limbata* (Ephemeroptera: Ephemeridae) are the primary component of secondary production.

Predators

RCC predictions either assume predator contributions remain constant along the continuum (Vannote *et al.*, 1980) or exclude them from predictions (Minshall *et al.*, 1985). Along the Ball Creek–Coweeta Creek–Little Tennessee River continuum macroinvertebrate predators are a dynamic component of benthic community functional organization. In Ball Creek and upper Coweeta Creek invertebrate predators account for over 20% of total secondary production; in downstream reaches, however, their contribution is greatly diminished (Fig. 2).

Low-order streams of the Coweeta catchment support limited populations of aquatic vertebrate predators; fish are absent and larval salamanders

account for little of total macrofaunal production (Lugthart & Wallace, 1992). Thus, relatively high contributions to production by invertebrate predators in these streams may reflect limited predation and competition pressures from vertebrates (Lugthart & Wallace, 1992).

In contrast, vertebrate predators such as fishes become an increasingly greater component of the aquatic macrofauna in the downstream reaches of the continuum. Freeman *et al.* (1988) reported ten fish species for Coweeta Creek, and McLarney (1990) found thirty species in the sixth-order reach of the Little Tennessee River and forty-four species in the seventh-order reach. Populations of hellbenders (*Cryptobranchus alleganiensis* Daudin), a large predatory salamander, also occur throughout lower Coweeta Creek and the Little Tennessee River. In these reaches invertebrate predators account for less than 10% of total invertebrate production (Fig. 2). Hildrew, Townsend & Francis (1984) reported similar findings for streams in southern England where proportions of large-insect predators were negatively related to fish numbers, which supports the contention that vertebrate predation influences contribution of invertebrate predators to benthic community structure. It is important to note that collector-filter production, which increases dramatically downstream, is primarily attributable to hydropsychids; Benke & Wallace (1980) and Ross & Wallace (1983) have shown that hydropsychids utilize a large portion of animal material in their diets. Thus, downstream changes in functional organization may reflect either a shift in the mode of invertebrate predation from engulfing to filter-feeding, changes in the influence of vertebrate predators, or a combination of both. To assess adequately the relative importance of invertebrate and vertebrate predation to benthic community functional organization, it is necessary to estimate production of both types of predators within the same system. Presently, such studies are rare.

Little research has been published addressing secondary production in rivers with discharges greater than $10 \text{ m}^3 \text{ s}^{-1}$, or that characterizes production-based patterns of functional organization along stream continua (Benke, 1993). Relative to the headwaters and low-order reaches, production in the large-stream and river reaches of the Ball Creek–Coweeta Creek–Little Tennessee River continuum are highly productive. Further, production in the headwater is dominated

by collector-gatherers and shredders; downstream reaches are increasingly dominated by collector-filterers as stream size increases. Lotic systems become less retentive for organic matter as stream order increases (Young *et al.*, 1978; Minshall *et al.*, 1983; Webster *et al.*, 1994). Shifting of functional composition from groups dependent on retained material (collector-gatherers and shredders) to those that use material entrained in the water column (collector-filterers) indicates the ability of the benthic community to track food-resource availability along the continuum. Huryn & Wallace (1987a), noting a similar pattern between retentive and erosional habitats in the Ball Creek headwaters, hypothesized that retentive habitats such as debris-dam pools were functionally analogous to low-order stream reaches, while erosional habitats supported communities characteristic of higher-order systems. Functional organization of the benthic community along the Ball Creek-Coweeta Creek-Little Tennessee River continuum supports this hypothesis. Differences among substrates imply that local geomorphology, with its concomitant influence on physical and biotic parameters associated with various habitats, strongly influences functional group production along this continuum. Clearly, adequately to characterize invertebrate functional composition along a continuum will require more than cobble-riffle samples within a given stream reach. Furthermore, to assess adequately whole stream production for larger stream reaches will require knowledge of substrate availability, and dynamics of animal populations associated with those substrates over extensive areas. Such data are not easily obtained and will require the development of new techniques and resources.

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