LOCAL GEOMORPHOLOGY AS A DETERMINANT OF MACROFAUNAL PRODUCTION IN A MOUNTAIN STREAM

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Abstract. By comparing distributions of functional group production among different habitats in an Appalachian mountain stream, the influence of site-specific geomorphology upon the overall functional group composition of the animal community was demonstrated. By replicated monthly sampling, substrate particle size distributions, current velocity, standing crops of benthic organic matter, and production of macrofauna were measured in each of three principal habitats: bedrock-outcrop, riffle, and pool. Samples were taken at randomly assigned locations and the relative number of samples taken from each habitat was assumed to be proportional to the area of the habitat within the stream. These proportions were used to weight production measured in each habitat and the resulting values were summed to obtain production per unit area of average stream bed.

The bedrock-outcrop habitat was characterized by high material entrainment and export as indicated by significantly higher current velocities and lower standing crops of detritus compared to the riffle and pool habitats. Pools were sites of low entrainment and high retention of organic matter as demonstrated by significantly lower current velocities and higher accumulations of detritus than other habitats. The riffle habitat was intermediate to the bedrock-outcrop and pool habitats in all parameters measured.

Annual production of collector-filterers was highest in the bedrock-outcrop (ash-free dry mass 1920 mg/m²), followed by riffle (278 mg/m²) and pool (32 mg/m²). Although constituting only 19% of the stream area, the bedrock-outcrop habitat contributed 68% of the habitat-weighted collector-filterer production. Annual production of shredders was highest in pools (2616 mg/m²), followed by riffles (1657 mg/m²) and bedrock-outcrop (579 mg/m²). The pool habitat, constituting 23% of stream area, contributed 36% of shredder production. Annual production of scrapers was highest in the riffle habitat (905 mg/m²), followed by bedrock-outcrop (517 mg/m²) and pool (238 mg/m²). Riffles constituted 58% of total stream area and were the source of 77% of the habitat-weighted scraper production. Annual production of engulfing predators was greatest in the pool habitat (2313 mg/m²), followed by riffles (1765 mg/m²) and bedrock-outcrop (687 mg/m²). The relatively lower production of engulfing predators in the bedrock-outcrop habitat reflects a functional shift in mode of resource acquisition by predators, with predaceous collector-filterers (Arctopsycheae: Trichoptera) predominating in the bedrock-outcrop. Collector-gatherer production was more evenly distributed, with the bedrock-outcrop, riffle, and pool habitats each contributing 14, 54, and 33% to the habitat-weighted production, respectively. Unlike all other functional groups, this distribution was not significantly different from the distribution of stream area among habitats and reflected lack of dependence on specific physical attributes of the local environment for access to food by members of this functional group.

Local geomorphology determined the diversity and spatial distribution of bedrock-outcrops, riffles, and pools in the study stream. In turn, the functional structure of the macrofauna, when viewed holistically, was the result of the integration of the relative contributions of each habitat type of total stream area. Total habitat-weighted annual production in the study stream was estimated at 5093 and 1921 mg/m² for primary and secondary consumers, respectively. The distribution of habitat-weighted production among functional groups was: collector-gatherers (39%), followed by shredders (22%), engulfing predators (22%), scrapers (13%), and collector-filterers (8%). This functional structure agrees favorably with current conceptual models of headwater streams draining forested catchments.

Key words: Appalachian Mountains; detritus; functional group composition; geomorphology; macrofauna; North Carolina; river continuum; secondary production; streams.

INTRODUCTION

The fundamental influence of landscape geomorphology on the structure and function of biotic com-
communities has been recognized for some time (Whittaker 1956, Swanson 1979), and is a theme central to recent conceptual models concerning the biotic zonation of stream continua (e.g., Vannote et al. 1980, Statzner and Higler 1986). However, these latter models tend to view stream segments representative of various locations along a continuum as generally uniform with respect to physical and biotic characteristics. This view, although of obvious heuristic value, obscures localized influences of geomorphology that underlie the diversity and spatial distribution of discrete mesoscale habitats (e.g., snags [woody debris], bedrock outcrops, riffles, pools) within a given stream segment (Brussock et al. 1985).

Mesoscale habitats are defined here as the hierarchical level between stream segments and individual substrate particles. Within a stream segment such habitats may be characterized by distinctly physical environments, and the boundaries between them are often abrupt and well defined. The contrast between physical attributes of mesoscale habitats may influence local depositional processes and consequently may be of great biological significance. For example, habitats with low substrate roughness and rapid current (e.g., bedrock-outcrops) are generally characterized by entrainment and export of materials entering the habitats’ boundaries. Conversely, habitats such as pools formed upstream of debris dams are regions of local deposition and may function as sites of organic matter accumulation (Bilby and Likens 1980). The communities of animals inhabiting these mesoscale habitats must conform functionally to widely different physical environments in order to obtain food resources. Therefore, habitats of great physical contrast may exhibit equally great contrasts in the functional structure of their respective animal communities (Benke et al. 1984). The proportion of stream bottom allocated to different habitats and the diversity of habitats incorporated into a given stream reach are determined by site-specific geomorphological characters, e.g., lithology and relief (Brussock et al. 1985). In turn, the mosaic of mesoscale habitats within a stream, when considered as a whole, determines its overall functional character.

High-gradient streams of the southern Appalachian Mountains are characterized by irregular debris-regulated channels with bedloads dominated by cobbles and boulders (Brussock et al. 1985). This results in stream channels composed of irregular mosaics of bedrock-outcrops, cascades, riffles, and debris-dam pools. These streams provide ideal physical settings to study the influences of geomorphology that underlie the diversity and spatial distribution of discrete mesoscale habitats and the functional structure of their resident animal communities.

Comparative studies addressing functional aspects of animal communities are often dependent upon standing stock abundances or biomass (e.g., Hawkins and Sedell 1981, Gurtz and Wallace 1984); however, data such as these represent measures of static quantities and give no indication of internal cycling of materials and associated energy flow. Measurements of secondary production account for discrepancies in rate of turnover between animal populations, are more reflective of resource utilization by consumers, and are therefore more appropriate for comparisons of functional group composition of animal communities (Nelson and Scott 1962, Whittaker 1975, Benke et al. 1984, Smock et al. 1985).

By comparing distributions of functional group production among different mesoscale habitats, we will demonstrate that the overall functional structure of the animal community of upper Ball Creek, a first- and second-order Appalachian mountain stream located in western North Carolina, USA, is largely determined by characteristics of site-specific mountain geomorphology.

**STUDY AREA**

Upper Ball Creek drains watershed 27 (WS 27), a high-elevation 38.8-ha catchment located at the Coweeta Hydrologic Laboratory (Macon County, North Carolina). The vegetation of WS 27 is characterized as mixed hardwoods and has remained generally undisturbed except for the chestnut blight (1930–1945) and chronic, partial defoliation of the canopy by the fall cankerworm (Alsophila pometaria [Harris]) during 1969 through 1977 (Swank et al. 1981). Riparian vegetation consists of occasional hemlocks (Tsuga caroliniana Engelmann) and a dense understory of rosebay rhododendron (Rhododendron maximum L.).

The topography of WS 27 is rugged and of high relief with an elevation ranging from 1035 to 1417 m above sea level, and the average gradient of Ball Creek is 28%.

The relatively high elevation of WS 27, its northnortheastern aspect, the seasonally dense forest cover, and intense shading by surrounding ridges combine to produce a perennially cool climate; therefore, Ball Creek accumulates only 2800 to 3300 degree-days/yr (Hyryn 1986). The mean annual precipitation at high-elevation sites within the Coweeta basin may approach 250 cm and is uniformly distributed throughout the year (Swank and Douglass 1977). During the sampling period (July 1983–June 1984) streamflow of Ball Creek was continuous. Stream discharge was 106% that of the 38-yr average (1947–1984) and ranged from 0.01 m³/s on 30 August 1983 to 1.8 m³/s (stormflow) on 13 February 1984. The highest and lowest annual discharges measured since 1949 occurred in 1979 and 1981, respectively (Coweeta Hydrologic Laboratory).

The channel of Ball Creek is a poorly sorted bedrock and cobble–boulder bed, typical for headwater streams of the Appalachian mountain region (Brussock et al. 1985). The channel form is heterogeneous, consisting of bedrock-outcrops, riffles, and pools. The patch size of these principal habitats varies from <1 m of linear stream channel to a maximum of ~2 m (pool), 9 m (riffle), and 30 m (bedrock-outcrop). However, the bedrock-outcrop habitat was generally much less exten-
sive. Woody debris within the stream channel is abundant and forms numerous retentive structures. Within the 500-m segment of Ball Creek studied, 83 debris dams spanning the stream channel were counted and many more partial structures were evident. The average vertical drop of the stream bed associated with these structures was 42 cm/dam (se = 3 cm, N = 83). Dimensions of the stream channel varied with location and discharge, with an average width of 224 cm (se = 2 cm, N = 59) and depth of 2 cm (se = 0.3 cm, N = 59) measured during July 1983, and corresponding values of 308 cm (se = 27 cm, N = 50) and 3 cm (se = 0.2 cm, N = 50) measured during January 1984 (Huryn and Wallace 1985). Stream chemistry and climatic and geological data for WS 27 and the Coweta basin is summarized in Swank and Crossley (in press). A more detailed description of Ball Creek can be found in Huryn (1986).

**Materials and Methods**

**Benthic sampling**

Twenty benthic samples were taken monthly (July 1983–June 1984) from randomly assigned locations along a 500-m section of Ball Creek extending upstream from the WS 27 wier. Before sampling, four locations within each 100-m section of the study reach were selected using a random number table. The stream bottom of Ball Creek is a mosaic of three primary habitats: bedrock-outcrop (BO), riffle (R), and pool (PL), and each sample was categorized accordingly. Due to differences in local current and substrate characteristics, three methods of sampling were utilized depending upon habitat. In pools a 400-cm$^2$ coring device was used. In riffles, a 930-cm$^2$ Surber Sampler (mesh = 230 µm) was employed. For areas of moss-covered outcrops of bedrock (BO), a 232-cm$^2$ area of moss was removed with a stiff brush, and the loosened material was washed into the Surber Sampler. At each location, samples were taken as close to the center of the stream as possible. Due to the coarse nature of the substrate material and fluctuating wetted perimeter, the margins of the stream were poorly developed and midstream samples were assumed to be representative of the entire stream. Prior to disturbance of each sample area, current velocity was measured at three locations using a Gessner bag meter (Gessner 1950) and a visual estimate of percent composition of substrate by particle size was made following the modified Wentworth scale (Cummins 1962). All samples were preserved in a 6–8% formalin solution containing a small amount of phloxine B dye.

Animals were removed from the coarse fraction (material retained by a 1-mm$^2$ sieve) of the samples by hand picking under 15× magnification. The fine fractions were subsampled ($\frac{1}{10}$ to $\frac{1}{5}$ of original sample) with a sample splitter (Waters 1969), and invertebrates were removed as above. A more detailed account of the sampling procedure is provided by Huryn and Wallace (1985).

**Production**

For the Trichoptera, larval ash-free dry mass (AFDM) was usually measured for a minimum of five individuals of the dominant instars present in each set of monthly samples (Huryn 1986); however, insufficient material occasionally necessitated the use of fewer specimens. For remaining taxa (see Appendix for list), individual AFDM for selected length classes of each taxon was estimated using significant ($P < .05$) least-squares regressions of log-transformed AFDM (in milligrams) on log body-length (in millimetres). The equations used are given in Huryn (1986). Specimens used for weighing were selected from formalin-preserved samples, dried (55°C) for 24 h, then desiccated (over CaCO$_3$) for an additional 24 h. Dried specimens were weighed to the nearest microgram (Cahn 23 Electrobalance) or 0.01 mg (Mettler H51) to obtain dry mass,ashed (490°C) for 1 h, then reweighed to obtain AFDM. For each sample, standing stock biomass was calculated as the sum of the products of abundance and AFDM for each length class (or instar) present and converted to milligrams AFDM per square metre.

In most cases production was calculated by the size-frequency method (Waters and Hokenstrom 1980) and corrected for the cohort production interval (CPI) (Benke 1979). Cohort production intervals were estimated from individual-length frequency histograms constructed for each series of monthly samples (Huryn 1986). The method of Kreuger and Martin (1980) was used to obtain 95% confidence intervals for size-frequency production estimates.

The presence of numerous taxa and overlapping cohorts in the non-tanypodine Chironomidae and the complex age structure of the crayfish population (Cambarus bartonii [Fabricius]: Cambaridae) precluded determination of CPI. For these taxa the instantaneous growth method was used to calculate production (Benke 1984). Instantaneous growth rates (IGR) for the non-tanypodine Chironomidae were obtained following the method of Huryn and Wallace (1986). Growth of crayfish was monitored using marked individuals released in Ball Creek. Individual crayfish were marked using a hot brand (Abrahamsson 1965, Huryn 1986). Subsequent recaptures allowed growth to be measured as a linear change in carapace length and IGR's were calculated from changes in AFDM estimated by a carapace length–AFDM regression (Huryn 1986). From the resulting data, IGR's were obtained for a range of crayfish sizes (Huryn 1986).

Production for the Nematoda, Turbellaria, and Oligochaeta were estimated as the product of standing stock biomass and a production to biomass ($P/B$) ratio of 5 (Benke 1984). Production of the Copepoda was estimated by assuming a $P/B$ of 18 (O'Doherty 1985). Since all samples were taken at randomly assigned
locations, the relative numbers of samples taken from BO, R, and PL were assumed to be directly proportional to the area of each habitat within the stream. Production specifically for BO, R, and PL was calculated by combining samples from the respective habitats. Production measured in BO, R, and PL was weighted by each habitat's relative contribution to the stream area and these values were summed to obtain production per square metre of average stream bed.

**Functional group designations**

Five functional feeding groups of animals were recognized collector-gatherers (CG), collector-filterers (CF), shredders (SHR), scrapers (SCR), and engulfing predators (EP). Most functional groups were assigned following Merritt and Cummins (1984) and/or personal observation of the fauna studied (see Appendix). Due to their diverse functional roles (e.g., Momot et al. 1978), crayfish production and standing stocks were divided evenly among the CG, SHR, and EP functional groups. Among vertebrates, only larval and recently transformed adult salamanders (Plethodontidae) occurred in Ball Creek and were assigned to the EP functional group (Appendix, Table A6). Larval plethodontids feed primarily on aquatic insect larvae (W. R. Woodall, Jr. and J. B. Wallace, personal observation).

**Benthic organic matter**

Following removal of macrofauna (animals retained by a 230-μm mesh), the sample material was air-dried and sieved into various sized fractions. Materials retained by a 1-cm² mesh were sorted into the following categories: wood > 1 cm²; leaves > 1 cm²; miscellaneous > 1 cm² (e.g., bark and hemlock cones); and moss. Material passing through the 1-cm² mesh but retained by a 1-mm² mesh was designated coarse particulate organic matter (CPOM) and the fraction passing through the latter mesh was designated fine particulate organic matter (FPOM). Materials of each category were weighed to the nearest 0.01 g and homogenized in a laboratory blender. Subsamples were oven dried (55°) for 24 h, then desiccated (over CaCO₃) for an additional 24 h. Oven-dried subsamples were weighed to obtain dry mass,ashed (490°) for ≈8 h, then reweighed to obtain % AFDM.

**RESULTS AND DISCUSSION**

**Characterization of habitats**

Estimates of the percent composition of each habitat's substrate by particle size class indicated a distinct trend in reduction of substrate particle size, where: BO > R > PL (A. D. Huryn and J. B. Wallace, personal observation). Current velocities differed significantly among habitats (ANOVA, P < .001), with mean velocity measured at 67.8 cm/s in BO, 31.0 cm/s in R, and 7.0 cm/s in PL (Student-Newman-Keuls test, P < .001).
TABLE 2. Total annual secondary production measured for functional groups and primary and secondary consumers in the bedrock-outcrop (BO), riffle (R), and pool (PL) habitats of upper Ball Creek, July 1983–June 1984.

<table>
<thead>
<tr>
<th>Functional group</th>
<th>BO</th>
<th>R</th>
<th>PL</th>
<th>Weighted*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collector-gatherer</td>
<td>2030</td>
<td>2635</td>
<td>4053</td>
<td>2846</td>
</tr>
<tr>
<td>Collector-filterer</td>
<td>1920</td>
<td>278</td>
<td>32</td>
<td>533</td>
</tr>
<tr>
<td>Shredder</td>
<td>579</td>
<td>1657</td>
<td>2616</td>
<td>1673</td>
</tr>
<tr>
<td>Scraper</td>
<td>517</td>
<td>905</td>
<td>238</td>
<td>678</td>
</tr>
<tr>
<td>Engulfing predator</td>
<td>687</td>
<td>1765</td>
<td>2313</td>
<td>1686</td>
</tr>
<tr>
<td>Primary consumer</td>
<td>3197</td>
<td>5419</td>
<td>6929</td>
<td>5344</td>
</tr>
<tr>
<td>Secondary consumer†</td>
<td>2536</td>
<td>1821</td>
<td>2323</td>
<td>2072</td>
</tr>
<tr>
<td>Total</td>
<td>5733</td>
<td>7240</td>
<td>9252</td>
<td>7416</td>
</tr>
</tbody>
</table>

* Production weighted by the proportion of each habitat to total stream area.
† Secondary consumer production includes all engulfing predators and Parapsyche (see Results and Discussion: Habitat-specific Secondary Production and Functional Organization).

of the R habitat was consistently intermediate to the BO and PL habitats (Table 1).

Habitat-specific secondary production and functional organization

On bedrock-outcrops, annual production of primary and secondary consumers (AFDM) was 3197 and 2536 mg/m², respectively, and was ordered among functional groups as follows: CG > CF > EP > SHR > SCR (Table 2). In riffles, annual production of primary and secondary consumers was 5419 and 1821 mg/m², respectively, and was distributed among functional groups in the following order: CG > EP > SHR > SCR > CF (Table 2). Annual production attributed to primary and secondary consumers in pools was 6929 and 2323 mg/m², respectively, and was ordered as follows: CG > SHR > EP > SCR > CF (Table 2).

Of 240 samples taken from Ball Creek during the period of study, 19, 58, and 23% were designated BO, R, and PL, respectively. These values are assumed to be directly proportional to the percent of total stream bottom occupied by each habitat type. Weighted production ($P_w$) was estimated for each functional group using the following formula:

$$P_w = (0.19 \times A) + (0.58 \times B) + (0.23 \times C),$$

where $A$, $B$, and $C$ represent production measured in BO, R, and PL, respectively. If the secondary production of a functional group were equivalent among habitats, then the distribution of each habitat’s proportional contribution to the weighted production of that functional group (e.g., for BO = $0.19 \times P_w$) would be mirrored by the distribution of stream area among habitats. For example, if the annual production of a particular functional group was 100 mg/m² in each habitat, the contributions of BO, R, and PL to weighted production in Ball Creek would be 19, 58, and 23 mg, respectively. In this example the distributions of the proportional contribution of each habitat to weighted production and the proportion of stream area occupied by each habitat would be identical. Differences in levels of functional group production among habitats are manifested as departures from the distribution of stream area among habitats (cf. Figs. 1–2).

The proportional contributions of each habitat to the weighted production of the CF, SHR, SCR, and EP functional groups exhibited significant departures from the distribution of stream area among habitats ($\chi^2$ goodness of fit, $P < .05$, Fig. 1). The productivity of the collector–filterers was highest in the BO habitat, undoubtedly subsidized by the apparently high material entrainment that is characteristic of these sites compared to the R and PL habitats (Table 2, Fig. 1). Similarly, the erosional character of the BO habitat resulted in little accumulation of BOM and coincided with low productivity of the collector–gathers and shredders in these sites (cf. Tables 1 and 2). Productivity of the collector–gathers and shredders was highest in pools and reflects utilization of leaf litter and sediments retained by physical structures within the stream channel (cf. Tables 1 and 2). Although intermediate in terms of BOM standing crops, substrate particle size, and current velocity, riffles were the sites of highest scraper production (Table 2). This phenomenon is undoubtedly related to physical instability of pebble-to-cobble-size particles that comprise much of the substrate of this habitat. Physical instability may contribute to occasional scouring of the particles, thus maintaining surfaces relatively free of mosses (cf. BO) and sediments (cf. PL) and more suitable for the mor-
disflies are members of the CF functional group their
Ross (see Appendix, Table A2). Although both cad-
dis (Banks) and P. car-
contributed by
Parapsyche apicalis
dicted for the BO habitat (Fig. 1). In addition, the BO
production is primarily derived from ingestion of an-
secondary consumer production in the BO habitat was
occupied by a distinct but less diverse assemblage
of engulfing predators compared to the R and PL hab-
was ordered among functional groups as follows:
CG > EP > SHR > SCR > CF (Table 2). It is apparent
that, due to dominance of taxa characterized by low
biomass organisms (e.g., Chironomidae, Copepoda),
conclusions about functional structure of Ball Creek
based on abundances would have greatly overesti-
ated the relative role of CG among the fauna of Ball
Creek (Fig. 3). Functional groups composed of taxa
with comparable life histories (e.g., SHR, EP, CF) gen-
eraly exhibit standing stock biomasses directly pro-
portional to levels of production; however, a discrep-
ancy arises when these are compared to other functional
groups (e.g., CG) dominated by taxa with markedly
different life cycles and P/B ratios (Fig. 3) (cf. Appendix
Table A1–A6). Unlike standing stock, production ac-
counts for discrepancies in rates of material turnover
and is more appropriate in comparing the relative func-
tional roles of animal populations (Benke et al. 1984).
Measurements of the production of animal popu-
lations are sensitive to various life history phenomena,
most notably the CPI (Benke 1979). Cohort production
intervals, specific assumptions used in calculations, and
the annual secondary production and standing stocks
for animal taxa occurring in the BO, R, and PL habitats
of Ball Creek are given in the Appendix (Tables A1–
A6). Other pertinent life history data concerning the
Ball Creek fauna can be obtained from Huryn (1986).

**GENERAL DISCUSSION**

The proportion of a headwater stream channel made
up of a particular habitat type is influenced by climate,
lithology, and relief (Brussock et al. 1985). In the Ap-

![Fig. 2. Comparison of percent of the stream bed comprising each habitat (H) with the percent contribution of each habitat to weighted production of the primary consumers (1°C), secondary consumers (2°C), and total secondary production (T). BO = bedrock-outcrop, R = riffle, PL = pool. Distributions of production do not depart significantly (x², P > .05) from the distribution of stream area among habitats.](image)

![Fig. 3. Relative apportionment of weighted production (P) and standing stock biomass (B) and abundances (A) among animal functional groups. CG = collector-gatherers, CF = collector-filterers, SHR = shredders, SCR = scrapers, EP = engulfing predators.](image)
palachian Mountains, climate and relief are the most variable on a local scale (Whittaker 1956) and should influence habitat type and distribution within streams as well as levels of production within particular habitats (Huryn 1986). The physical characteristics of specific mesoscale habitats determine resource availability and mode of delivery to consumers; therefore, the functional structure of any stream reach is the result of the integration of these phenomena occurring in each of its distinct mesoscale habitats (e.g., BO, R, and PL habitats of Ball Creek). The overall contribution of each habitat type to total stream area will greatly influence the ecosystem efficiency of a stream (sensu Fisher and Likens 1973) when considered holistically.

The influence of functional group production within each mesoscale habitat identified in Ball Creek, upon weighted production is illustrated in Fig. 1. The production of the CG functional group was generally evenly distributed among habitats, reflecting a lack of dependence on specific physical attributes of the local environment for access to trophic resources. However, the CF, SHR, and SCR functional groups are dependent upon specific physical characteristics of their definitive habitats for resource delivery (CF, SHR) or substrate maintenance (SCR). These functional groups exhibited striking specificity to different habitats, and it was the relative proportion of these habitats to total area that lent Ball Creek its functional character (Table 2, Weighted).

Although Ball Creek was spatially diverse in terms of functional composition of its animal community, a consistent level of primary and secondary consumer production occurred throughout the stream (Fig. 2); which suggests some limiting factor(s) (e.g., nutrients, temperature, space; see Benke [1984]) operating at a hierarchical level above that of the mesoscale habitats chosen for study. Weighted secondary production measured for each functional group recognized in Ball Creek indicated a dominance of CG activity (53% of annual primary consumer production, Table 2). Major contributors to CG production were generally the Chiromidae, Copepoda, and Oligochaeta (see Appendix, Table A1). The former two taxa are characterized by high turnover rates (O’Doherty 1985, Huryn and Wallace 1986) which contributed to their high production. Shredders also contributed substantially (31% of annual primary consumer production, Table 2), whereas CF and SCR contributions were substantially smaller. The distribution of weighted production among the functional groups occurring in Ball Creek reflects a primarily allochthonous resource base and agrees well with predictions of the River Continuum Concept (RCC) for headwater streams in forested regions (Vannote et al. 1980, Minshall et al. 1985).

Within a given stream reach, mesoscale regions that are analogous to various sites along the river continuum of Vannote et al. (1980) may be identified. In Ball Creek, the highly retentive PL habitat, dominated by CG and SHR (Table 2), is analogous to the headwater reaches of the RCC (Vannote et al. 1980, Minshall et al. 1985). In contrast, production in the BO habitat is dominated by CG and CF, resulting in a functional structure thought to be characteristic of higher order stream communities (Vannote et al. 1980, Minshall et al. 1985). This contrast between the PL and BO habitats reflects a physical transition from a highly retentive to an erosional environment, requiring adjustment in mode of food acquisition by consumers. Therefore, a shift from the benthos (CG, SHR) to the water column (CF) occurs; a shift which is also predicted, on a much larger scale, between middle order and higher order stream segments along the river continuum. In the RCC, the middle order reaches are predicted to be regions of enhanced SCR activity, generally due to a more open canopy and related increases in periphyton production. In Ball Creek, the R habitat with intermediate current, BOM standing crops, and particle size, exhibited the greatest SCR production, indicating that the production of this functional group is related to aspects of substrate maintenance (e.g., McAuliffe 1983).

Streams are mosaics of habitat types (Hynes 1970, Resh 1977, Benke et al. 1984, Brussock et al. 1985) and each may possess a characteristic community which is functionally structured to exploit the distinct physical characteristics imposed by site-specific geomorphy. Furthermore, the relative proportions of a stream occupied by each of these habitats determine its overall functional character. The unit usually chosen for investigations of stream ecology, the stream segment, obscures relationships operating at an intermediate spatial scale that may be critical in understanding broader concepts applicable to the entire river continuum. Examination and quantification of resource linkages within and between these mesoscale communities may be an appropriate and manageable scale for future investigation of physical and biotic structure and function within stream ecosystems.

Acknowledgments

This work was supported by grants from the National Science Foundation (BSR-8516497 and BSR-8514328), Georgia Power Company, and the Southeastern Forest Experiment Station, U.S.D.A. Forest Service. The authors thank the following individuals for assisting with lab and field work: B. Canamella, I. Goldman, E. Jacubowski, A. Lingle, D. A. Crossley and J. L. Meyer provided helpful criticism and encouragement throughout the study. S. G. Fisher, T. F. Waters, and an anonymous reviewer provided thoughtful commentary on an earlier draft of this paper. We are especially grateful to B. Caldwell and B. Kondratieff for providing names for various mayflies, stoneflies, and midges, and to J. O’Hop for his programming expertise.

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<table>
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<tr>
<th>Taxon</th>
<th>CPI (d)#</th>
<th>Bedrock-outcrop</th>
<th>Rifflle</th>
<th>Pool</th>
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<tbody>
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<td></td>
<td>A</td>
<td>B</td>
<td>P ±1/2 CI</td>
<td>A</td>
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<td>298 3 30 ± 18</td>
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<td>0 0 0 (… …)</td>
<td>30 1 5 ± 2</td>
<td>87 4 15 ± 6</td>
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<td>E 330 2476 161 1112 ± 417</td>
<td>210 10 72 ± 19</td>
<td>24 1 7 ± 5</td>
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<td>199 12 87 ± 67</td>
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<td>21 &lt;1 2 ± 1</td>
<td>0 0 0 (… …)</td>
<td></td>
</tr>
<tr>
<td>Chironomidae§</td>
<td>D … … 12 186 45 689</td>
<td>9668 66 1326</td>
<td>27773 130 2532</td>
<td></td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>… … 934 6 29</td>
<td>3499 77 386</td>
<td>8070 6 29</td>
<td></td>
</tr>
<tr>
<td>Copepod</td>
<td>… … 3116 3 56</td>
<td>15 122 15 272</td>
<td>43814 47 842</td>
<td></td>
</tr>
<tr>
<td>Nematoda</td>
<td>… … 1191 1 6</td>
<td>2363 2 12</td>
<td>7352 7 37</td>
<td></td>
</tr>
<tr>
<td>Decapoda§</td>
<td>… … 0 0 0</td>
<td>5 645 361</td>
<td>8 872 455</td>
<td></td>
</tr>
<tr>
<td>Sum</td>
<td>20879 229 2030</td>
<td>31 159 917 2635</td>
<td>87 642 1098 4053</td>
<td></td>
</tr>
</tbody>
</table>

* E = Ephemeroptera, P = Plecoptera, T = Trichoptera, D = Diptera.
† Confidence intervals for production values were calculated following Kreuger and Martin (1980).
‡ Chironominae exclusive of Tanypodinae.
§ Production estimated by the Instantaneous Growth Method (see Materials and Methods: Production).
¶ Assuming P/B = 18 (O'Doherty 1984).
# CPI = Cohort Production Interval.

TABLE A2. Collector-filterers.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>CPI (d)#</th>
<th>Bedrock-outcrop</th>
<th>Rifflle</th>
<th>Pool</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>P ±1/2 CI</td>
<td>A</td>
</tr>
<tr>
<td>Dolophilodes</td>
<td>T 95</td>
<td>4 &lt;1 2 ± 3</td>
<td>7 &lt;1 6 ± 4</td>
<td>0 0 0 (… …)</td>
</tr>
<tr>
<td>distinctus§</td>
<td>T 279</td>
<td>0 0 0 (… …)</td>
<td>5 &lt;1 3 ± 2</td>
<td>5 &lt;1 1 ± 2</td>
</tr>
<tr>
<td>Wormaldia moesta‡</td>
<td>T 63</td>
<td>3 &lt;1 2 ± 4</td>
<td>2 &lt;1 3 ± 2</td>
<td>0 0 0 (… …)</td>
</tr>
<tr>
<td>W. moesta§</td>
<td>T 269</td>
<td>25 3 15 ± 12</td>
<td>35 5 21 ± 8</td>
<td>21 2 9 ± 9</td>
</tr>
<tr>
<td>Polycentropus</td>
<td>T 332</td>
<td>0 0 0 (… …)</td>
<td>30 1 7 ± 2</td>
<td>33 1 5 ± 3</td>
</tr>
<tr>
<td>maculatus</td>
<td>T 332 112 75 323 ± 200</td>
<td>14 9 23 ± 11</td>
<td>16 2 10 ± 12</td>
<td></td>
</tr>
<tr>
<td>Parapsycha</td>
<td>T 352</td>
<td>169 330 1526 ± 559</td>
<td>11 7 33 ± 33</td>
<td>0 0 0 (… …)</td>
</tr>
<tr>
<td>apanicus</td>
<td>P. cardis T 332 2 &lt;1 2 ± 3</td>
<td>92 34 168 ± 39</td>
<td>12 1 7 ± 8</td>
<td></td>
</tr>
<tr>
<td>Diplectrona modesta</td>
<td>T 332 2 5 47 ± 13</td>
<td>12 1 6 ± 3</td>
<td>0 0 0 (… …)</td>
<td></td>
</tr>
<tr>
<td>Simuliidae</td>
<td>D 180</td>
<td>138 5 47 ± 13</td>
<td>12 1 6 ± 3</td>
<td>0 0 0 (… …)</td>
</tr>
<tr>
<td>Sum</td>
<td>487 414 1920</td>
<td>207 57 278</td>
<td>85 7 32</td>
<td></td>
</tr>
</tbody>
</table>

* T = Trichoptera, D = Diptera.
† See Table A1.
‡ Summer cohort.
§ Winter cohort.
## Table A3. Shredders.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Insect order*</th>
<th>CPI (d)t</th>
<th>Bedrock-outcrop</th>
<th>Rifle</th>
<th>Pool</th>
</tr>
</thead>
<tbody>
<tr>
<td>Allocaopia spp.</td>
<td>P</td>
<td>90</td>
<td>47 1 18 ± 19</td>
<td>90 1 23 ± 22</td>
<td>224 2 44 ± 36</td>
</tr>
<tr>
<td>Leuctra spp.</td>
<td>P</td>
<td>540</td>
<td>213 8 33 ± 13</td>
<td>1327 54 245 ± 41</td>
<td>2821 79 416 ± 30</td>
</tr>
<tr>
<td>Peltoperlidae</td>
<td>P</td>
<td>340</td>
<td>775 48 419 ± 131</td>
<td>481 73 369 ± 116</td>
<td>92 6 32 ± 28</td>
</tr>
<tr>
<td>Pycnotyche genilis</td>
<td>T</td>
<td>275</td>
<td>2 &lt;1 1 ± 3</td>
<td>9 18 138 ± 75</td>
<td>70 17 194 ± 143</td>
</tr>
<tr>
<td>P. sonso</td>
<td>T</td>
<td>299</td>
<td>0 0 0 (…•)</td>
<td>1 16 60 ± 54</td>
<td>4 39 180 ± 228</td>
</tr>
<tr>
<td>Lepidostoma griseum</td>
<td>T</td>
<td>246</td>
<td>0 0 0 (…•)</td>
<td>17 2 12 ± 5</td>
<td>28 7 39 ± 14</td>
</tr>
<tr>
<td>L. lydia</td>
<td>T</td>
<td>241</td>
<td>0 0 0 (…•)</td>
<td>23 2 13 ± 5</td>
<td>50 2 17 ± 37</td>
</tr>
<tr>
<td>Psilota amara</td>
<td>T</td>
<td>335</td>
<td>0 0 0 (…•)</td>
<td>11 10 38 ± 22</td>
<td>21 15 60 ± 46</td>
</tr>
<tr>
<td>Fatigina pele</td>
<td>T</td>
<td>664</td>
<td>0 0 0 (…•)</td>
<td>49 47 173 ± 297</td>
<td>78 63 179 ± 63</td>
</tr>
<tr>
<td>Lipodiopa sp.</td>
<td>D</td>
<td>310</td>
<td>1 &lt;1 2 ± 3</td>
<td>9 2 6 ± 5</td>
<td>10 5 18 ± 12</td>
</tr>
<tr>
<td>Limonia sp.</td>
<td>D</td>
<td>340</td>
<td>1 &lt;1 1 ± 3</td>
<td>6 &lt;1 2 ± 2</td>
<td>0 0 0 (…•)</td>
</tr>
<tr>
<td>Molophilius spp.‡</td>
<td>D</td>
<td>365</td>
<td>0 0 0 (…•)</td>
<td>11 2 7 ± 3</td>
<td>174 20 84 ± 39</td>
</tr>
<tr>
<td>Tipula sp. A</td>
<td>D</td>
<td>310</td>
<td>0 0 0 (…•)</td>
<td>5 43 196 ± 129</td>
<td>23 226 898 ± 523</td>
</tr>
<tr>
<td>Tipula sp. B</td>
<td>D</td>
<td>310</td>
<td>13 21 105 ± 92</td>
<td>2 4 16 ± 11</td>
<td>0 0 0 (…•)</td>
</tr>
<tr>
<td>Decapoda</td>
<td>……</td>
<td>0 0</td>
<td>5 645 361</td>
<td>8 872 455</td>
<td></td>
</tr>
<tr>
<td>Sum</td>
<td></td>
<td>1051</td>
<td>79 579</td>
<td>2045 916 1657</td>
<td>3605 1352 2616</td>
</tr>
</tbody>
</table>

* P = Plecoptera, T = Trichoptera, D = Diptera.
† See Table A1.
‡ Life history unclear; cohort production interval of 365 d assumed.

## Table A4. Scrapers.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Insect order*</th>
<th>CPI (d)t</th>
<th>Bedrock-outcrop</th>
<th>Rifle</th>
<th>Pool</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ameletus cryptostimulus</td>
<td>E</td>
<td>330</td>
<td>3 3 7 ± 11</td>
<td>40 17 78 ± 64</td>
<td>30 10 51 ± 23</td>
</tr>
<tr>
<td>Baeosgus nr. dispar</td>
<td>E</td>
<td>120</td>
<td>84 1 14 ± 12</td>
<td>109 22 43 ± 19</td>
<td>3 &lt;1 4 ± 4</td>
</tr>
<tr>
<td>E. pleuralis</td>
<td>E</td>
<td>240</td>
<td>0 0 0 (…•)</td>
<td>18 8 56 ± 19</td>
<td>0 0 0 (…•)</td>
</tr>
<tr>
<td>Stenacron carolina</td>
<td>E</td>
<td>340</td>
<td>7 &lt;1 0 (…•)</td>
<td>135 17 89 ± 25</td>
<td>89 12 57 ± 38</td>
</tr>
<tr>
<td>Stenomena merrirvanum</td>
<td>E</td>
<td>340</td>
<td>0 0 0 (…•)</td>
<td>34 32 205 ± 43</td>
<td>17 7 45 ± 34</td>
</tr>
<tr>
<td>Leuctrocata sp.</td>
<td>E</td>
<td>330</td>
<td>0 0 0 (…•)</td>
<td>13 5 25 ± 9</td>
<td>3 1 7 ± 6</td>
</tr>
<tr>
<td>Nice sp.</td>
<td>E</td>
<td>270</td>
<td>0 0 0 (…•)</td>
<td>41 4 30 ± 8</td>
<td>0 0 0 (…•)</td>
</tr>
<tr>
<td>Strophopteryx limata</td>
<td>P</td>
<td>180</td>
<td>44 6 71 ± 34</td>
<td>12 1 20 ± 8</td>
<td>0 0 0 (…•)</td>
</tr>
<tr>
<td>Neophylax mitchelli</td>
<td>T</td>
<td>213</td>
<td>222 12 144 ± 115</td>
<td>128 11 141 ± 20</td>
<td>48 2 27 ± 34</td>
</tr>
<tr>
<td>Goeria sensata‡</td>
<td>T</td>
<td>655</td>
<td>288 89 228</td>
<td>0 0 0</td>
<td>0</td>
</tr>
<tr>
<td>Oulimnus laticusculus‡</td>
<td>C</td>
<td>365</td>
<td>24 &lt;1 1 ± 2</td>
<td>70 1 5 ± 2</td>
<td>98 2 7 ± 4</td>
</tr>
<tr>
<td>Ophiocoma australis</td>
<td>C</td>
<td>365</td>
<td>77 4 21 ± 10</td>
<td>82 4 22 ± 5</td>
<td>31 3 12 ± 4</td>
</tr>
<tr>
<td>Ectopia thoracica‡</td>
<td>C</td>
<td>365</td>
<td>0 0 0 (…•)</td>
<td>22 43 110 ± 102</td>
<td>4 3 15 ± 16</td>
</tr>
<tr>
<td>Sum</td>
<td></td>
<td>751</td>
<td>120 517</td>
<td>817 154 905</td>
<td>362 39 238</td>
</tr>
</tbody>
</table>

* E = Ephemeroptera, P = Plecoptera, C = Coleoptera, T = Trichoptera.
† See Table A1.
‡ From Huryn and Wallace (1985).
§ Life history unclear; cohort production interval of 365 d assumed.
### TABLE A5. Engulfing predators: Invertebrata.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>CPI (d)</th>
<th>Bedrock-outcrop</th>
<th>Rifle</th>
<th>Pool</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>P ±½ CI</td>
<td>A</td>
</tr>
<tr>
<td>Beloneuria spp.</td>
<td>P</td>
<td>660</td>
<td>17</td>
<td>6</td>
</tr>
<tr>
<td>Desmognathus spp.</td>
<td>P</td>
<td>300</td>
<td>152</td>
<td>28</td>
</tr>
<tr>
<td>Malirekus hastatus</td>
<td>P</td>
<td>340</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Sveltsa lateralis</td>
<td>P</td>
<td>630</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Lanthis vernalis</td>
<td>O</td>
<td>660</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Rhyacophila carpenteri</td>
<td>T</td>
<td>340</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R. glabberima</td>
<td>T</td>
<td>209</td>
<td>33</td>
<td>3</td>
</tr>
<tr>
<td>R. minora</td>
<td>T</td>
<td>299</td>
<td>2</td>
<td>&lt;1</td>
</tr>
<tr>
<td>R. nigrita</td>
<td>T</td>
<td>340</td>
<td>32</td>
<td>23</td>
</tr>
<tr>
<td>R. torva</td>
<td>T</td>
<td>241</td>
<td>66</td>
<td>42</td>
</tr>
<tr>
<td>Pseudogoaera singularis</td>
<td>T</td>
<td>660</td>
<td>81</td>
<td>11</td>
</tr>
<tr>
<td>Dicranota spp.</td>
<td>D</td>
<td>310</td>
<td>212</td>
<td>4</td>
</tr>
<tr>
<td>Hexatoma sp. A‡</td>
<td>D</td>
<td>365</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>Hexatoma sp. B‡</td>
<td>D</td>
<td>365</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Hexatoma sp. C‡</td>
<td>D</td>
<td>365</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Hexatoma sp. D‡</td>
<td>D</td>
<td>365</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>ar. Pedicia</td>
<td>D</td>
<td>340</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pilaria spp.‡</td>
<td>D</td>
<td>365</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Empididae sp. A</td>
<td>D</td>
<td>340</td>
<td>132</td>
<td>3</td>
</tr>
<tr>
<td>Empididae sp. B</td>
<td>D</td>
<td>340</td>
<td>83</td>
<td>3</td>
</tr>
<tr>
<td>Empididae sp. C‡</td>
<td>D</td>
<td>365</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Dolichopodida</td>
<td>D</td>
<td>300</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td>Ceratopogonidae§</td>
<td>B</td>
<td>365</td>
<td>264</td>
<td>3</td>
</tr>
<tr>
<td>Tanytubidida</td>
<td>D</td>
<td>340</td>
<td>581</td>
<td>6</td>
</tr>
<tr>
<td>Decapoda</td>
<td> </td>
<td> </td>
<td>600</td>
<td>0</td>
</tr>
<tr>
<td>Turbellaria§</td>
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<td> </td>
<td>127</td>
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<tr>
<td>Sum</td>
<td></td>
<td></td>
<td>1806</td>
<td>138</td>
</tr>
</tbody>
</table>

* O = Odonata, P = Plecoptera, T = Trichoptera, D = Diptera.
† See Table A1.
‡ Life history unclear; cohort production interval of 365 d assumed.
§ Assuming P/B = 5 (Benke 1984).


<table>
<thead>
<tr>
<th>Taxon</th>
<th>CPI (d)</th>
<th>Bedrock-outcrop</th>
<th>Rifle</th>
<th>Pool</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A</td>
<td>B</td>
<td>P ±½ CI</td>
<td>A</td>
</tr>
<tr>
<td>Desmognathus spp.</td>
<td>330</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>D. quadramaculatus</td>
<td>600</td>
<td>0</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>Sum</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
</tbody>
</table>

† See Table A1.