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The Exopterygote Insect Community of a Mountain Stream in North Carolina, USA: Life Histories, Production, and Functional Structure

by

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Life histories and production of the Exopterygota inhabiting a first to second order mountain stream in North Carolina, USA, were studied by replicated monthly sampling of three different habitats (BO = boulder-outcrop, R = riffle, PL = pool). Life histories were diverse, ranging from multi-voltine (e.g. *Baetis*) to semi-voltine (e.g. *Leuctra ferruginea*, *Sweltsa lateralis*).

Habitat-weighted annual production was 1862 mg (ash-free dry weight)/m² with > 50% being based on four taxa (of 21 considered): *Serratella* sp. (16%), Peltoperlidae (16%), *Leuctra* spp. (13%), and *Beloneuria* spp. (8%). The Odonata, Ephemeroptera, and Plecoptera contributed 36, 760, and 1066 mg/m² to annual production, respectively. Production was distributed evenly among four functional groups with collector-gatherers, shredders, scrapers, and engulfing-predators contributing 21%, 33%, 23%, and 23%, respectively. Production by functional groups followed broad taxonomic categories with the Ephemeroptera, euholognathous Plecoptera, and systelognathous Plecoptera contributing 93%, 90%, and 92% of the scraper, shredder, and engulfing-predator production, respectively. *Serratella* sp. contributed 77% of the collector-gatherer production.

Annual production by the Exopterygota was greatest in the BO habitat (2056 mg) > R (1981 mg) > PL (951 mg). Production in the BO was attributable to a unique combination of taxa compared with R and PL. Sixty-five percent of the BO production was based on *Serratella* sp., a collector-gatherer. Collector-gatherers constituted only 2% and 8% of PL and R production, respectively. The remainder of the PL and R production was generally distributed evenly among scrapers, shredders, and engulfing-predators.

Comparison of the functional structure of the exopterygote communities of headwaters with higher order streams indicated a shift from a dominance of detritivory to predation. In higher order, low gradient streams characterized by limited stable substrate, the majority of the Exopterygota are unable to use entrained food resources directly, and predation upon the filter-feeding Endopterygota (e.g. Chironomidae) may be the predominant method of feeding.

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INTRODUCTION

Insect communities inhabiting streams of temperate regions are generally dominated by 5 orders: Ephemeroptera, Odonata, Plecoptera, Trichoptera, and Diptera. The first 3 orders are members of the division Exopterygota and are

thus characterized by external wing pads throughout post-embryonic growth and development (Hinton 1963; Daly et al. 1978).

The Exopterygota arose early in insect evolution (Ross et al. 1983) and the long period of coexistence is thought to have facilitated an apparent functional segregation among the stream dwelling orders (Wiggins & Mackay 1978). Whereas the Ephemeroptera appear to be mostly collector-gatherers and scrapers, most Plecoptera are shredders or engulfing-predators (Wiggins & Mackay 1978; cf. Edmunds 1984; Stewart & Harper 1984) although there are a number of exceptions (Edmunds 1984; Harper & Stewart 1984). This functional complementarity suggests that investigations of the ecological roles of these orders in streams should consider the exopterygote community as a whole.

As part of a larger study addressing aspects of secondary production in upper Ball Creek (UBC), a 1st and 2nd order stream located in the southern Appalachian mountains of North Carolina, USA (Huryn 1986), we have obtained life history and production data for 21 exopterygote insect taxa. The objectives of this paper are to: (i) demonstrate the life history patterns of the Ephemeroptera, Odonata, and Plecoptera inhabiting UBC, (ii) present habitat specific secondary production for each taxon and functional group, and (iii) use the above information to suggest factors that influence the functional structure of exopterygote insect communities in stream ecosystems.

STUDY AREA

Upper Ball Creek drains watershed 27 (WS 27) of the Coweeta Hydrologic Laboratory (Macon County, North Carolina). Watershed 27 is a 38.8 hectare reference catchment with a rugged topography ranging from 1035 to 1417 m a.s.l. The vegetation is characterized as a mixed hardwood forest that has remained generally undisturbed. Mean annual precipitation may approach 250 cm and is generally uniformly distributed throughout the year (Swank & Douglass 1977). During the study period, streamflow was continuous with lowest and highest discharges occurring during the early fall and late winter months, respectively. Due to a perennially cool climate, the stream accumulates only 2800 to 3300 degree days/year. The average gradient of UBC is circa 28% and its channel form is heterogeneous and debris regulated, consisting of ca. 19% bedrock-outcrop, 58% riffle, and 23% pool (% total stream bottom) (Huryn 1986). More complete descriptions of UBC are given in Huryn (1986) and Huryn & Wallace (1985). Additional information concerning climate, and geology of WS 27 and the Coweeta basin is given in Swank & Crossley (in press).

MATERIALS AND METHODS

Benthic Sampling

Twenty benthic samples were taken monthly (July 1983 – June 1984) from locations that were randomly assigned along a 500 m section of Ball Creek upstream from the WS 27 weir. To facilitate location of sampling sites, the study reach was marked at 5 m intervals. Three methods of sampling were used depending upon local flow and substrate characteristics: (i) In pools a 400 cm² coring device was used, (ii) in riffle areas, a 930 cm² Surber Sampler (mesh = 230 μ m) was employed, and (iii) in areas of moss-covered bedrock-outcrops, a 232 cm² area of moss was removed with a stiff brush, and the loosened material was washed into the Surber Sampler. All samples were preserved in a 6 to 8% formalin solution containing a small amount of phloxine B dye. A more detailed account of the sampling procedure is given in Huryn & Wallace (1985).

Invertebrates were removed from the coarse fraction (material retained by a 1 mm sieve) of the samples by hand picking under 15X magnification. The fine fractions were subsampled (1/8 to 1/64 of original sample) with a sample splitter (Waters 1969) and invertebrates removed as above.

Life History

For calculation of secondary production by the size-frequency method (Hamilton 1969), knowledge of the cohort production interval (CPI) is mandatory (Benke 1979) and can be adequately determined only through detailed study of the life histories (Waters 1979).

Flight periods of mayflies and stoneflies were monitored by collections (malaise or emergence traps) of adults. Adult Ephemeroptera and Plecoptera were determined by B.C. Kondratieff (Colorado State University, Fort Collins). Larvae were identified by association of larvae with adult collections and by use of current taxonomic literature (e.g. Brigham et al. 1982; Merritt & Cummins 1984). Apparent patterns of voltinism and larval growth were elucidated from length-frequency histograms constructed for each series of monthly benthic samples. Larval lengths were measured from the anterior margin of the head to the terminus of the abdomen.

Production

Larval ash-free dry weight (AFDW) for each taxon was estimated from significant ($p < 0.05$) least-squares regressions of \ln AFDW versus \ln length (Huryn 1986). Specimens were selected to represent every 1 mm length class increment. Weight of larvae within each length class was estimated from the median of the length class boundaries and the appropriate length-weight regression. Larvae used in weighings were selected from formalin preserved samples and dried (55°C) for 24 hr and desiccated (CaCO₃) for an additional 24 hr. Specimens were weighed on a Cahn 23 Electrobalance to the nearest μ g to obtain dry mass and ashed (500°C) for 1 hr and reweighed to obtain AFDW.

Larval production was calculated by the size-frequency method (Hamilton 1969) and corrected for CPI (Benke 1979). CPI's were calculated as the interval in days from peak occurrence of larvae of the smallest size class until onset of emergence. In cases where substantial difference in definitive larval sizes was apparent, the boundaries of the ultimate size class were adjusted in attempt to include the range of mature larval sizes and avoid inflation of production estimates due to an artificially high "times-loss" factor (Waters & Crawford 1973). The method of Kreuger & Martin (1980) was used to obtain 95% CI for the size frequency production estimates.

Since all samples were taken at randomly assigned locations, the resulting mean densities derived from combination of all samples were considered to be proportional to the amount of each habitat within the stream. Habitat-weighted production was obtained by combining all samples and utilizing the grand mean annual density for the various size classes. Production in specific habitat types (BO = bedrock-outcrop, R = riffle, PL = pool) was calculated using samples from the respective substrates.

RESULTS

Life Histories and Functional Assignments

In UBC, exopterygote insects were represented by the Ephemeroptera (10 genera, ca. 12 spp.), Odonata (2 genera, 2 spp.) and Plecoptera (14 genera, ca. 27 spp.). Taxa were assigned to functional groups following Merritt & Cummins (1984) or personal knowledge of the fauna. A complete list of taxa is given in Tables 1 and 2. Functional group assignments are given in Tabel 3.

Table 1. List of Ephemeroptera and Odonata collected from upper Ball Creek (July 1983-June 1984).

Ephemeroptera	Ephemerellidae
Siphonuridae	<i>Serratella</i> sp.
<i>Ameletus cryptostimulus</i> Carle	Leptophlebiidae
Baetidae	<i>Habrophlebia vibrans</i> Needham
<i>Baetis</i> sp.	<i>Paraleptophlebia assimilis</i> (Banks)
Heptageniidae	<i>P. guttata</i> (McDunnough)
<i>Epeorus</i> nr. <i>dispar</i> (Traver)	Odonata
<i>E. pleuralis</i> (Banks)	Cordulegastridae
<i>Leucrocuta</i> sp.	<i>Cordulegaster erronea</i> Hagen ¹
<i>Nixe</i> sp.	Gomphidae
<i>Stenacron carolina</i> (Banks)	<i>Lanthus vernalis</i> Carle
<i>Stenonema meririvulatum</i> Carle	

¹ rare in upper Ball Creek, not treated in present study.

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Ephemeroptera

A well synchronized cohort of *Baetis* (Baetidae) was apparent from January through June (Figure 1A); however, collections throughout the remainder of the year yielded an unpatterned assortment of length classes. During warmer months, the growth and development of *Baetis* was probably rapid relative to the collection schedule which resulted in inability to distinguish cohorts. A similar situation was observed by Wallace & Gurtz (1986) and short developmental periods have been widely reported for various *Baetis* species (Brittain 1982; Humpesch 1979; Ciborowski & Clifford 1983). A conservative CPI representative of the winter cohort (120 d) was utilized in production calculations.

The Heptageniidae, represented by *Epeorus*, *Leucrocuta*, *Nixe*, *Stenacron* and *Stenonema*, was the most generically diverse exopterygote family occurring in UBC. The preceding genera are assigned to the scraper and/or gathering-collector functional groups (Edmunds 1984). In UBC, these taxa were generally observed on mineral surfaces (personal observation) and are considered scrapers.

The life cycle of *E. nr. dispar* could not be interpreted from length-class frequency histograms (Figure 1B); no clear pattern of growth was evident and a CPI of 340 days was assumed. *Epeorus pleuralis* exhibited a synchronized, fast-seasonal (Hynes 1970) life cycle (Figure 1C) which was generally similar to that described for a population in a Kentucky stream (Minshall 1967). She reported that recruitment generally occurred in late September through

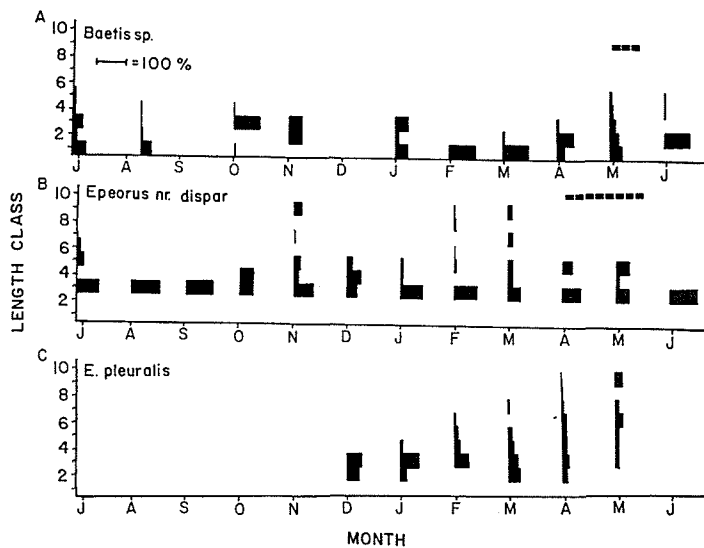


Fig. 1. Monthly length-frequency histograms for: A) *Baetis* sp., B) *Epeorus nr. dispar*, and C) *Epeorus pleuralis* in upper Ball Creek (July 1983-June 1984). Length increment = 1 mm. Width of each bar represents the percentage of total individuals occurring in a given instar. Dashed line indicates flight period.

October. In UBC, the smallest larvae with gills sufficiently developed for determination were first observed in December and it is probable that earlier stages were assigned to *E. nr. dispar*. Assuming that hatching of *E. pleuralis* occurred in October, an appropriate CPI is ca. 240 days.

The life cycles of *Nixe* sp. and *Leucrocuta* sp. followed slow-seasonal patterns (Hynes 1970). *Nixe* emerged during late spring. Early instar larvae were first observed in September (Figure 2A). *Leucrocuta* emerged during early summer and recruitment of larvae commenced by July (Figure 2B).

Stenacron carolina and *Stenonema meririvulanum* were characterized by non-seasonal growth patterns (Hynes 1970) with most larval size classes being present on every collection date (Figures 2C, 3A). The life history of *Stenacron interpunctatum* (Say) was described by McCafferty & Huff (1978) and was found to be complex with as many as 3 cohorts present on a given date. Development times reported by these authors ranged from ca. 86 to 355 days. Univoltine life cycles are thought to be typical for *Stenonema* although bivoltinism has been reported for some species (see Krueger & Cook (1984) for review). Cohort production intervals derived from life history studies of other *Stenonema* species ranged from ca. 150 d for the summer cohort of the bivoltine *S. modestum* (Banks) (Kondratieff & Voshell 1980) to ca. 300 days for *S. vicarium* (Walker) (Krueger & Cook 1984). For both species in UBC, a conservative CPI of 340 was applied in production calculations.

Ameletus cryptostimulus (Siphonuridae) followed a slow-seasonal developmental cycle (Figure 3B). The adult flight period extended from March through

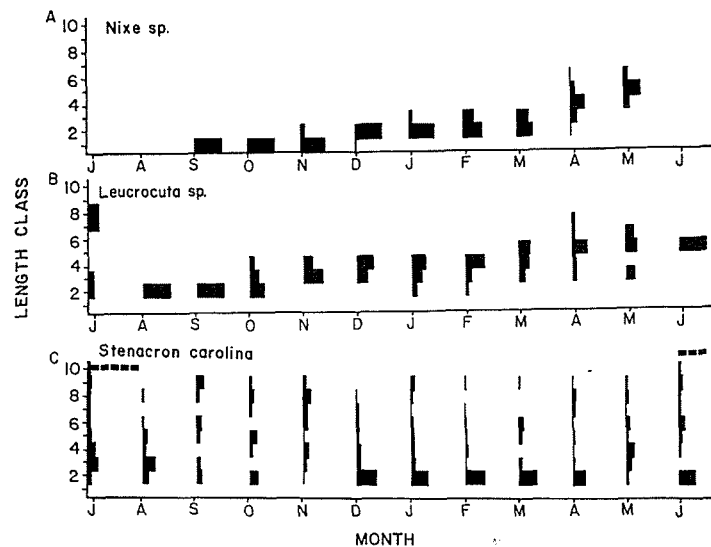


Fig. 2. Monthly length-frequency histograms for: A) *Nixe* sp., B) *Leucrocuta* sp. and, C) *Stenacron carolina* in upper Ball Creek (July 1983-June 1984). Length increment = 1 mm.

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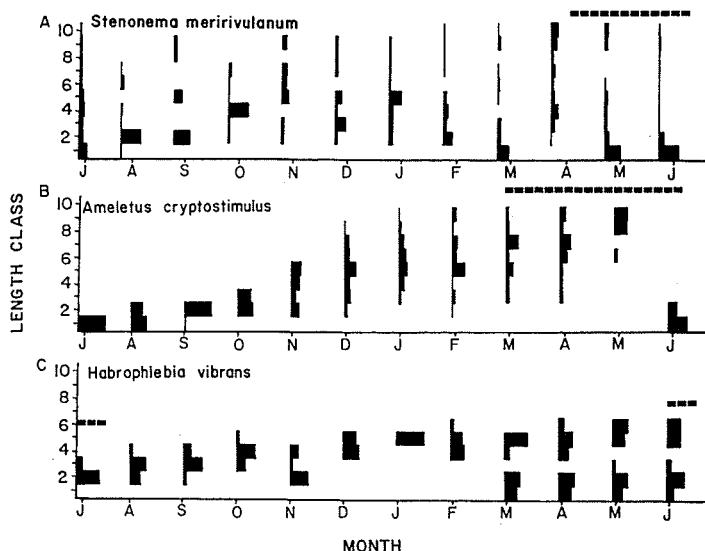


Fig. 3. Monthly length-frequency histograms for: A) *Stenonema meririvulatum*, B) *Ameletus cryptostimulus*, and C) *Habrophlebia vibrans* in upper Ball Creek (July 1983-June 1984). Length increment = 1 mm.

June and early instar larvae were first observed in June. Mackay (1969) and Barton (1980) reported similar life cycles.

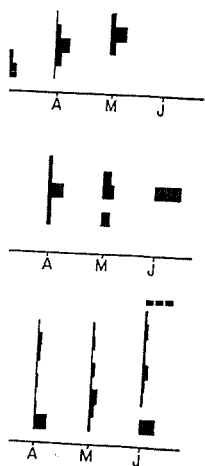
Habrophlebia vibrans (Leptophlebiidae) was semi-voltine with a 16 month life cycle (Figure 3C), markedly longer than the 8 to 12 months estimated by Edmunds et al. (1979). Larvae reached the final length class by February following a period of growth during the late fall and early winter. The adult flight period extended from mid-June through mid-July. Early instar larvae were first observed in March, suggesting a ca. 7-8 month egg diapause.

Paraleptophlebia spp. (Leptophlebiidae) followed a markedly asynchronous slow-seasonal growth pattern (Figure 4A). The slow-seasonal growth pattern is typical for members of the genus (Edmunds et al. 1979) although a 2 month, fast-seasonal pattern was reported by Barton (1980). Early instar larvae reached peak densities during July through September and the final length class was attained by April. The flight period of *P. assimilis* extended from April through August. The flight period of *P. guttata* was restricted to late June.

The growth pattern of *Serratella* sp. (Ephemerellidae) was slow-seasonal with a rapid period of growth occurring during April through June (Figure 4B). Maximum densities of early instar larvae occurred during August through October.

Odonata

Lanthus vernalis (Gomphidae) was semivoltine (Figure 4C), following a pattern



B) *Leucrocuta* sp. and, C) *Leucrocuta* sp. Length increment = 1 mm.

apparently similar to the 2 year cycle reported by Folsom & Manuel (1982). Adults of *L. vernalis* were observed from May through early July and initial larval recruitment occurred in August. Larvae of *Cordulegaster erronea* (Cordulegasteridae) were rare and are not considered further.

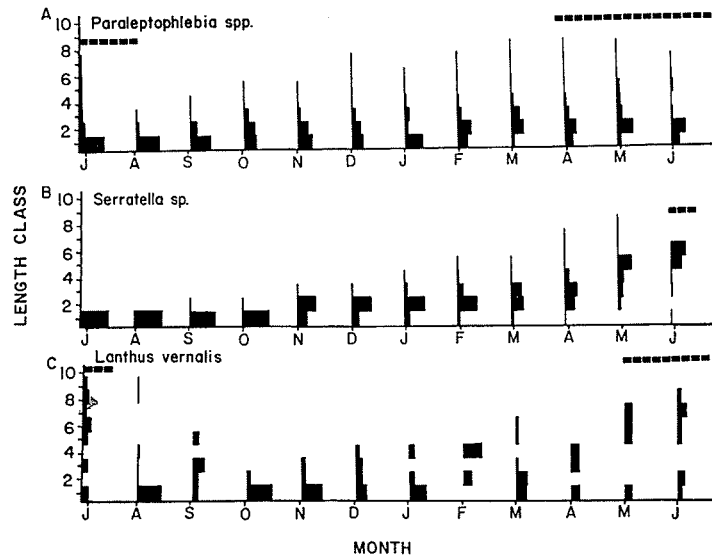


Fig. 4. Monthly length-frequency histograms for: A) *Paraleptophlebia* spp., B) *Serratella* sp., and C) *Lanthus vernalis* in upper Ball Creek (July 1983-June 1984). Length increment = 1 mm (A,B) or 2 mm (C).

Plecoptera

The Nemouridae were represented by *Amphinemura wui* and *Soyedina carolinensis*. *Soyedina* was rare in benthic collections and is not considered further. Two synchronized developmental groups of *Amphinemura* were apparent: i) December - August, and ii) June - March (Figure 5A). *Amphinemura* followed a similar developmental pattern in other Coweeta streams (J.B. Wallace & M. Gurtz, unpublished) and, at present, we are uncertain as to whether two cohorts or one cohort divided into separate developmental groups were involved in forming the observed developmental patterns. Mackay (1969) reported a univoltine, single cohort life cycle for *A. wui*. Harper (1973a) reported a generally similar annual growth pattern to that reported here except each cohort originated from a different species, *Amphinemura delosa* Ricker (October-June) and *Amphinemura linda* Ricker (March-July). Ernst & Stewart (1985) reported a fast-seasonal life cycle for *A. delosa* with emergence in April-May and initial larval recruitment in December.

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Table 2. List of Plecoptera collected from upper Ball Creek (July 1983-June 1984).

Peltoperlidae	Capniidae
<i>Tallaperla maria</i> (Needham & Smith)	<i>Allocaupnia fumosa</i> Ross
<i>Tallaperla anna</i> (Needham & Smith)	<i>A. stannardi</i> Ross
<i>Viehopera ada</i> (Needham & Smith)	
Taeniopterygidae	Perlidae
<i>Strophopteryx limata</i> (Frison)	<i>Beloneuria georgiana</i> (Banks)
Nemouridae	<i>B. stewarti</i> Stark & Szczytko
<i>Amphinemura wui</i> (Claassen)	<i>Eccoptura xanthenes</i> (Newman) ¹
<i>Soyedina carolinensis</i> (Claassen) ¹	
Leuctridae	Perlodidae
<i>Leuctra biloba</i> Claassen	<i>Isoperla holochlora</i> (Klapalek)
<i>L. carolinensis</i> Claassen	<i>I. orata</i> Frison
<i>L. ferruginea</i> (Walker)	<i>I. similis</i> "complex"
<i>L. grandis</i> Banks	<i>Malirekus hastatus</i> (Banks)
<i>L. mitchellensis</i> Hanson	<i>Oconoperla innubilis</i> (Needham & Claassen) ¹
<i>L. monticola</i> Hanson	
<i>L. sibleyi</i> Claassen	Chloroperlidae
<i>L. triloba</i> Claassen	<i>Alloperla usa</i> Ricker
	<i>Sweltsa lateralis</i> (Banks)
	<i>Sweltsa nanina</i> (Banks)

¹ rare in upper Ball Creek, not treated in present study.

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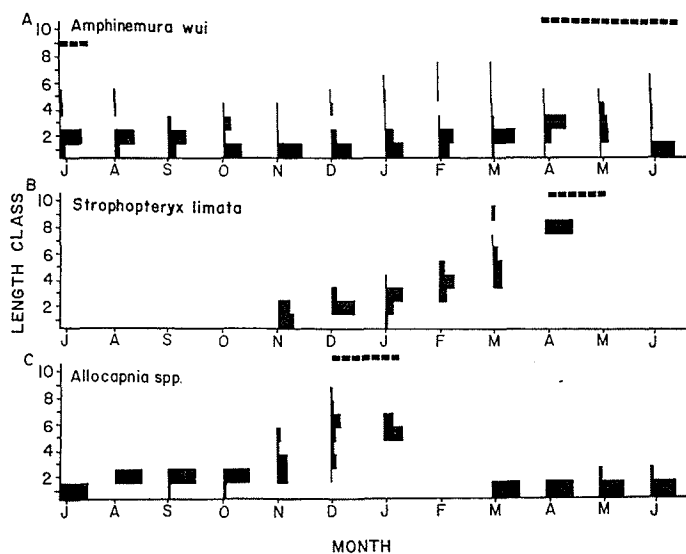


Fig. 5. Monthly length-frequency histograms for: A) *Amphinemura wui*, B) *Strophopteryx limata*, and C) *Allocaupnia* spp. in upper Ball Creek (July 1983-June 1984). Length increment = 1 mm.

Strophopteryx limata (Taeniopterygidae) followed a fast-seasonal growth pattern. Early instar larvae were first observed in November. Growth was slow through early winter followed by rapid growth from February until emergence in April (Figure 5B). A long period of larval diapause (April–November) has been reported for *Strophopteryx fasciata* (Burmeister) by Harper & Hynes (1970).

Early instar larvae of *Allocapnia* spp. (Capniidae) were first observed in March. During July and August, larvae were found in the characteristic posture of diapause (Harper & Hynes 1970). Rapid growth commenced in November and emergence occurred during December and January (Figure 5C). The growth pattern reported here is similar to that reported for *Allocapnia rickerti* Ricker by Ernst & Stewart (1985). A CPI of 90 days (period of active growth) was applied to estimate *Allocapnia* production (Figure 5C).

At least 8 species of *Leuctra* (Leuctridae) were present (Table 2). Based on emergence records, *L. biloba*, *L. ferruginea* and *L. triloba*, were most abundant with peak emergence periods during April–May, July–August, and October–November, respectively (Figure 8). *Leuctra ferruginea* was, by far, the most abundant adult leuctrid collected in emergence traps (Figure 8). Although species determination of larval specimens is currently unfeasible, the length-frequency histogram of *Leuctra* spp. is dominated by 2 well synchronized cohorts of a semi-voltine taxon with a mid-summer emergence (Figure 6A) which are assumed to be *L. ferruginea*. Although some larval growth prior to emergence times of *L. biloba* and *L. triloba* is apparent, overall growth patterns are obscured (Figure 6A). Harper (1973a) described a 1 to 2 year life cycle for a population of *L. ferruginea* and Harper (1973a) and Ernst & Stewart (1985) reported a fast-seasonal life cycle for *Leuctra tenuis* (Walker). Although *Leuctra* spp. other than *L. ferruginea* in UBC may be univoltine, a conservative CPI of 540 d was used to calculate production for the genus as a whole.

The Peltoperlidae followed a semi-voltine life cycle similar to that described by O'Hop et al. (1984) for populations in other Coweeta streams (Figure 6B) (CPI = 540 days). Genera were indistinguishable in their early instars and all taxa combined exhibited a synchronized growth pattern; hence, a single production estimate was made for the family as a whole.

Isoperla spp. (Perlodidae) followed a slow-seasonal growth pattern (Figure 6C). Possible confusion of early instars with other perlodid and perlid taxa, the potential presence of 2 or more species, and extended hatching, resulted in a poorly synchronized apparent growth pattern with larvae of the smallest size classes being present on all sampling dates (Figure 6C). Mackay (1969) reported well synchronized, but temporally offset growth patterns for *I. similis* and *I. holochlora* which, if combined, would yield a pattern similar to that described here. Harper (1973b), Kreuger & Cook (1981), Barton (1982) and Jop & Szczytko (1984) all report slow-seasonal growth patterns for various *Isoperla* species. The flight period of *I. holochlora* extended from mid-July through mid-August. Adult *Isoperla orata* were collected only in mid-June. The flight

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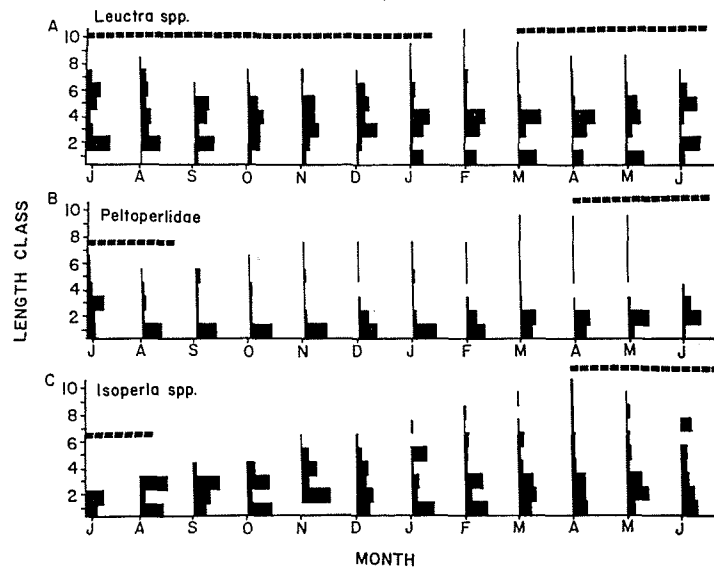


Fig. 6. Monthly length-frequency histograms for: A) *Leuctra* spp., B) *Peltoperlidae*, and C) *Isoperla* spp., in upper Ball Creek (July 1983-June 1984). Length increment = 1 mm.

period of *I. similis* complex was longer, from mid-April through mid-July. The extended flight period of the *I. similis* complex indicates a CPI substantially less than one year and 300 d was considered representative.

Malirekus hastatus (Perlodidae) followed a clearly synchronous slow-seasonal growth pattern (Figure 7A) (CPI = 340 days). Early instar larvae were observed in June with little growth occurring until December. Steady and relatively rapid growth was observed from December through May. The adult flight period extended from early June through July.

Beloneuria spp. (Perlidae) followed an apparent semi-voltine life cycle (Figure 7b). Semivoltinism has been reported for many perlid species (Harper 1973b; Barton 1982; Ernst & Stewart 1985) and Unzicker & McCaskill (1982) report a semi-voltine life cycle for *Beloneuria*. We assume that *Beloneuria* followed a 2 year life cycle with a CPI of 660 d.

Sweltsa lateralis was by far the most numerous chloroperlid (Table 2) and the life history described here is probably most applicable to this taxon. *Sweltsa* followed a clearly synchronous 2-year life cycle (Figure 7C) (CPI = 630 days). Early instar larvae were observed in August and September and both cohorts grew slowly throughout the year. Two year life cycles are typical for *Sweltsa* spp. (Harper 1973b; Cushman et al. 1977).

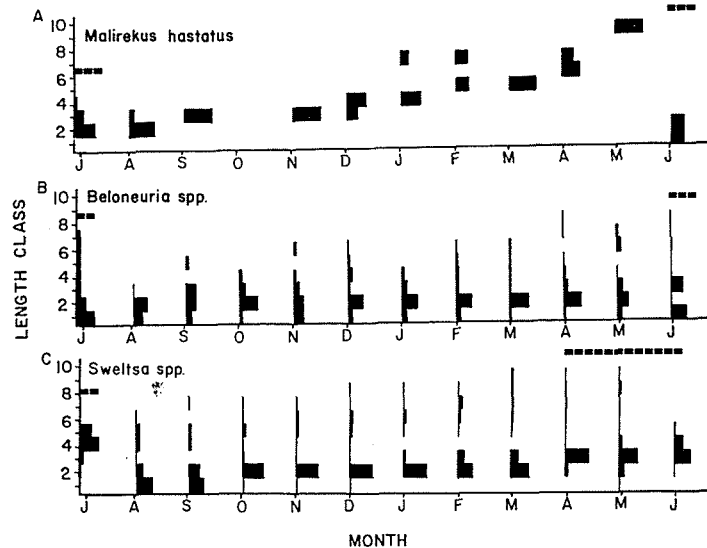


Fig. 7. Monthly length-frequency histograms for: A) *Malirekus hastatus*, B) *Beloneuria* spp., and C) *Sweltsa* spp. in upper Ball Creek (July 1983-June 1984). Length increment = 2 mm (A,B) or 1 mm (C).

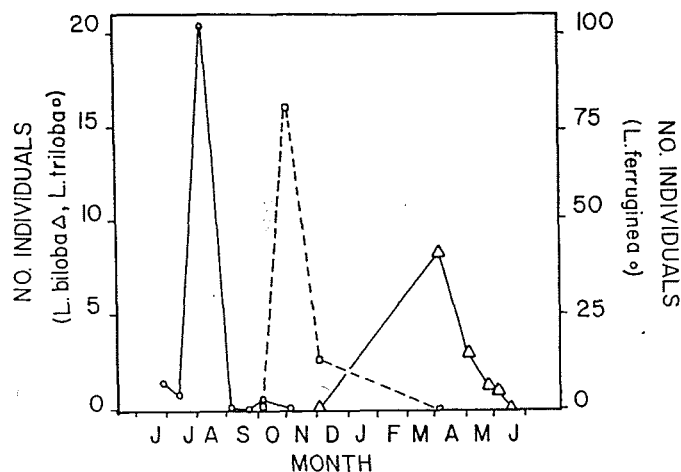


Fig. 8. Emergence phenology of *Leuctra biloba*, *L. ferruginea*, and *L. triloba* in upper Ball Creek at the Coweeta Hydrologic Laboratory, Macon County, NC (June 1983-July 1984). Numbers of individuals reported for each collection date are the average of four 1 m² emergence traps.

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Habitat-weighted production: Taxonomic aspects

Total habitat weighted exopterygote production was 1862 mg AFDW $m^{-2} yr^{-1}$ with a mean standing stock biomass of 338 mg AFDW/ m^2 (Table 3) ($P/B = 5.5$). Fifty three percent of the exopterygote production was attributable to 4 taxa (19% of all taxa considered): *Serratella* sp. (16%), Peltoperlidae (16%), *Leuctra* spp. (13%), and *Beloneuria* (8%). The following taxa constituted an additional 36% of exopterygote production: *Sweltsa* spp. (6%), *Stenonema meririvulatum* (6%), *Amphinemura wui* (4%), *Isoperla* spp. (4%), *Stenacron carolina* (4%), *Paraleptophlebia* spp. (3%), *Ameletus cryptostimulus* (3%), *M. hastatus* (3%), and *Epeorus* nr. *dispar* (3%).

Habitat-weighted annual production for the Ephemeroptera was 760 mg AFDW/ m^2 (41%). Annual production of the Odonata and Plecoptera was 36 (2%) and 1066 (57%) mg/ m^2 , respectively. Mean standing stock biomasses were 112 mg/ m^2 ($P/B = 6.8$), 18 mg/ m^2 ($P/B = 2$) and 208 mg/ m^2 ($P/B = 5.1$) for the Ephemeroptera, Odonata, and Plecoptera, respectively. *Serratella* sp. accounted for 39% of mayfly production and *Stenonema meririvulatum* and *Stenacron carolina* contributed an additional 25%. Peltoperlidae and *Leuctra* spp. constituted 50% of total stonefly production. *Amphinemura wui*, *Beloneuria* spp. and *Sweltsa* spp. contributed an additional 32%. The major contributors to exopterygote production were characterized by high densities and standing stocks but generally slow-seasonal (e.g. *Serratella*) or semi-voltine life cycles (e.g. Peltoperlidae, *Leuctra*, *Beloneuria*, *Sweltsa*).

All tissue losses due to cast exuviae were not accounted for and probably rendered production estimates conservative. During development, Ephemeroptera, Odonata, and Plecoptera may undergo numerous molts (as many as 23 and 50 reported for taxa within the Plecoptera and Ephemeroptera, respectively (Hynes 1976; Brittain 1982)) and losses as cast exuviae may represent more than 40% of total production (Sweeney 1978).

Production to biomass ratios generally followed patterns reflecting assigned CPI's and fell within ranges cited by Waters (1977) for a series of aquatic invertebrates. Exceptions include *E. nr. dispar*, *Paraleptophlebia* spp. and *Isoperla* spp. (Table 3). In these 3 cases, the P/B is reflective of the number of size classes selected (e.g. the "times loss" factor of Hamilton (1969) which may have been artificially high due to variation in size of mature larvae (Waters & Crawford 1973). The unusually high P/B of *Serratella* sp. and the Peltoperlidae is related to the rapid growth near completion of the life cycle (Figures 4B, 6B) that resulted in low annual standing stock biomass yet relatively high production.

Habitat-specific production: Taxonomic aspects

Exopterygote production (mg AFDW $m^{-2} yr^{-1}$) was greatest in the BO habitat (2056 mg) > R (1981 mg) > PL (951 mg) (Table 4). Ninety-five percent of the BO exopterygote production was attributable to *Serratella* sp., Peltoperlidae, *Isoperla* spp., *Amphinemura wui* and *Strophopteryx limata*. *Serratella* sp. alone

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contributed 60% to exopterygote production in the BO. Only 30 and 16% of production was attributable to this combination of taxa in the R and PL habitats, respectively. *Serratella* sp. was the only exopterygote taxon considered to be restricted to the BO (cf. Table 4). The relatively high production of Peltoperlidae in the BO was due to large numbers of early instars (e.g. although peltoperlid production was essentially equal in the BO and R (Table 4), mean annual densities in the BO were 970 ± 610 (\pm SD, $n = 46$) versus 500 ± 428 individuals/ m^2 in R ($n = 127$)).

In the R habitat, production was more evenly distributed among taxa. The 5 most productive taxa (Peltoperlidae, *Leuctra* spp., *Beloneuria* spp., *Sweltsa* spp., and *Stenonema meririvulanum*) were responsible for only 55% of the total. The Heptageniidae dominated ephemeropteran production in riffles with *Epeorus* spp. and *Nixe* sp. occurring exclusively in the R habitat while production of *Stenonema meririvulanum* and *Leucrocuta* sp. was significantly higher in the R versus BO or PL. Only *Stenacron carolina* showed no significant difference in production between R and PL. *Stenacron* has been shown to prefer regions of lower current than *Stenonema* (Lamp & Britt 1981). Production of *M. hastatus* was similarly restricted to the R habitat. Relative levels of production of *Lanthus vernalis*, *Ameletus cryptostimulus*, *Baetis* sp., *Leuctra* spp., and *Sweltsa* spp. were similar among the R and PL (Table 4).

Of the 5 major contributors in the R and PL, *Leuctra* spp. and *Sweltsa* spp. were common to both habitats. *Leuctra* spp., *Sweltsa* spp., *Stenacron carolina*, *Lanthus vernalis* and *Ameletus cryptostimulus* accounted for 73% of total PL exopterygote production. *Leuctra* spp. alone contributed 42% to exopterygote production in the PL. In the BO and R habitats, 2 and 29% of production were attributed to this combination of taxa, respectively. Apparently no exopterygote taxa were restricted to the PL habitat.

Habitat-weighted production: Functional aspects

Habitat-weighted exopterygote primary (collector-gatherers, shredders, scrapers) and secondary (engulfing-predators = EP) consumer production was 1441 (77%) and 421 (23%) mg AFDM $m^{-2} yr^{-1}$, respectively. Shredders (SHR), collector-gatherers (CG), and scrapers (SCR) contributed 627 (33%), 388 (21%), and 426 (23%) mg, respectively. Substrate-weighted production was distributed remarkably evenly among the 4 recognized functional categories (Figure 10).

The distribution of production among the various functional groups followed broad taxonomic categories. The Ephemeroptera, euholognathous Plecoptera, and systelognathous Plecoptera contributed 93%, 90%, and 92% of the SCR, SHR and EP production, respectively (Figure 9). Collector-gatherer production was attributable to *Amphinemura wui* (23%) and *Serratella* spp. (77%).

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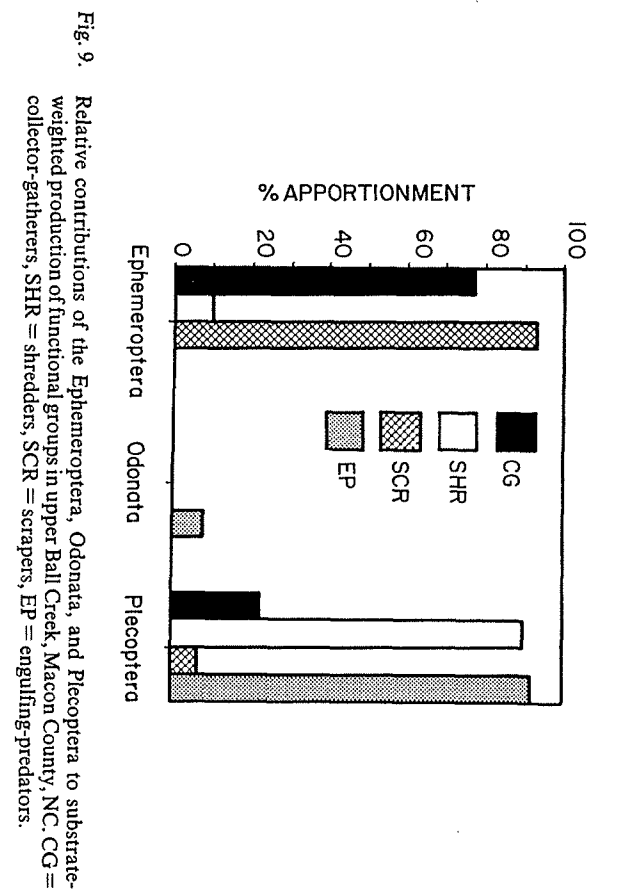


Fig. 9. Relative contributions of the Ephemeroptera, Odonata, and Plecoptera to substrate-weighted production of functional groups in upper Ball Creek, Macon County, NC. CG = collector-gatherers, SHR = shredders, SCR = scrapers, EP = engulfing-predators.

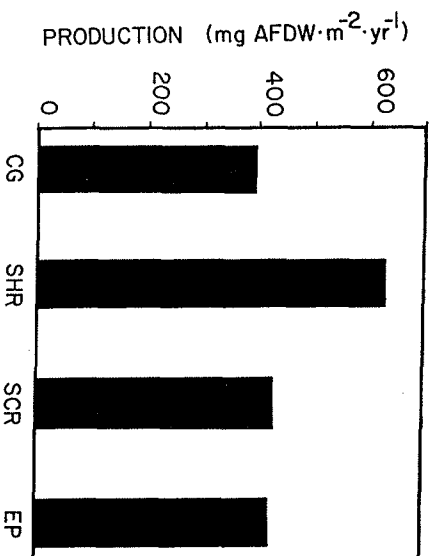


Fig. 10. Apportionment of habitat-weighted exopterygote insect production among functional groups in upper Ball Creek. CG = collector-gatherers, SHR = shredders, SCR = scrapers, EP = engulfing-predators.

30 and 16% of the R and PL axon considered production of (e.g. although Table 4), mean is 500 ± 428 individuals. The 5 long taxa. The 5 p., *Swelusa* spp., of the total. The les with *Epeorus* e production of higher in the R ant difference in prefer regions of n of *M. hastatus* iction of *Lantlus* 'welsa' spp. were and *Swelusa* spp. *macron carolina*, 73% of total PL to exopterygote production were tly no exoptery-

shredders, scra- lution was 1441 redders (SHR), 627 (33%), 388 production was ional categories groups followed ous Plecoptera, 2% of the SCR, atherer produc- i spp. (77%).

Habitat-specific production: Functional aspects

Exopterygote production in the BO habitat was primarily attributable to CG's (64%) (Figure 11). Collector-gatherers contributed only 2% and 8% to PL and R production, respectively. In contrast to the BO and PL habitats, the R habitat exhibited a more even apportionment of production between the 4 functional categories (CG = 8%, SHR = 36%, SCR = 30%, EP = 26%) (Figure 11). Unlike both BO and R, production in PL was strongly skewed toward SHR production (SHR = 55%).

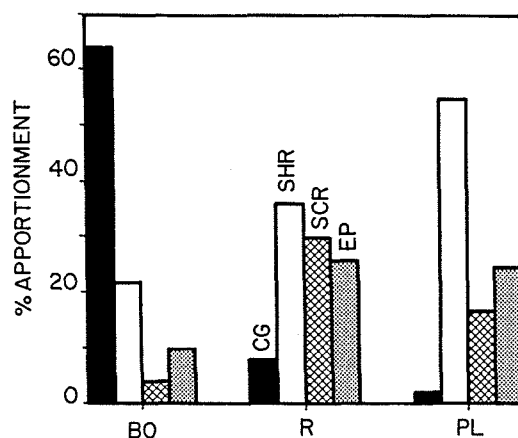


Fig. 11. Apportionment of habitat-specific exopterygote insect production among functional groups in upper Ball Creek. CG = collector-gatherers, SHR = shredders, SCR = scrapers, EP = engulfing-predators.

DISCUSSION

In the oligotrophic UBC, annual production levels of individual exopterygote insect taxa fell within the low range of those reported in the literature; the majority being less than 500 mg AFDW $m^{-2} yr^{-1}$ (Waters 1977; Neves 1979, Short & Ward 1980; MacFarlane & Waters 1982; Kreuger & Waters 1983; Mortensen & Simonsen 1983; Benke et al. 1984; Jop & Szczytko 1984; O'Hop et al. 1984; Smock et al. 1985; Wallace & Gurtz 1986). In more enriched systems, the range of production is considerably higher. Estimates for annual production of single ephemeropteran taxa range up to 8600 mg DW/ m^2 for *Trichorythodes atratus* McDunnough (Ephemeroptera) in Minnesota (Hall et al. 1980). The highest reported levels of lotic odonate and plecopteran annual production are 1800 mg DW/ m^2 of snag surface reported for *Neurocordulia molesta* (Walsh) (Corduliidae) in the Satilla River (Benke et al. 1984) and 2100 mg DW for *Stenoperla prasina* (Newman) (Eustheniidae) in New Zealand (Winterbourn 1974), respectively. Low nutrient availability combined with shading and cool climate are

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probably the primary factors limiting production in UBC (e.g. Wallace & Gurtz 1986).

We are aware of no comprehensive studies treating secondary production in a headwater mountain stream similar to UBC. However, estimates of the annual production of exopterygote communities inhabiting cobble riffles of 2nd order streams in Massachusetts ($2592\text{--}2927\text{ mg DW/m}^2 = \text{ca. } 2333\text{--}2634\text{ mg AFDW}$ (Neves 1979)) and Minnesota ($9020\text{--}15620\text{ mg WW/m}^2 = \text{ca. } 812\text{--}1406\text{ mg AFDW}$ (Kreuger & Waters 1983)) are comparable to that found in UBC (1920 mg AFDW/m^2).

Macroinvertebrate production estimates for all major effective habitats (*sensu* Resh 1977) of a stream segment have been reported only for southeastern USA Coastal Plain blackwater streams: Cedar Creek (SC) (Smock et al. 1985) and the Satilla River (GA) (Benke et al. 1984). Substrate-weighted exopterygote annual production for the second order, headwater Cedar Creek was 522 mg DW/m^2 (mean of 3 sites; calculated from data of Smock et al. 1985) of which 88% and 12% was attributable to the Ephemeroptera and Odonata, respectively. For the Satilla River, Benke et al. (1984) reported total annual substrate weighted production of the exopterygote fauna as 231 mg DW/m^2 (mean of 2 sites; calculated from data of Benke et al. 1984) of which 18%, 21%, and 60% was contributed by the Ephemeroptera, Plecoptera and Odonata, respectively. Substrate weighted exopterygote production in these 2 coastal blackwater streams is substantially lower than that of upper Ball Creek (1920 mg AFDW). This disparity is related, in part, to a low proportion of stable substrate in the Coastal Plain streams in the form of snags (Benke et al. 1984; Wallace & Benke 1984; Smock et al. 1985) which greatly reduces their contribution to weighted estimates.

Indirectly, production levels are influenced by temperature, nutrients, food quality (Benke 1984; Sweeney et al. 1986), and factors contributing to mortality (e.g. predation, disease). However, the relative proportions of effective habitat also influence the overall production of a stream reach (Resh 1977; Benke et al. 1984; Huryn 1986). In order to obtain resources, animal communities characteristic of specific habitats (e.g. BO, PL, R) may be specifically adapted to exploit the habitat's physical characteristics. This has been demonstrated for the trichopteran community of UBC (Huryn 1986); however, adaptive constraints of the Exopterygota have apparently reduced their relative access to all major habitat types.

The relatively high production of the Exopterygota in the BO habitat was attributable to CG production which far exceeded that measured in other habitats (Figure 11). In the BO, characterized as shallow channels of water flowing over moss-covered bedrock-outcrops, collector-gatherers feed upon fine particulate organic materials (FPOM) intercepted by the moss matrix. Although standing stocks of FPOM are generally low in the BO habitat (ca. $7.6 \pm 7.5\text{ mg AFDW/m}^2$ (\pm SD), Huryn 1986), annual turnover rates can be high (6X is a conservative estimate, Huryn 1986) which would support the levels of

CG production observed. Additional factors, such as higher levels of autochthonous primary production within the BO habitat compared with other habitats (Webster et al. 1983) and coprophagy (e.g. Fisher & Gray 1983) within the moss matrix, probably also play important roles.

Scraper production was highest in the R habitat and was primarily due to the heptageniid mayflies. In the R habitat, substrate particle surfaces are continually scoured by combined action of water current and physical instability of substrate particles which deters moss growth compared with the more physically stable BO habitat (e.g. McAuliffe 1983). The morpho-behavioral adaptations of the heptageniid mayflies in UBC are highly suited to function upon these scoured surfaces. The presence of moss in the BO habitat and the accumulation of fine sediments and organic materials in the PL may functionally exclude these mayflies. In contrast to such erosional factors thought to enhance heptageniid production, the formation of leaf packs among larger mineral particles of the R habitat during fall and winter (Huryn 1986) probably supported plecopteran SHR production which exceeded that of other habitats.

Pools upstream of debris dams are important in regulating release of particulate organic matter (POM) (Bilby & Likens 1980). In contrast to the erosive and highly entraining character of the BO (and to a lesser degree, the R habitat), the PL habitats in upper Ball Creek are sites of local deposition and seasonal storage of POM (Huryn 1986). Production by Exopterygota in the PL habitat was dominated by shredding Plecoptera, e.g. *Leuctra* and Peltoperlidae, which coincides with high POM retention (Huryn 1986). However, PL production was < 50% of that estimated for the BO and R habitats. In contrast, Trichoptera and Chironomidae (Diptera) inhabiting the PL habitat exhibited levels of production similar to or exceeding those of the BO and R habitats (Huryn 1986). The relatively higher production by Trichoptera and Chironomidae in pools may be related to the evolution of tubular cases and retreats which allows efficient regulation of water currents over respiratory surfaces (e.g. Wiggins 1977); the absence of such adaptation among the plecopteran taxa of UBC may reduce their ability to function in the PL habitat.

Functional groups of Ephemeroptera and Plecoptera followed broad taxonomic groups as noted by Wiggins & Mackay (1978). The Ephemeroptera contributed most of the CG (Ephemerellidae) and SCR (Heptageniidae) production while the euholognathous and systelognathous Plecoptera contributed most of the SHR and EP production (Figure 10). In UBC, the major exopterygote orders present a diverse but functionally complementary assemblage which may be related to a long coevolutionary history (Wiggins & Mackay 1978).

In stream habitats characterized by material entrainment, the major endopterygote insect orders (Trichoptera, Diptera) have evolved various adaptations based on silk production which allow them to filter-feed (Wiggins & Mackay 1978; Wallace & Merritt 1980). Conversely, most exopterygote groups (e.g. all Odonata, Plecoptera; most Ephemeroptera) lack this ability. These feeding adaptations (or lack thereof) should be reflected in community changes

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Taxon

Lanthus
Ameletus
Baetis
E. nr. disp.
E. pleuralis
Leucrocotus
Nixe
Stenacron
Stenonema
Habrophlebia
Paraleptotriton
Serratella
Peltoperla
Leuctra
Allocaenis
Strophopteryx
Amphipetura
Isoperla
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Table 3. Habitat-weighted production of the exopterygote community of upper Ball Creek. Production was calculated by the size-frequency method. The 95% confidence intervals (CI) were calculated following Kreuger & Martin (1980). Production (P) = mg AFDW m⁻² yr⁻¹. Biomass (B) = mg AFDW/m². Abundance (A) = individuals/m². # = total number of specimens examined. FG = functional group, cg = collector gatherer, shr = shredder, scr = scraper, ep = engulfing predator. CPI = cohort production interval.

Taxon	FG	CPI	P	±95% CI	B	A	P/B	#
<i>Lanthus</i>	ep	660	36	17	18	9	2.0	109
<i>Ameletus</i>	scr	330	57	35	13	32	4.5	565
<i>Baetis</i>	scr	120	31	13	2	71	18.7	3253
<i>E. nr. dispar</i>	seccr	340	50	15	6	76	8.7	1452
<i>E. pleuralis</i>	scr	240	35	12	5	10	7.0	181
<i>Leucrocota</i>	scr	330	16	6	3	8	5.1	163
<i>Nixe</i>	scr	270	18	5	3	26	7.1	471
<i>Stenacron</i>	scr	340	73	18	14	113	5.4	1760
<i>Stenonema</i>	scr	340	117	29	22	36	5.3	623
<i>Habrophlebia</i>	shr	480	6	3	2	40	3.9	582
<i>Paraleptophlebia</i>	shr	340	58	9	7	310	8.7	5352
<i>Serratella</i>	cg	330	300	99	38	691	8.0	5026
Peltoperlidae	shr	540	299	73	53	503	5.7	7321
<i>Leuctra</i>	shr	540	237	76	52	1542	4.6	22656
<i>Allocapnia</i>	shr	90	27	11	1	114	27.6	1701
<i>Strophopteryx</i>	scr	180	30	11	2	17	13.1	189
<i>Amphinemura</i>	cg	300	88	49	11	352	8.0	4147
<i>Isoperla</i>	ep	300	75	16	10	175	7.7	2753
<i>Malirekus</i>	ep	340	53	23	9	4	5.8	120
<i>Beloneuria</i>	ep	660	140	70	39	41	3.6	2753
<i>Sweltsa</i>	ep	630	117	43	32	302	3.7	4923
Sum			1862		338	4471	5.5	64122

along a river continuum as the proportion of habitats dominated by entrainment increase (Vannote et al. 1980; Minshall et al. 1983). Although distinctly different stream types, comparison of the exopterygote insect communities of UBC (1st-2nd order, cool-oligotrophic) and Cedar Creek (2nd order, warm-blackwater) (Smock et al. 1985) with that of the middle order (5th-6th, warm-blackwater) Satilla River (Benke et al. 1984) serves to illustrate this shift in function of the invertebrate community.

In UBC and Cedar Creek, ca. 22 and 12% of total habitat weighted annual exopterygote production was contributed by engulfing-predators (e.g. Odonata, systellognathous Plecoptera). However, in the Satilla River ca. 80% of the production of the Exopterygota was contributed by engulfing-predators (Odonata, Plecoptera) and *Stenonema* spp. contributed most of the remaining 20%. Exopterygote production in the headwater streams, UBC and Cedar Creek, is generally attributable to herbivores or detritivores, whereas that of the Satilla River is based on predation. The major resource available to the primary consumers inhabiting snags in the Satilla is entrained FPOM and only that material which is intercepted by or produced autochthonously on snag surfaces

is available to collector-gatherers. Hence, direct access to the continuous supply of sestonic materials is available only to filter-feeding organisms, e.g. Trichoptera and Chironomidae (Benke et al. 1984; Wallace et al. 1987). In the Satilla, collector-filterers are extremely productive (Benke et al. 1984) and apparently support a substantial proportion of EP production among the exopterygote community (e.g. Wallace et al. 1987). Preliminary data from another Coastal Plain river in Georgia, the Ogeechee River (6th order, warm-blackwater), indicates that EP production may exceed 50% of the total exopterygote production (standing stocks from Wallace & Benke 1984; P/B ratios from Benke et al. 1984). The relatively greater levels of exopterygote CG production estimated for the snag habitat in the Ogeechee compared to the Satilla rivers may be related to the ca. 5X greater snag surface area and thus greater overall retentiveness in the Ogeechee (Wallace & Benke 1984). In terms of functional structure, the exopterygote community of the Ogeechee River is intermediate to the headwater streams, UBC and Cedar Creek, and the Satilla River. With the exception of a few mayflies (Edmunds et al. 1976; Wallace & Merritt 1980), the Exopterygota are evolutionarily restricted from direct access to entrained food resources. In larger, low-gradient streams (e.g. > 4th order) with limited stable substrate and

low overall retentiveness, ces by capitalizing on the: these environments the p nated by the engulfing-pr

This research was supported b Georgia Power Company, and Service. The authors thank B. C in the lab and field. Adult Ephr Crossley, J.L. Meyer and an a paper.

Table 4. Production of the exopterygote community measured in specific habitats of upper Ball Creek. Production was calculated by the size-frequency method. The 95% confidence intervals (CI) were calculated following Kreuger & Martin (1980). Production (P) = mg AFDW m⁻² yr⁻¹.

Taxon	Bedrock-Outcrop		Riffle		Pool	
	P	±95% CI	P	±95% CI	P	±95% CI
<i>Lanthus</i>	0	0	30	14	53	37
<i>Ameletus</i>	0	0	79	64	51	23
<i>Baetis</i>	15	12	43	19	4	4
<i>E. nr. dispar</i>	0	0	80	63	0	0
<i>E. pleuralis</i>	0	0	57	19	0	0
<i>Leucrocuta</i>	0	0	25	9	7	6
<i>Nixe</i>	0	0	29	8	0	0
<i>Stenacron</i>	0	0	96	25	62	38
<i>Stenonema</i>	0	0	167	43	44	34
<i>Habrophlebia</i>	0	0	5	2	15	6
<i>Paraleptophlebia</i>	0	0	89	13	30	18
<i>Serratella</i>	1230	417	72	19	7	5
Peltoperlidae	404	131	357	116	30	28
<i>Leuctra</i>	32	13	236	41	44	36
<i>Allocapnia</i>	17	19	23	12	44	36
<i>Strophopteryx</i>	72	34	20	8	0	0
<i>Amphinemura</i>	88	49	89	68	14	10
<i>Isoperla</i>	161	43	65	14	24	12
<i>Malirekus</i>	0	0	91	42	3	7
<i>Beloneuria</i>	37	27	189	86	35	29
<i>Sweltsa</i>	0	0	142	60	127	35
Sum	2056		1981		951	

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low overall retentiveness, the Exopterygota gain indirect access to such resources by capitalizing on the adaptive modes of the filter-feeding Endopterygota. In these environments the production of exopterygote communities will be dominated by the engulfing-predators.

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