Community structure of Trichoptera in a mountain stream: spatial patterns of production and functional organization

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SUMMARY. 1. Annual production was estimated for Trichoptera occurring in each of three distinct habitats of a mountain stream: bedrock-outcrops, riffles and pools. Production was greatest on bedrock-outcrops (2608 mg ash-free dry weight m$^{-2}$), followed by riffles (1038) and pools (950).

2. Annual production in bedrock-outcrops and pools was dominated by single functional groups, with collector-filterers and shredders contributing 73% and 15% of the annual production, respectively. Production in riffles was due primarily to shredders (46%), followed by collector-filterers (27%).

3. Taking account of the amount of stream area occupied by each habitat type, total annual production was estimated at 1336 mg AFDW m$^{-2}$. 53% of this production was attributable to four taxa: Parapsyche cardis Ross (25%), Pycnopsyche gentilis (MacLachlan) (10%), Neophylax mitchelli Carpenter (9%) and Rhyacophila nigrita Banks (9%).

4. Habitat-weighted production was distributed among functional groups as follows: collector-filterers (41%), shredders (29%), engulfing-predators (15%), scrapers (13%) and collector-gatherers (2%).

5. The distinct taxonomic and functional structures of trichopteran sub-communities were shaped by the distinct physical characteristics of their principal habitats. Bedrock-outcrops were characterized by low roughness and high current and were sites of low deposition or organic matter; thus the predominance of collector-filterers. In contrast, the other habitats of greater roughness (riffles) and/or lower current (pools) were sites of deposition of food (e.g. leaf litter) and greatest shredder production.

6. By distinguishing discrete mesoscale habitats, each with a functionally distinct caddisfly sub-community, we speculate that small mountain streams provided the diverse physical templates essential for the evolution of the major feeding tactics (e.g. scraping, shredding, filter-feeding) of the Trichoptera.
Introduction

With the exception of the Chironomidae (Coffman & Ferrington, 1984; Pinder, 1986), stream dwelling Trichoptera are generally represented by more species than are other groups of animals using the same resources (Mackay & Wiggins, 1979). These authors attribute this great ecological diversity to the secretion of silk which is utilized in various ways to enhance exploitation of resources. Among trichopteran genera, all major functional feeding groups are represented and are geographically widespread (Wiggins & Mackay, 1978; Wiggins, 1984); accordingly, the functional composition of communities occurring in different habitats should serve as a general index to food availability and mode of its acquisition.

Although certainly not a new development (Hayes, 1971; also see Statzner & Higler, 1985), a recent trend in stream ecology has been to emphasize the influence of hydraulics and geomorphology (Brussock, Brown & Dixon, 1985; Statzner & Higler, 1985; 1986; Frissel et al., 1986; Huryn & Wallace, 1987). Channel form determines the spatial distribution of physically distinct habitats, e.g. riffle versus pool, and the mode of food delivery, e.g. entrained versus deposited, to their resident consumers (Brussock et al., 1985; Huryn & Wallace, 1987). The remarkable diversity among the Trichoptera should enhance their ability to respond at the community level, taxonomically, and functionally to the physiologically singularities of any given stream.

The objectives of this study were to examine the autecologies of twenty-two species of Trichoptera inhabiting upper Ball Creek, in the southern Appalachian mountains (U.S.A.), and to evaluate the influence of channel form on spatial patterns of community structure, production, and functional organization.

Study area

General description

Upper Ball Creek drains watershed 27 of the Coweeta Hydrologic Laboratory (Macon County, North Carolina, U.S.A.). Watershed 27 is a 38.8 ha reference catchment with a rugged topography ranging from 1085 to 1417 m a.s.l. The vegetation of watershed 27 is a mixed hardwood forest that has remained generally undisturbed. Mean annual precipitation approaches 250 cm and is evenly distributed throughout the year (Swank & Douglass, 1977). During the study, streamflow was continuous with lowest and highest discharges in the early autumn and late winter, respectively. Because of the perennially cool climate, the stream accumulates only 2800–3300 degree days y⁻¹. A more complete description of Ball Creek is given by Huryn & Wallace (1987).

Channel form and principal habitats

The physical characteristics of the major habitats of Ball Creek were treated in detail by Huryn & Wallace (1987). However, the most important features are summarized here. The channel form of Ball Creek is heterogeneous and debris regulated, with about 19% bedrock-outcrop, 58% riffle and 23% pool (% total stream bottom). Current velocities among these principal habitats were significantly different as follows: bedrock-outcrop > riffle > pool (Fig. 1A).

Bedrock-outcrops were characterized by low retention coupled with high entrainment of materials as indicated by significantly lower standing crops of detritus compared to riffles and pools. In contrast, pools were characterized as habitats of relatively high retention and low transport. In terms of benthic organic matter accumulation, riffles were consistently intermediate to the bedrock-outcrops and pools (Fig. 2A).

Materials and Methods

Benthic sampling

Twenty benthic samples were taken monthly (July 1983 to June 1984) from randomly assigned locations along a 500 m section of Ball Creek that extended upstream from the watershed 27 weir. Two methods of sampling were utilized depending upon local flow and substrate characteristics. In pools a 400 cm² coring device was used. In riffle areas and moss-covered bedrock outcrops, a 930 cm² Surber Sampler (mesh=230 μm) was used. All samples were preserved in 6–8% formalin
Comparison of habitat characteristics with production of selected trichopteran functional groups in upper Ball Creek: (A) water velocity, biomass of aquatic mosses and median substrate particle size measured in bedrock-outcrops, riffles and pools. Units of left y-axis are cm s\(^{-1}\) for water velocity and g AFDW m\(^{-2}\) for mosses. Water velocity and moss biomass are from Huryn & Wallace (1987). (B) Annual production (mg AFDW m\(^{-2}\) y\(^{-1}\)) calculated for collector-filterers, scrapers and engulfing-predators.

Life histories and functional feeding group assignment

Flight periods of adult caddisflies were assessed by collecting with malaise or emergence traps. Unless otherwise indicated, larval instars were distinguished from head-width frequency histograms. Seasonal changes in larval instars was assessed by examination of successive samples. Growth patterns were described from plots of larval ash-free dry weight (AFDW) (see below) against time from initial occurrence in the benthic samples. Functional feeding groups were assigned following Wiggins (1984) or personal observation.

Production

Most monthly estimates of larval AFDW were based upon weights of at least five individuals of the dominant instars present. For first instar larvae of several taxa, five larvae were weighed together and the mean weight calculated. Average monthly AFDW was calculated as the sum of the product of each instar's mean AFDW and the instars relative frequency within its respective cohort. Larvae weighed were selected from formalin...
preserved samples, dried (55°C) for 24 h and desiccated (CaCO₃) for an additional 24 h. Dried specimens were weighed to the nearest μg on a Cahn 23 Electrobalance to obtain dry mass, ashed (500°C) for 1 h and reweighed to obtain AFDW.

Larval production was calculated by the size frequency method (Hamilton, 1969) and corrected for cohort production interval (CPI) (Benke, 1979). Cohort production intervals were calculated as the interval in days from the peak occurrence of first instar larvae until the onset of pupation. The method of Kreuger & Martin (1980) was used to obtain 95% CI for size-frequency production estimates. For taxa that spent a disproportionate amount of time in a particular instar, the duration of that stage was subdivided and each division treated as a separate weight class (Benke & Wallace, 1984). Temporal patterns of production (e.g. Fig. 3A-C) were obtained from monthly standing stocks and the instantaneous growth method (Benke, 1984). Growth was assumed to be exponential and growth rates were calculated from changes in average monthly AFDW. Due to low recovery of early instars of Palaegapetes celsus (Ross) (Hydroptilidae), production was calculated for the final instar only using the instantaneous growth method.

Since all samples were taken at randomly assigned locations, the resulting mean standing stocks of all samples combined were assumed to be weighted by the relative amount of each habitat in the stream. Habitat-weighted production was obtained by combining all samples and utilizing the grand mean annual density for the various size classes.

Leaf litter biomass and substrate particle size distributions

Leaf litter (>1 cm²) was removed from samples, air-dried, weighed to nearest 0.01 g and homogenized in a laboratory blender. Subsamples were oven dried (55°C) for 24 h, then desiccated over CaCO₃ for an additional 24 h. Subsamples were then weighed to obtain dry mass, ashed (500°C) for about 8 h, then reweighed to obtain % AFDW. These data were used to demonstrate monthly changes in leaf litter biomass.

Estimates of per cent composition of substrate by particle size was made within the area of each sample unit following Gurtz & Wallace (1984) and was used to estimate median Phi values (Cummins, 1962) for each habitat.

Results

Life histories

Estimation of secondary production by the size-frequency method requires knowledge of the CPI (Benke, 1984) which can be determined by detailed study of life histories. Therefore the following discussion of the life histor-
ies of the Bali Creek trichopteran fauna is an integral part of the production data provided below. A complete list of trichopteran taxa and functional assignments is provided in Table 1. Figures of monthly instar frequency distributions are provided only for those species for which such information is not readily available in the literature.

*Rhyacophila minor*a (Rhyacophilidae) followed a 12-month developmental period as reported by Mackay (1969) and Manuel & Folsom (1982), whereas *Rhyacophila glaberrima* had a short developmental period of about 8 months starting in October. *Rhyacophila torva* had an unusually long adult flight period (February-August) and a long period of continuous recruitment (Fig. 4A). Other *Rhyacophila* studied exhibited shorter flight periods (<2 months). The life cycle of *Rhyacophila nigrita*, the most abundant *Rhyacophila* in the study area, was the most difficult to interpret. First instar larvae were present throughout the year suggesting continuous recruitment from delayed hatching of eggs (e.g. Thut, 1969). *Rhyacophila nigrita* and *Rhyacophila carpenteri*, which was rare, were assumed to be univoltine with CPI of 340 days.

Prepupa and pupae of *Palaegapetes celsus* occurred in May and June, respectively. The flight period extended from early June to July. Development proceeded rapidly with larvae attaining the penultimate instar by late July. All *P. celsus* reached the final larval instar by August and grew steadily until prepupation in May.

Four species of Philopotamidae occurred in upper Ball Creek: *Dolophilodes distinctus*, *D. major*, *D. sisko* and *Wormaldia moesta*. Lar-

### Table 1. Habitat-weighted production measured for Ball Creek Trichoptera. FG = functional group, cg = collector-gatherer, cf = collector-filterer, shr = shredder, scr = scraper, ep = engulfing-predator. CPI = cohort production interval. Production (P) = mg AFDW m$^{-2}$ y$^{-1}$. CL = 95% confidence limit, biomass (B) = mg AFDW m$^{-2}$, abundance (A) = individuals m$^{-2}$.

<table>
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<tr>
<th>Taxon</th>
<th>FG</th>
<th>CPI</th>
<th>P ±CL</th>
<th>B</th>
<th>A</th>
<th>P/B</th>
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<td>4</td>
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<td>3</td>
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<td>&gt;1</td>
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<td>241</td>
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<td>8</td>
<td>2</td>
<td>16</td>
</tr>
<tr>
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<td>39</td>
<td>17</td>
<td>10</td>
<td>14</td>
</tr>
<tr>
<td><em>Psilotreta amena</em> (Ross)</td>
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<td>39</td>
<td>17</td>
<td>10</td>
<td>14</td>
</tr>
<tr>
<td><em>Pseudogotia similis</em> Carpenter</td>
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<td>1009</td>
<td>16</td>
<td>3</td>
<td>2</td>
<td>17</td>
</tr>
<tr>
<td><em>Fartagia pelita</em> (Ross)</td>
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<td>604</td>
<td>112</td>
<td>120</td>
<td>14</td>
<td>40</td>
</tr>
</tbody>
</table>

Sum | 1336 | 272 | 703 |

1 Rate in upper Ball Creek, not considered in the present study. 2 Production calculated by method of instantaneous growth; 'summer cohort'; 'autumn - spring cohort'. 3 Hryyn & Wallace (1985).
FIG. 4. Monthly instar frequency distributions for: (A) *Rhyacophila torva*, (B) *Dolophilodes distinctus*, (C) *Wormaldia moesta*, (D) *Polycentropus maculatus*, (E) *Lype diversa*, (F) *Parapsyche apicula*, and (G) *P. cardis* in upper Ball Creek (July 1983 to June 1984). Instars are designated 1-5. Width of each bar represents the percentage of total individuals (combined from 20 samples m$^{-1}$) occurring in a given instar on each sampling date. Dashed lines indicate flight periods.

Vae of *D. major* occupy regions of underground flow (personal observation), and were encountered rarely. Although adults of *D. sisko* were collected in emergence traps (late July to August), larvae were never distinguished and may have been mis-identified as *D. distinctus*. *Dolophilodes distinctus* was bivoltine (Fig. 4B), with a short summer cohort and a longer autumn-spring cohort. Prepupae, pupae, and adults were collected throughout the spring, summer and winter months. Benke & Wallace (1980) and Ross & Wallace (1983) reported multivoltinism for *D. distinctus*. *Wormaldia moesta* had at least two distinct cohorts (Fig. 4C). Growth of the autumn-spring cohort was rapid during October and November but slower, yet relatively constant, from January to June. Pupae and adults were collected throughout the
winter, spring and summer months. Ross & Wallace (1983) reported three generations y for a population of W. moestus in another Coweta stream.

*Polycentropus maculatus* (Polycentropodidae) was univoltine with first instar larvae appearing in July (Fig. 4D). Growth proceeded rapidly in autumn and spring but was greatly retarded during the winter months. The adult flight period lasted from June to July.

Larvae of *Lype diversa* (Psychomyiidae) are collector-gatherers which construct tubular retreats on wood (Dudley & Anderson, 1982). In Ball Creek, *L. diversa* was univoltine with first instar larvae appearing in July (Fig. 4E). The flight period extended from June to October.

Two hydropsychids, *Diplecetria modesta* and *Parapsycha apicalis*, had univoltine life cycles (e.g. Fig. 4F) as did most *Parapsycha cardis* (Fig. 4G). However, a small proportion of the *P. cardis* recruited in early summer may have attained the fifth instar by July or August, or possibly a proportion of the previous years cohort remained as larvae through a second winter as suggested by Mackay (1969) for *P. apicalis* in a Quebec stream. Pupation of the hydropsychids occurred during June and

![Graph](image-url)
July. The flight period extended from June to September.

Pecnopsycha gentilis (Limnephilidae) and Pecnopsycha sonso were univoltine (Fig. 5A). First instar larvae of P. gentilis appeared in September and October and grew steadily through June. Pupation occurred in August and the flight period extended from August to October. Pecnopsycha sonso followed a similar pattern. Neophylax mitchelli (Limnephilidae) was univoltine with an extended period of aestivation through the summer months (Fig. 5B). First instar larvae appeared in October and were most abundant by November. Growth was slow through January but increased abruptly from February until the closure of the larval case in June. The flight period extended from August to October.

Lepidostoma griseum and Lepidostoma lydia (Lepidostomatidae) exhibited discrete univoltine cohorts (Figs. 5C, D). First instar larvae of L. griseum appeared in October and pupated in late July. The flight period extended from July to October. In contrast, first instar larvae of L. lydia appeared in July and pupated the following March and April. The flight period of L. lydia extended from April to June. Although adults Theliopsyche melas (Lepidostomatidae) were collected in an emergence trap in early June (1983 and 1984), larvae were never found.

The head-width frequency-histogram for the Ball Creek population of Fatigia pele (Sericostomatidae) did not reveal discrete larval instars and, therefore, a range of size classes was selected to follow development. The presence of at least two cohorts on each collection date indicated a 2-year life cycle (Fig. 5E), although some individuals may be univoltine. Semivoltinism is reported for the European S. persona-
tis (Iverson, 1973). Pupae of S. persona-
tis are attributed to accelerated growth and, depending upon voltinism, fell within the expected ranges cited by Waters (1977) for various aquatic invertebrates (Table 1). Unusually low ratios were observed for Waters (1977) for various aquatic invertebrates (Table 1). Unusually low ratios were observed for R. carpe-
teri, L. diversa, P. celsus and P. anser (Table 2), and are attributed to accelerated growth early in the life cycle followed by a prolonged period in the final instar which resulted in high biomass (e.g. Figs. 4E, 5F).

Habitat-specific production: taxonomic aspects

Trichopteran production (mg AFDW m^{-2} y^{-1}) was greatest on bedrock-outcrops (2608) followed by riffles (1038) and pools (950) (Table 2). Production on bedrock-outcrops may require 2 years to mature (see Par-

psycha, above). Females carrying extruded egg masses were observed in early July. Low densities of Pseudogastria singularis (Odonto-
toceridae) made conclusions about its life cycle tenuous, although a 2-year cycle was indicated. Adults were reared from field collected pupae in late July.

Habitat-weighted production: taxonomic aspects

Total habitat-weighted trichopteran produc-
tion was 1336 mg AFDW m^{-2} y^{-1} with a mean biomass of 275 mg AFDW m^{-2} (Table 1) (P B = 5). These values do not include case and net silk which may represent about 20% of caddisfly production (Iverson, 1980; Huryn & Wallace, 1985). Four taxa contributed 52% of total trichopteran production: P. cardis (25%), P. gentilis (10%), N. mitchelli (9%) and R. nigrita (9%). Fatigia pele (8%), D. modesta (7%), P. apicalis (7%), P. sonso (6%), Goeri-
ta senata (4%), R. torva (3%) and P. amera (3%) contributed an additional 38%. Most production was attributable to taxa with high final larval weights (i.e. P. cardis, F. pele), or a combination of short CPIs, high IGRs, and high densities (i.e. P. gentilis, N. mitchelli).

Neophylax mitchelli was the most abundant caddisfly in the stream (134±17 ind. m^{-2}) (X ±SE, n=240) followed by R. nigrita (119±14 ind. m^{-2}). Other taxa had substantially lower abundances (Table 1). Total trichopteran density was 706 m^{-2}.

Production to biomass ratios (P/B) generally reflected the CPIs assigned to the various taxa and, depending upon voltinism, fell within the expected ranges cited by Waters (1977) for various aquatic invertebrates (Table 1). Unusually low ratios were observed for R. carpe-
teri, L. diversa, P. celsus and P. anser (Table 2), and are attributed to accelerated growth early in the life cycle followed by a prolonged period in the final instar which resulted in high biomass (e.g. Figs. 4E, 5F).
TABLE 2. Trichopteran production measured in specific habitats in Ball Creek. Production (P = mg AFDW m⁻² y⁻¹; ±CL = 95% confidence limit. Condensed in part from Huryn & Wallace (1985).

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<th>Riffle</th>
<th>Pool</th>
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<td>P ± CL</td>
<td>P ± CL</td>
<td>P ± CL</td>
</tr>
<tr>
<td>Rhvacophila carpenteri</td>
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<td>0.10 ± 0.00</td>
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<td>R. glabrata</td>
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<tr>
<td>P. apicalis</td>
<td>323.200 ± 3.23</td>
<td>0.33 ± 0.03</td>
<td>0.11 ± 0.00</td>
</tr>
<tr>
<td>Diplectrona modesta</td>
<td>2.3 ± 0.3</td>
<td>0.168 ± 0.02</td>
<td>0.08 ± 0.00</td>
</tr>
<tr>
<td>Pycnopsyche genialis</td>
<td>1.3 ± 0.1</td>
<td>0.141 ± 0.02</td>
<td>0.075 ± 0.00</td>
</tr>
<tr>
<td>P. sonso</td>
<td>0.00 ± 0.00</td>
<td>0.61 ± 0.04</td>
<td>0.183 ± 0.03</td>
</tr>
<tr>
<td>Neophylax mitchelli</td>
<td>145.115 ± 1.45</td>
<td>0.142 ± 0.03</td>
<td>0.027 ± 0.00</td>
</tr>
<tr>
<td>Goerita semata</td>
<td>237.000 ± 2.37</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>Lepistoma griseum</td>
<td>0.00 ± 0.00</td>
<td>0.12 ± 0.02</td>
<td>0.037 ± 0.00</td>
</tr>
<tr>
<td>L. lydia</td>
<td>0.00 ± 0.00</td>
<td>0.12 ± 0.02</td>
<td>0.040 ± 0.00</td>
</tr>
<tr>
<td>Psilothera amera</td>
<td>0.00 ± 0.00</td>
<td>0.37 ± 0.04</td>
<td>0.22 ± 0.03</td>
</tr>
<tr>
<td>Pseudogeta singularis</td>
<td>27.11 ± 1.27</td>
<td>0.00 ± 0.00</td>
<td>0.00 ± 0.00</td>
</tr>
<tr>
<td>Fattigia pele</td>
<td>0.00 ± 0.00</td>
<td>0.172 ± 0.01</td>
<td>0.297 ± 0.03</td>
</tr>
<tr>
<td>Sum</td>
<td>26.07 ± 2.60</td>
<td>1.038 ± 0.10</td>
<td>0.950 ± 0.09</td>
</tr>
</tbody>
</table>

¹Production calculated by instantaneous growth method; ²summer cohort; ³autumn-spring cohort; ⁴from Huryn & Wallace (1985).

was attributable to a unique combination of taxa compared to the other habitats (Table 2). 94% of the trichopteran production on bedrock-outcrops was contributed by P. cardis (59%), P. apicalis (12%), G. semata (9%), R. torva (8%) and N. mitchelli (6%), whereas in riffles and pools they contributed only 20% and 4% of total annual trichopteran production, respectively. Goerita semata, R. torva, P. cardis and P. apicalis were restricted primarily to bedrock-outcrops (Table 2). Fattigia pele (17%), D. modesta (16%), P. genalis (14%), N. mitchelli (14%) and Rhvacophila nigrita (13%) contributed 74% of trichopteran production in riffles. Diplectrona modesta was essentially restricted to riffles (Table 2).

Pycnopsyche genialis (21%), P. sonso (19%), F. pele (19%), R. nigrita (12%) and L. diversa (10%) contributed 80% of annual production of pools. Compared to riffles, two of the top five contributors to production in pools were of different taxa with P. sonso and L. diversa were restricted mainly to pools (Table 2). Neophylax mitchelli and Rhvacophila nigrita had the most catholic habitat preferences and exhibited relatively high production in all habitats.

Habitat-weighted production: functional aspects

Trichopteran production attributable to primary and secondary consumers was 707 (=53%) and 629 (=47%) mg AFDW m⁻² y⁻¹, respectively. Production by primary consumers was apportioned between shredders (388 mg m⁻²=55%) > scrapers (170 mg m⁻²=24%) > filtering-collectors (119 mg m⁻²=17%) > collector-gatherers (31 mg m⁻²=4%). Collector-filterers (Parapsycha) and engulfing-predators (mainly Rhvacophila) contributed c. 430 mg m⁻² (=68%) and 199 mg m⁻² (=32%) mg to the annual production of the secondary consumers. Total habitat-weighted annual production was
broken down among functional feeding groups as follows: collector-filterers (548 mg m\(^{-2}\) = 41\%) > shredders (388 mg m\(^{-2}\) = 29\%) > engulfing-predators (199 mg m\(^{-2}\) = 15\%) > scrapers (170 mg m\(^{-2}\) = 13\%) > collector-gatherers (31 mg m\(^{-2}\) = 2\%).

Habitat-specific production: functional aspects

Qualitatively, the functional structure of the trichopteran community occurring in pools, riffles and bedrock-outcrops could be broken down in three groups. Production in pools and on bedrock-outcrops was dominated by single functional groups (Figs. 1B, 2B). Shredders and collector-filterers contributed 75\% and 73\% of the annual production in pools and bedrock-outcrops, respectively (Figs. 1B, 2B), whereas production in riffles was more evenly apportioned among the various functional groups (Figs. 1B, 2B).

Leaf litter biomass and substrate particle size distributors

The annual pattern of leaf litter biomass in pools and riffles exhibited a distinct peak in autumn (Fig. 6). Apparently, litter accumulated in riffles (October) and later accumulated in pools (November-December). Leaf litter biomass on bedrock-outcrops was negligible.

The median Phi values for substrates of each of the principal habitats exhibited the following trend: bedrock-outcrop > riffle > pool. Median Phi values are given in Fig. 1A.

Biology of dominant taxa

Collector-filterers

Both Parapsyche apicalis and Parapsyche cardis exhibited significantly higher production on bedrock-outcrops than riffles and pools (see 95\% CIs, Table 2), with P. cardis exhibiting a significantly higher level of production than P. apicalis (Table 2). Production of Diplectrona modesta occurred almost exclusively in riffles, where it was significantly greater than production measured for other hydropsychids. In Ball Creek, a rather obvious separation of habitat between the Arctopsychiinae and Diplectroniinae is apparent, with the former primarily utilizing moss covered bedrock-outcrops and the latter occurring upon unconsolidated rubble. A similar habitat distribution was observed for the hydropsychid community of Hugh White Creek, a lower elevation stream at Coweeta (Gurtz & Wallace, 1986).

Other than the Hydropsychidae, collector-filtering caddisflies contributed little to total production. The bivoltine philopotamids were dominated by Wormaldia moestus. Dolophilodes distinctus exhibited significantly lower production. This pattern was similar to that observed by Ross & Wallace (1983) with W. moestus the dominant philopotamid at the highest altitude site which was replaced by D. distinctus throughout the remainder of the Dryman Fork basin. Ross & Wallace (1983) observed a rather consistent level of philopotamid production along Dryman Fork and attributed this to the uniform supply of ultrafine organic seston throughout the stream continuum.
Most shredders, therefore, had spatial and temporal patterns of production which were: (i) either closely linked to periods and locations of litter accumulation, i.e. *L. llydia*, or (ii) showed two phases: a period of relatively high production which coincided with litter accumulation in pools and an intense period of production in riffle areas which were low litter biomass. During late spring, available litter consists of primarily robust and slowly conditioned leaves such as *Rhododendron*. Perhaps movement from pools to riffles by *P. gentilis* and *L. griseum* is related to utilization of these initially more refractory materials.

Scrapers

Despite heavy shading by the seasonally dense forest canopy and high ridges surrounding the Ball Creek catchment, substantial production of scraping Trichoptera was found (13% of total). *Goerita semata* contributed to scraper production only on bedrock-outcrops (Huryn & Wallace, 1985). Most production of *N. mitchelli* and *G. semata* occurred from March until May and was correlated with rising stream temperatures as seasonal insolation increased. As much as 84% of the production of *G. semata* occurred during this period, and 54% of the annual production was attributed to consumption of diatoms (Huryn & Wallace, 1985).

Collector-gatherers

The only caddisfly designated a collector-gatherer was *Lepidostoma diversum* which is well known for its association with submerged wood (e.g. Wiggins, 1977). Annual production was greatest in pools where wood was most abundant.

Engulfing-predators

Production of engulfing-predators, *Rhyncophila* spp., was low with *R. nigrita* and *R. torva* being most productive. *Rhyncophila nigrita* was remarkably widespread, with similar levels of production (c. 100 mg AFDW m⁻²) in all habitats sampled (Table 2). Final instar larvae of *R. nigrita* are large (c. 3–10 x the
AFDW of the other *Rhvacophilus* spp., a characteristic which may facilitate relatively rapid movement through diverse habitats. *Rhvacophilus torva* occurred almost exclusively on bedrock-outcrops where its production was significantly higher than that of *R. nigriia*. The other *Rhvacophilus* species contributed little to total engulfing-predator production and were confined primarily to riffles (Table 2). *Pseudoagoera singularis* contributed little to engulfing-predator production and, like *R. torva*, was exclusively confined to bedrock-outcrops.

**Discussion**

Spatial patterns of production: importance of habitat

The ability of a stream channel to retain and cycle dissolved and particulate materials influences consumer production (Leopold, 1941). Retention may be mediated physically through characteristics of channel form or biotically by activities of consumers. Additionally, channel form and the resultant habitat structure serves as a physical template which is a major determinant of the structure and functional feeding group composition of the trichopteran community. Production of the discrete trichopteran sub-communities found in pools, riffles and on bedrock-outcrops is strongly subsidized by the primary physically characteristics of these distinctive meso-scale habitats.

Physical retention is a function of channel form (Likens & Bilby, 1982; Brussock et al., 1985) and catchment history (Likens & Bilby, 1982; Molles, 1982). Bilby & Likens (1980) and Bilby (1981) demonstrated that pooled areas upstream of debris dams are important in regulating release of particles. In Ball Creek, accumulation of leaf litter in pools during late autumn indicates that pools are primary sites for physical retention and storage of organic matter. Accordingly, shredder production predominated in pools (72%), Fig. 2) and collector-filterer production was minimal (4%, Fig. 1). Trichopteran production in riffles was distributed more evenly among functional groups than in pools and on bedrock-outcrops, which reflects the greater diversity of physical conditions within this habitat. The major proportion of production in riffles (46%) was contributed by shredders (cf. Figs. 1B and 2B), mainly *F. pele* and *P. gentilis*. Apparently the physical retention of leaf litter predominated transport characteristics in riffles, at least at baseflow. Although a substantial amount of the production by *P. gentilis* occurred in pools during autumn, the spatial pattern of production shifted from pools to riffles during early spring and coincided with the decline of leaf litter in the former habitat. Taxa occupying pools and, to a lesser degree, riffles, are exploiting areas of stream channel that are sites of physical retention.

An obvious form of biotic retention is mediated by collector-filtering organisms which ingest suspended materials. 42% of the total trichopteran production in Ball Creek was attributable to collector-filterers (Table 1). Similar or higher proportions of collector-filterer production appear to be general for stream reaches where there are suitable sites for retreat attachment [e.g. outcrop (Nelson & Scott, 1962; Flossner, 1976), cobble (Neves, 1979; Kreuger & Waters, 1983), snags and emergent macrophytes (Cudney & Wallace, 1980; Smock Gilinsky & Stoneburner, 1985)]. In Ball Creek, the dependence of the collector-filtering caddisfly community upon regions of adequate current and stable attachment sites was shown by the relatively high production attained in bedrock-outcrop habitats which were characterized as shallow sluiceways of water over moss-covered bedrock-outcrops. Low physical retention and high potential for entrainment of materials over these outcrops can be inferred from their lower standing crops of accumulated organic matter compared with riffles and pools (Fig. 2A: Huryn & Wallace, 1987). Furthermore, the thick moss cover apparently provides retreat sites for *Parapsyche*, particularly those of *P. cardis*. Although constituting only 19% of the stream area, bedrock-outcrops contributed 64% of the production of filter-feeding Trichoptera. Collector-filterers, through use of silken nets, primarily exploit erosional characteristics of the bedrock-outcrop habitat.

Production of engulfing-predators followed that of collector-filterers, being greatest on bedrock-outcrops > riffles > pools (Fig. 1). Engulfing-predator production on outcrops was primarily attributable to the habitat specialist, *R. torva*. The specific adaptations and trophic relations of *R. torva* are unclear.
and, at present, we have no simple explanation
for the above trend of engulfing-predator pro-
duction among habitats.
Physically stable mineral surfaces are most
suited for epilithon attachment and growth
(Wallace & Gurtz, 1986). Trichoptera which
consume epilithon frequently have mouthparts
(Cummins & Merritt, 1984) and case forms
(Molles, 1984) that are highly adapted to
exploit physical characteristics of such local
environments. Therefore, the contribution of
scrapers to total trichopteran production in
Ball Creek is probably related to the amount
of stream area occupied by stable mineral
surfaces (Fig. 1). Scraper production in the
bedrock-outcrop and riffle habitats was sig-
ificantly higher than rates measured in pools.

Importance of habitat: evolutionary
considerations
It has often been proposed that the Tricho-
ptera originated in cool lotic habitats (Ross,
1967; Lepneva, 1969; Wiggins, 1977; Mackay
& Wiggins, 1979); however, the implications of
stream channel form with respect to the evolu-
tion of the functional diversity found among
the recent fauna have never been developed
(cf. Ross, 1967; Mackay & Wiggins, 1979;
Weaver & Morse, 1986). The present study, by
distinguishing discrete mesoscale habitats each
with a functionally distinct caddisfly sub-
community, demonstrates that small streams
situated in mountainous terrain may have
provided the diversity of physical templates
essential for the initial adaptive radiation of
the Trichoptera. Headwater streams in moun-
tainous regions tend to be remarkably diverse
in channel form and habitat structure, thus
presenting suites of unique selective pressures
that, on an evolutionary time scale, may con-
strain and shape the functional adaptations of
their fauna. These site-specific factors, when
combined with the potential for isolation of
individual catchments in rugged and moun-
tainous landscapes for long periods of time
(Ross, 1950, 1972), as well as the apparently
low vagility of many stream inhabiting insects
occurring in such regions (e.g. Wallace, Vogel
& Cuffney, 1986) may have promoted the
isolation of small populations leading to the
evolution of taxa representing the ancestors of
all the present-day functional feeding groups.
Subsequent periods of dispersal, perhaps re-
lated to coalescence of catchments and streams
during prolonged periods of downwasting,
would allow for development of the function-
ally distinct sub-communities presently occup-
ying physically discrete habitats of mountain
streams. These ecologically diverse trichopter-
an communities may have in turn provided
fortuitously adapted forms which invaded the
more spatially homogenous habitats such as
ponds, lakes and larger rivers and resulted in
their characteristically more derived fauna
(Ross, 1956).

Weaver & Morse (1986) presented a revised
phylogeny based upon a more logical and
well-documented systematic analysis than the
widely cited phylogeny of Ross (1967). These
authors stated that the ancestral trichopteran
probably occurred along ‘aquatic environments
such as littoral regions, slowly moving water-
ways, or marshes’. In essence, it was implied
that this hypothetical animal occurred within
detritus rich margins of depositional zones of
the ancestral environment. Similar to those of
the present, the mountain streams of Pangea
must have had substantial regions of organic
matter deposition within and along their mar-
gins to provide just the type of habitat deduced
to be ancestral by Weaver & Morse (1986). It
seems that the ecological aspects of the phy-
logeny proposed by these authors are consist-
ent with the more traditional and well
documented idea that the Trichoptera evolved
in association with low-order, cool, moderately
high-gradient woodland streams (Ross, 1956,
1967; Lepneva, 1969; Wiggins, 1977; Mackay

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Trichopteran community structure

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