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Author(s): G. John Lugthart and J. Bruce Wallace

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Effects of disturbance on benthic functional structure and production in mountain streams

G. JOHN LUGTHART¹ AND J. BRUCE WALLACE²

Department of Entomology, University of Georgia, Athens, Georgia 30602 USA

Abstract. To assess the role of macrofauna consumers in organic matter dynamics of headwater streams, we applied seasonal insecticide treatments to a southern Appalachian Mountain stream and compared benthic community structure between this and two other streams. Production was estimated in the two major habitats: mixed cobble-gravel-sand substrate and bedrock outcrop. Using the proportional availability of the habitats in each stream, production over the entire stream was measured.

Annual habitat-weighted production in the untreated streams during the two study years ranged from 8.9 to 14.0 g AFDM m⁻² yr⁻¹, 81 to 86% of which was attributed to insects. Habitat-weighted production was distributed rather evenly among the collector-gatherer (32-41%), shredder (23-31%), and predator (28-33%) functional groups. Collector-filterer and scraper groups accounted for less than 9% of total habitat-weighted production in all three streams.

Insecticide applications resulted in dramatic changes in the macrofaunal community. Annual habitat-weighted production (4.4 g m⁻² yr⁻¹) in the treated stream decreased by 62% from Yr 1 to Yr 2, with insects contributing only 45% to total production. Oligochaetes, several Diptera, dragonflies, and copepods composed most of the production during treatment. Although habitat-weighted production of all functional groups was lower in the treatment year than in the pre-treatment year, collector-gatherer production decreased the least (21% reduction) and dominated overall production during treatment. Production of the other functional groups decreased by 71-94% between the two years. The changes in macrofaunal community structure and production observed in the insecticide treated stream were much greater than between-year changes in the reference stream, despite the occurrence of a record drought in Yr 2. The effect of the two different disturbances on overall production differed not only in magnitude but also in direction, with production in the reference stream increasing (12% over Yr 1) during the drought year.

Resource ingestion was estimated using values of functional group production. Estimates of ingestion suggested that the major functional groups were ingesting a fairly large portion of available resources in the untreated streams. Collector-gatherers consumed 34-64% of total annual habitat-weighted fine particulate organic matter. Shredders consumed an estimated 28-47% of average annual standing crop of leaves, and predators ingested 67-79% of total macrofaunal production. Insecticide treatments resulted in much lower levels of resource ingestion: 26%, 4%, and 50% for collector-gatherers, shredders, and predators, respectively.

Our results show the importance of using estimates of production when assessing disturbance effects on macrofaunal communities, since abundances greatly underestimated the impact of insecticide treatments. Biomass estimates, though providing better measures of disturbance than abundances, tended to overestimate overall macrofaunal losses because of the disproportionate influence of large, slow growing taxa such as crayfish.

Key words: secondary production, disturbance, insecticide, macroinvertebrates, macrofauna, functional structure, drought, organic matter.

In a review of stream bioenergetics, Benke et al. (1988) noted that studies estimating production for entire macroinvertebrate communities are uncommon. They cited the need for a better understanding of how production varies within and across biomes. Comparisons of faunal pro-

duction between streams of a particular region indicate the variability that occurs among physically similar streams and provide a necessary background against which comparisons between regions can be made. Furthermore, multi-year studies that simultaneously estimate production in different streams may reveal some of the physical and biological factors controlling production (Krueger and Waters 1983).

¹ Present address: Sequoia Hall, Dalton College, 213 N. College Drive, Dalton, Georgia 30720 USA.

² To whom reprint requests should be addressed.

Studies of secondary production offer an im-

portant means of examining the effects of disturbances (Benke 1984). Since the late 1940s, when early attempts to control forest insects were made using DDT and other insecticides, many studies have documented the effects of insecticides on stream fauna (see Wallace and Hynes [1981] and Muirhead-Thompson [1987] for comprehensive reviews). Direct toxic effects include the elimination of many organisms and subsequent reduction in benthic standing stocks. Indirect effects of pesticide application may include increased numbers of some taxa, presumably because of reduced predation or competition for food or both (Hurlbert 1975). Most studies that have assessed the impact of insecticides on aquatic macroinvertebrates have examined only changes in abundances of taxa. To our knowledge, changes in secondary production have not been addressed. Secondary production measurements account for differences in turnover rates among taxa. Therefore, these measurements permit a better understanding of the relative roles of animals within the stream community, and provide a more appropriate means of assessing the effects of community-level changes on ecosystem-level processes (Benke 1984).

Our primary objective in the present study was to examine the effects of insecticide on macroinvertebrate and larval salamander community structure and production in a 1st-order Appalachian stream. To accomplish this objective, faunal structure and production and organic matter relationships in the two major habitats were assessed in three undisturbed streams in the first year (Yr 1). This information was then used as a base against which we examined the effects of insecticide treatment of one stream in Yr 2. A severe drought in Yr 2 provided a rare opportunity to compare effects of this natural disturbance with those of the insecticide treatment on macrofaunal communities of these streams.

Study Sites

The three streams examined are within the Coweeta Hydrologic Laboratory (US Forest Service) in western North Carolina. Coweeta is a 1625-ha drainage basin in the Blue Ridge Province of the southern Appalachian Mountains. Detailed descriptions of the Coweeta basin can be found in Swank and Crossley (1988). The

TABLE 1. Physical parameters of study streams in Coweeta Hydrologic Laboratory. Elevations were measured at the gauging flumes. Year 1 = 11 Oct 1984–13 Nov 1985; Year 2 = 14 Nov 1985–22 Nov 1986. Annual precipitation was 139.4 cm in 1985 and 113.8 cm in 1986.

	C 53	C 54	C 55
Catchment			
Area (ha)	5.2	5.5	7.5
Elevation (m asl)	829	841	810
Channel length (m)	135	260	170
Substrate (%)			
Bedrock outcrop	27	35	13
Mixed substrate			
Boulder	7	4	3
Cobble	19	17	29
Pebble & sand	14	12	49
Silt	33	32	6
Discharge (L/s)			
Average Year 1	0.58	0.91	0.94
Year 2	—	0.54	0.47
Temperature (°C)			
Average Year 1	12.9	12.4	12.7
Year 2	—	12.4	12.5
Maximum Year 1	18.7	17.7	18.2
Year 2	—	19.5	19.4
Minimum Year 1	2.8	4.9	4.4
Year 2	—	3.3	1.6
Annual degree-days			
Year 1	4696	4524	4626
Year 2	—	4541	4567

study streams are 1st order, and drain Catchments (C) 53, 54, and 55. Catchment vegetation consists of mixed hardwoods, dominated by oaks and hickories. Dense growths of understory rhododendron result in heavy shading of the streams for most of the year. Elevation, area drained, thermal regime, discharge, and aspect (southern) are similar for the three streams (Table 1). Discharge was gauged continuously using FW-1 stage recorders attached to H-flumes at the base of each catchment.

Substrate particle size distribution was assessed visually at 1-m intervals along the entire length of each stream (Table 1). Sixty-five to 87% of the substrate in the three streams consisted of a heterogeneous mixture of cobbles, pebbles, gravel, sand, and silt. Areas composed

of this mixture are referred to in this paper as the mixed substrate habitat. The remaining substrate was composed of stretches of bedrock outcrop with growths of moss. The overall roughness of the streambed topography resulted in high retention, with abundant accumulations of leaves and wood. Additional information about the study streams has been reported by Wallace et al. (1986) and Cuffney et al. (1990).

In Yr 1 of the present study, C 53 was in its fifth year of recovery from insecticide treatment. The insecticide methoxychlor had been applied to C 53 in 1980 during a previous study that examined the role of invertebrates in the processing of leaves and the export of organic matter (Wallace et al. 1982, 1986, Cuffney et al. 1984).

Precipitation during our study was 77% of average during Yr 1 and 63% of average during Yr 2 (Table 1). During the second year, the southeastern US experienced the most severe drought in 56 yr of record keeping at Coweeta Hydrologic Laboratory.

Methods

Benthic sampling

Macrofauna and benthic organic matter were sampled by two methods. The mixed substrate habitats were sampled with a 400-cm² corer. All material within the corer was removed by hand and with a cup to a depth of approximately 10 cm or bedrock. Following sample removal, water depths were measured at five locations to obtain an average depth of water remaining in the corer for volume estimates. Following agitation, a subsample of the water in the corer was removed for later organic matter quantification. Bedrock outcrops were sampled by scraping and brushing moss and associated material from a 15 × 15-cm area into a plastic bag pressed to the rock surface. In Yr 1 (October 1984 to September 1985), samples were collected monthly from all three streams, C53, C54, and C55. In Yr 2 (January 1986 to November 1986), samples were collected during alternate months from two streams, C54 and C55. Seven benthic samples, four from mixed substrates and three from bedrock outcrops, were collected from each stream on each sampling date. Sample locations were selected from a random number table. If the appropriate habitat type was

not present at the preselected location, the sample was collected at the closest upstream site.

Organic matter in samples, including invertebrates and salamanders, was elutriated from the inorganic substrate, passed through nested 1-mm and 250- μ m sieves, and preserved in a 6–8% formalin solution containing Phloxine B dye. All animals were removed from the coarse particulate organic matter (CPOM) on the 1-mm sieve by hand picking under 15× magnification and were preserved in 6–8% formalin solution. CPOM was separated into leaf, wood, seed, moss, and miscellaneous categories, then dried, weighed to the nearest 0.01 g, ashed (12 h), and reweighed. Fine particulate organic matter (FPOM) was composed of three fractions: fine benthic organic matter (FBOM: <1 mm > 250 μ m), very fine benthic organic matter (VFBOM: <250 μ m), and organic matter in water (OMW: <1 mm) that remained in the core following removal of other material. FBOM (material on the 250- μ m sieve) was placed in graduated bucket with a known volume of water, stirred, and subsampled (<1% removed) with a graduated syringe. The remainder of the sample was concentrated on a 250- μ m sieve and preserved (6–8% formalin) for later sorting of invertebrates. The subsample was filtered onto a pre-ashed, pre-weighed glass fiber filter (Gelman A/E). Filters were oven dried (60° for 7 d), weighed to the nearest 0.01 mg, ashed (500°C for 2–12 h), and reweighed to determine ash free dry mass (AFDM). For all material passing through the 250- μ m sieve (VFBOM), volume was recorded and a subsample taken and processed as described above for FBOM. No invertebrates were removed from the <250 μ m fraction. OMW was estimated by measuring the concentration of organic matter in the subsample removed from the corer. A 10–20-mL subsample was filtered and processed as described for FBOM.

Material in the <1-mm > 250- μ m size fraction was subsampled ($\frac{1}{8}$ to $\frac{1}{64}$ of whole sample) using a sample splitter (Waters 1969) prior to removal of invertebrates. Animals were removed by hand using a stereomicroscope (15× magnification). Invertebrates and larval salamanders were identified and counted. Identifications of most insects were made to species or genus. Larval chironomids were identified as either Tanypodinae or non-Tanypodinae. Most non-insect invertebrates were identified to the ordinal level or higher. The body length

of each individual was measured to the nearest mm using $12\times$ magnification and a graduated stage or an ocular micrometer. We measured snout-vent lengths of salamanders and carapace lengths of crayfish. For Copepoda, Hydra-carina, Nematoda, and Cladocera, biomass (AFDM) was obtained from mean mass of >50 individuals in subsamples of representative size classes. For other taxa, biomass was obtained using length-weight regressions derived from animals in the study streams, nearby Coweeta streams (Huryn 1986), or, for several taxa of Trichoptera, other North Carolina streams (Smock 1980).

Production

Annual production estimates for most taxa were calculated using the size-frequency method (Hamilton 1969) and were corrected for the cohort production interval (CPI; Benke 1979). Invertebrate CPIs were estimated using length-frequency histograms constructed from monthly samples of each taxon in the study streams (Lugthart, unpublished) or in another Coweeta stream (Huryn and Wallace 1987b, Huryn and Wallace 1988). For salamanders, we used larval period lengths determined for salamander populations in the Coweeta basin, nearby Station Creek, or Wolf Creek in Jackson County, North Carolina (Bruce 1988a, 1988b, 1989).

Production of non-Tanytopodinae chironomids was estimated using the community-level method of Huryn and Wallace (1986) and Huryn (1990), and has been discussed by Lugthart et al. (1990). The product of standing stock biomass and annual production/biomass (P/B) ratio was used to estimate production for the remaining taxa. Empirically derived P/B values of 0.58 for crayfish (*Cambarus bartonii*, Huryn and Wallace 1987c) and 18 for Copepoda (O'Doherty 1988) were assumed. Theoretical P/B values of 5 and 10 were used for eight taxa considered to be univoltine and bivoltine, respectively (Waters 1977) (see Appendix 1). With the exception of oligochaetes, these taxa formed a very small portion of total biomass. Because oligochaete taxa were grouped, and voltinism was uncertain, production was estimated using a P/B value of 5. We recognize that these estimates may be conservative given that high reproductive rates have been observed in some oligochaete taxa (Brinkhurst and Cook 1980).

Production was estimated separately for the mixed substrate and bedrock outcrop substrate. Production for an entire stream was calculated according to the proportion of bedrock outcrop and mixed substrates shown in Table 1.

Animals were assigned to the following functional feeding groups: shredder, collector-gatherer (=gatherer), scraper, collector-filterer (=filterer), or predator. Designations were made following Merritt and Cummins (1984) or based on our knowledge of the local fauna (see Appendix 1). Because crayfish use several feeding mechanisms (Momot et al. 1978), their production was divided among the shredder ($\frac{1}{2}$), gatherer ($\frac{1}{4}$), and predator ($\frac{1}{4}$) functional groups. Salamanders were the only vertebrates found in the study streams; their larvae were assigned to the predator functional group because they feed almost exclusively on aquatic invertebrates (Lugthart 1991). Adult salamanders are amphibious and consume much terrestrial prey (Hairston 1949, Krzysik 1979); their production was not estimated in our study.

Food ingestion by major functional groups was estimated by dividing production values by the product of assimilation efficiency (AE) and net production efficiency (NPE) (Benke and Wallace 1980). Efficiencies were obtained from the literature. An AE of 85% and an NPE of 50% were assumed for predators (Lawton 1970). An AE of 13% and an NPE of 38% were used for shredders (McDiffett 1970, Perry et al. 1987). We used the values of Ross and Wallace (1983) from a nearby Coweeta stream for estimates of ingestion and bioenergetic efficiencies for different taxa of filterers. An AE of 5% and an NPE of 33% were assumed for gatherers. These values are slightly lower than those generally assumed for detritivores (Benke and Wallace 1980). Fisher and Gray (1983) calculated assimilation efficiencies of 7–15% for several gatherer taxa that fed on material collected from algal mats. Ingestion and production estimates were placed into primary and secondary consumer levels. The secondary consumer level included all predators and the proportion of production and ingestion attributable to animals in the diets of the filter feeders *Parapsyche* and *Diplectrona* (Ross and Wallace 1983). The primary consumer level included the gatherers, shredders, scrapers, and the remainder of the ingestion and production of the filter feeders. Our estimates of ingestion are coarse since assimilation and net production

efficiencies were applied to entire functional groups which probably contained taxa with varying diets.

Cluster analysis was used to assess similarities of animal communities among streams and between the two study years. Analyses were performed on untransformed habitat-weighted production estimates of all taxa, and on habitat-weighted and habitat-specific estimates of functional group production. The cluster analysis used the chord distance measure and the flexible strategy (with $\beta = -0.25$) (Ludwig and Reynolds 1988).

Pesticide treatment

The insecticide methoxychlor (1,1,1-trichloro-2,2-bis [p-methoxyphenyl]ethane; CAS no. 72-43-5) was applied seasonally to C 54 during the second year of the study, as described by Wallace et al. (1989). Briefly, the procedure was to treat the entire stream channel from flume to spring seeps. Two hand-sprayers were used to apply the insecticide for 4 h (December 1985) and 2 h (March, June and September 1986) at a rate (based on discharge at the flume) that would result in a concentration of 10 mg/L in the water column. C 55 served as a reference stream during both study years.

Results

Benthic organic matter

Habitat-weighted standing crops of CPOM and FPOM in the three streams showed the same pattern: C 53 > C 54 > C 55 (Table 2). Considering mixed substrates alone, standing crops of total CPOM and FPOM were significantly lower in C 55 than in the other two streams during Yr 1 (Table 2). In Yr 2, total CPOM standing crop in the mixed substrate of C 55 was again lower than that in C 54; total FPOM did not differ significantly between streams. The higher total CPOM standing crops in C 53 and C 54 were primarily a result of wood standing crops which were 26–39% higher in these streams than in C 55. The estimates of wood standing crops in all three streams are very conservative since logs and large debris dams were not sampled. For example, separate measurements of mass of bankful woody debris made using line intercept

techniques (Wallace and Benke 1984), and incorporating woody debris from 2 mm diameter to large logs (0.5 m diameter), indicate 22.7 to 26.3 kg AFDM of wood per linear meter of stream, which is much greater than that indicated from benthic sampling (Table 2). The higher total FPOM standing crops in the mixed substrates of C 53 and C 54 compared with C 55 during Yr 1 resulted from significantly higher levels of VFBOM in both streams, and significantly higher levels of FBOM in C 53. There were no significant differences in Yr 1 versus Yr 2 levels of mixed substrate CPOM or FPOM standing crops within either C 54 or C 55.

Although CPOM standing crops on the bedrock outcrops followed the same trends observed for the mixed substrates (i.e., C 53 and C 54 > C 55), much lower detrital standing crops and higher variability resulted in no significant differences between streams in either year (Table 2). However, in C 55, standing crops of leaves and total CPOM on the bedrock outcrops were significantly higher in Yr 2 compared with Yr 1. A similar increase in CPOM standing crops was observed on the bedrock outcrops of C 54, but between-year differences were not significant. Standing crops of VFBOM and total FPOM in C 53 were significantly higher than in C 55 in Yr 1.

Production in year 1

Annual habitat-weighted production of macrofauna in Yr 1 was highest in C 53 (14.0 g/m²), intermediate in C 54 (Yr 1 = 11.5 g/m²), and lowest in C 55 (Yr 1 = 8.9 g/m²) (Table 3). Cluster analysis indicates that the communities in C 54 and C 55 during Yr 1 were most similar and that the community in C 53 was similar to that in C 55 during Yr 2, with each of these pairs forming a distinct cluster (Fig. 1A). Production in mixed substrates was 1.5 to 3.4× greater than that on bedrock outcrops (Table 4).

Diptera were the largest contributors (38–41%) to total macrofaunal production in all communities (Table 3). The family Chironomidae accounted for most of this production (see Appendix 1). Trichoptera, Plecoptera, and Odonata also made substantial contributions to total production in the untreated streams (Table 3).

Insects composed 81–86% of total production in Yr 1. Oligochaeta were the dominant non-insect contributors to total production (4–7%),

TABLE 2. Mean standing crop of benthic organic matter in two substrate types in C 53, C 54, and C 55 during year 1 (pre-treatment: October 1984–September 1985) and in C 54 and C 55 in year 2 (January 1986–November 1986) when C 54 received insecticide. Values within an organic matter category and followed by the same letter are not significantly different ($p < 0.05$, ANOVA and Tukey multiple comparison tests on transformed ($\log [x + 1]$) values.

Categories	Year 1			Year 2	
	C 53	C 54	C 55	C 54	C 55
Mean standing crop (g ash-free dry mass/m ²)					
Mixed substrate					
CPOM ¹					
Leaves	183.6 ^b	245.0 ^{ab}	146.5 ^b	315.4 ^a	217.1 ^{ab}
Wood	755.3 ^a	678.0 ^a	461.0 ^{bc}	674.0 ^{ab}	499.6 ^c
Moss	0	0	0	0	0
Other ²	49.5 ^a	18.6 ^c	18.6 ^{bc}	23.4 ^{abc}	28.7 ^{ab}
Misc.	217.6 ^{abc}	241.9 ^{ab}	175.5 ^{bc}	283.3 ^a	138.5 ^c
Total	1206.0 ^{ab}	1183.4 ^a	801.7 ^c	1296.2 ^a	883.9 ^{bc}
FPOM ³					
FBOM	157.8 ^a	142.4 ^{abc}	73.9 ^c	141.5 ^{ab}	63.2 ^{bc}
VFBOM	456.9 ^a	556.4 ^a	335.4 ^b	655.9 ^a	480.3 ^{ab}
OMW	84.0 ^a	102.7 ^a	92.0 ^a	260.1 ^a	158.4 ^a
Total	703.8 ^a	784.1 ^a	517.7 ^b	1050.3 ^a	683.5 ^{ab}
Bedrock outcrop					
CPOM ¹					
Leaves	16.3 ^{abc}	9.7 ^{bc}	6.5 ^c	24.2 ^{ab}	43.7 ^a
Wood	11.3 ^a	6.0 ^a	5.6 ^a	7.7 ^a	17.4 ^a
Moss	10.7 ^a	6.2 ^a	6.0 ^a	6.5 ^a	1.9 ^a
Other ²	3.6 ^{ab}	0.2 ^b	0.9 ^{ab}	0.0 ^{ab}	2.6 ^a
Misc.	7.2 ^a	5.2 ^a	4.1 ^a	5.5 ^a	8.3 ^a
Total	49.1 ^{ab}	27.3 ^{ab}	23.2 ^b	44.0 ^{ab}	73.9 ^a
FPOM ³					
FBOM	8.0 ^a	6.3 ^a	5.6 ^a	6.6 ^a	9.2 ^a
VFBOM	31.4 ^a	24.5 ^{ab}	17.9 ^b	16.5 ^{ab}	26.1 ^{ab}
OMW	—	—	—	—	—
Total	39.9 ^a	30.8 ^{ab}	23.5 ^b	23.3 ^{ab}	36.4 ^{ab}
Habitat weighted					
CPOM total	887.7	775.9	699.3	854.8	777.4
FPOM total	521.2	518.6	452.7	688.3	598.4

¹ Coarse particulate organic matter: Miscellaneous = material <23 mm² and >1 mm²; remaining categories are >23 mm².

² Other = seeds and roots.

³ Fine particulate organic matter: FBOM = fine benthic organic matter <1 mm² and >0.06 mm²; VFBOM = very fine benthic organic matter <0.06 mm²; OMW = organic matter in corer water after removal of other particulates.

with the notable exception of Copepoda in C 53, whose production in C 53 was >1 g/m² and formed 8% of total production. Larval salamander production was highest in C 53.

Functional group habitat-weighted production was similar among communities in Yr 1 and was distributed fairly evenly among the

gatherer (32–41%), shredder (23–31%), and predator (28–33%) functional groups (Figs. 2A, 3).

A very different picture was obtained when habitat-weighted abundance estimates were used to illustrate macrofaunal functional structure (Fig. 2B). Gatherers dominated total abun-

TABLE 3. Macrofaunal community composition in the study streams, C 53, C 54, and C 55, during year 1 (pre-treatment: October 1984–September 1985) and in C 54 and C 55 in year 2 (January 1986–November 1986) when C 54 received insecticide treatment. Values are annual habitat-weighted secondary production estimates ($\text{g m}^{-2} \text{yr}^{-1}$). Percent contribution of each taxon to total stream production is given in parentheses.

	Year 1			Year 2	
	C 53	C 54	C 55	C 54	C 55
Insect Taxa					
Ephemeroptera	0.31 (2)	0.63 (5)	0.45 (5)	<0.02 (<1)	0.11 (1)
Odonata	1.25 (9)	0.58 (5)	0.47 (5)	0.57 (13)	1.24 (12)
Plecoptera	1.08 (8)	2.21 (19)	1.67 (19)	<0.01 (<1)	1.08 (11)
Coleoptera	<0.01 (<1)	0.04 (<1)	0.06 (1)	0.01 (<1)	0.05 (<1)
Diptera	5.76 (41)	4.58 (40)	3.37 (38)	1.30 (30)	4.28 (42)
Trichoptera	2.93 (21)	1.85 (16)	1.59 (18)	0.08 (2)	1.71 (17)
Total	11.34 (81)	9.88 (85)	7.61 (86)	1.99 (45)	8.46 (83)
Non-insect Taxa					
Invertebrates					
Oligochaeta	0.51 (4)	0.65 (6)	0.58 (7)	1.68 (38)	0.52 (5)
Nematoda	0.06 (<1)	0.02 (<1)	0.02 (<1)	0.04 (1)	0.04 (<1)
Turbellaria	0.06 (<1)	0.02 (<1)	0.02 (<1)	0.06 (1)	<0.01 (<1)
Cladocera	<0.01 (<1)	<0.01 (<1)	<0.01 (<1)	0.01 (<1)	<0.01 (<1)
Copepoda	1.05 (8)	0.38 (3)	0.33 (4)	0.52 (12)	0.40 (4)
Acari	0.08 (1)	0.04 (<1)	0.04 (<1)	0.06 (1)	0.05 (1)
Decapoda	0.13 (1)	0.30 (3)	0.10 (1)	0 (0)	0.58 (6)
Vertebrates					
Caudata	0.75 (5)	0.20 (2)	0.16 (2)	0.05 (1)	0.05 (<1)
Total	2.65 (19)	1.61 (15)	1.25 (14)	2.41 (55)	1.64 (17)
TOTAL	13.99	11.49	8.86	4.40	10.10

dances in all streams (82–87%). Functional group composition based on standing stock biomasses (Fig. 2C) was fairly similar to that based on production estimates, however, the contributions of gatherers and predators were proportionally lower and higher, respectively.

In Yr 1, the relative contributions of the functional groups to total production in the mixed substrate habitat (Table 4) were similar to those described for habitat-weighted production (Fig. 2A), a consequence of the predominance of this habitat in the streams (Table 1). In contrast, on the bedrock outcrop, production of filterers and predators accounted for a greater (13–48%) and lesser (13–17%) proportion of total production, respectively (Table 4).

In the bedrock outcrop habitat, the greatest differences in functional group production were observed for the filterer and shredder groups. Filterer production in C 53 was about 2.7–4.5 \times lower than in C 54 and C 55 in Yr 1, and shredder production in C 53 was about 1.2–2.8 \times

higher than in C 54 and C 55 in Yr 1 (Table 4 and Appendix 1). The dendrogram in Figure 1B shows the similarity between the untreated mixed substrate communities as well as the distinction between these communities and those on the bedrock outcrop.

Production in C 55 in year 2

Although C 55 served as a reference stream, the record low precipitation (56-yr) in Yr 2 offered a unique opportunity to examine the influence of severe drought on invertebrate production in this stream. Habitat-weighted production increased from 8.9 g/m^2 in Yr 1 to 10.1 g/m^2 in Yr 2 in C 55. Production levels varied between years for a number of taxa. Plecoptera production decreased by 35% from Yr 1 to Yr 2; stoneflies formed a large portion (19%) of total production in C 55 and C 54 during Yr 1, but only 11% of total production in C 55 during Yr 2 (Table 3). Stonefly production and per-

TABLE 4. Annual secondary production as AFDM ($\text{g m}^{-2} \text{yr}^{-1}$) of functional groups and community P/B ratios in mixed substrate and bedrock outcrop habitats of C 53, C 54, and C 55, during year 1 (pre-treatment: October 1984–September 1985) and in C 54 and C 55 in year 2 (January 1986–November 1986) when C 54 received insecticide treatment.

Functional group	Mixed substrate			Bedrock outcrop		
	C 53	C 54	C 55	C 53	C 54	C 55
Year 1						
Filterer	0.5	0.1	0.4	0.7	1.8	3.0
Gatherer	7.1	4.7	3.0	2.4	2.1	1.8
Predator	5.6	4.6	2.8	0.9	0.8	0.9
Scraper	0.1	0.2	0.2	<0.1	0.2	0.1
Shredder	4.0	5.0	2.8	1.1	0.9	0.4
Total	17.37	14.59	9.27	5.09	5.79	6.14
P/B (total)	5.0	4.1	4.7	4.8	6.0	5.8
Year 2						
Filterer		<0.1	0.5		0.1	0.9
Gatherer		3.9	3.7		1.2	1.5
Predator		1.3	3.8		0.2	0.7
Scraper		<0.1	<0.1		<0.1	0.2
Shredder		0.7	3.0		<0.1	0.9
Total		5.97	10.98		1.52	4.30
P/B (total)		4.9	3.5		6.4	3.8

cent contribution to total production in C 55 in Yr 2 resembled those in C 53 in Yr 1 (Table 3). This similarity was primarily due to relatively low production of Peltoperlidae in both streams (Appendix 1, Fig. 4). Ephemeroptera production in C 55 decreased by 76% between years because of lower production of taxa such as *Paraleptophlebia* (Fig. 4) and *Serratella*. Production of *Parapsyche*, a filter-feeding caddisfly that we found almost exclusively on bedrock outcrop, decreased by 80% (Fig. 4). Other groups, such as Chironomidae and Decapoda, had substantially higher levels of production in Yr 2 (Fig. 4). Odonata production increased by 62%, a result of much higher production of *Lanthus* (Fig. 4). As a consequence of faunal changes between years in C 55, the community there during Yr 2 clustered with that in C 53 in Yr 1, rather than with the community in C 55 in Yr 1 (Fig. 1A).

Production in C 54 during insecticide treatment

A dramatic change in community structure was seen in C 54 during insecticide treatment in Yr 2 when the fauna was compared with the previous year. Total annual production in C 54

decreased by 62%, whereas a 12% increase was seen in C 55 from Yr 1 to Yr 2. In C 54, Oligochaeta accounted for 38% of macrofaunal production (Table 3), increasing 61% between years. Diptera (primarily Chironomidae) production in C 54 decreased by 72% between years, yet this order remained important, accounting for 30% of total production. Production of Trichoptera, Plecoptera, and Ephemeroptera was severely reduced (96–99%) during the treatment year. Although Odonata production changed very little with treatment, they constituted a greater proportion (13%) of total production. In addition to Oligochaeta, copepods were also important contributors to the production of non-insect invertebrates. Most of the increase in total copepod production in Yr 2 occurred on bedrock outcrop. Little change in copepod production occurred in mixed substrate habitat (see Appendix 1). Large changes in community structure during treatment are reflected by the dissimilarity between this community and others (dendrogram, Fig. 1A).

Total numbers of taxa in C 53, C 54, and C 55 were very similar in Yr 1: 73, 74, and 71, respectively. During year 2, only 48 were recorded in C 54 versus 67 in C 55.

The relative contribution of functional groups

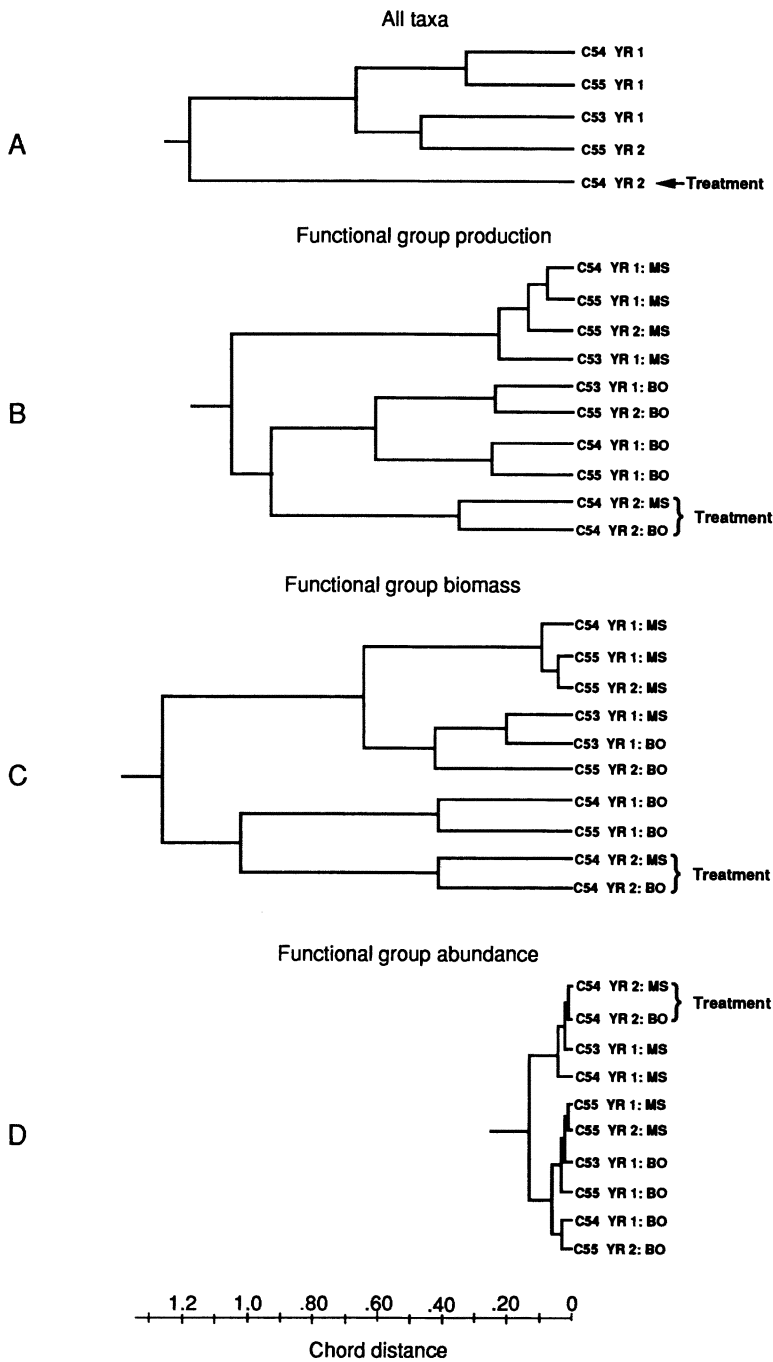


FIG. 1. Dendrograms resulting from cluster analysis of untransformed benthos data from three streams, C 53, C 54, and C 55, in Yr 1 (October 1984–September 1985) and in C 54 and C 55 in Yr 2 (January 1986–November 1986) when C 54 received insecticide. A.—Habitat-weighted production estimates for all taxa. B.—Production estimates of functional groups in mixed substrate (MS) and bedrock outcrop habitats (BO). C.—Biomass estimates of functional groups in both MS and BO habitats. D.—Abundance estimates of functional groups in both habitats. Clustering was performed using the chord distance measure and flexible strategy (beta = -0.25).

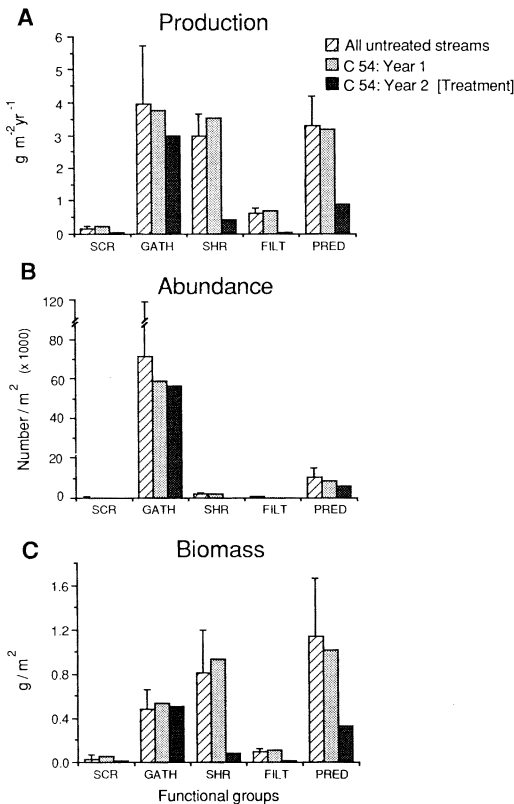


FIG. 2. Annual habitat-weighted functional group (A) production ($\text{mg AFDM m}^{-2} \text{ yr}^{-1}$), (B) abundance (number/m^2), and (C) biomass (mg AFDM/m^2) of macrofauna in all untreated streams (mean \pm 1 SE, $n = 4$) and C 54 during Yr 1 (pre-treatment) and C 54 during Yr 2 (treatment).

to habitat-weighted macrofaunal community production in C 54 during Yr 2 contrasted sharply with that of the previous year (Figs. 2A, 3). The marked difference between the insecticide disturbed community and the others, in terms of habitat-weighted functional composition and level of production, is illustrated by cluster analysis (Fig. 3). The disturbance of functional structure in C 54 in Yr 2 was also revealed by estimates of standing stock biomass (Fig. 2C); however, little change was seen in terms of abundances (Fig. 2B).

Gatherers were the dominant functional group in C 54 during treatment. Although gatherer production accounted for more community production than other functional groups in C 54 during Yr 2, its contribution was 21% lower

in Yr 2 compared with the previous year (Fig. 3). The three gatherer taxa in C 54 that contributed most (78%) to production in Yr 1—Chironomidae, Oligochaeta, and Copepoda—dominated production of gatherers (98%) in Yr 2 and were the principal contributors to production of the entire macrofaunal community (Fig. 4, Appendix 1). Although habitat-weighted chironomid production decreased by 64% in Yr 2, copepod and oligochaete production increased by 26% and 62%, respectively, during treatment of C 54. The increase in habitat-weighted copepod production was a consequence of their 14-fold increase on the bedrock outcrop, whereas production increased very little in the mixed substrate (Appendix 1). Although the actual increase in production of oligochaetes was greatest in the mixed substrate, the relative change in production on the bedrock outcrop was much

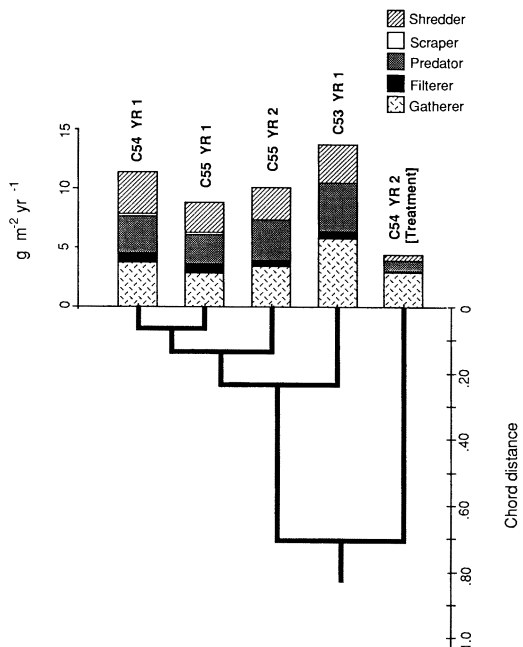


FIG. 3. Annual habitat-weighted production ($\text{g AFDM m}^{-2} \text{ yr}^{-1}$) of macrofaunal functional feeding groups in C 53, C 54 and C 55 in Yr 1 (October 1984–September 1985) and in C 54 and C 55 in Yr 2 (January 1986–November 1986) when C 54 received insecticide. The dendrogram indicates the dissimilarity between communities based on cluster analysis of the habitat-weighted functional group data. The analysis was performed as in Figure 1.

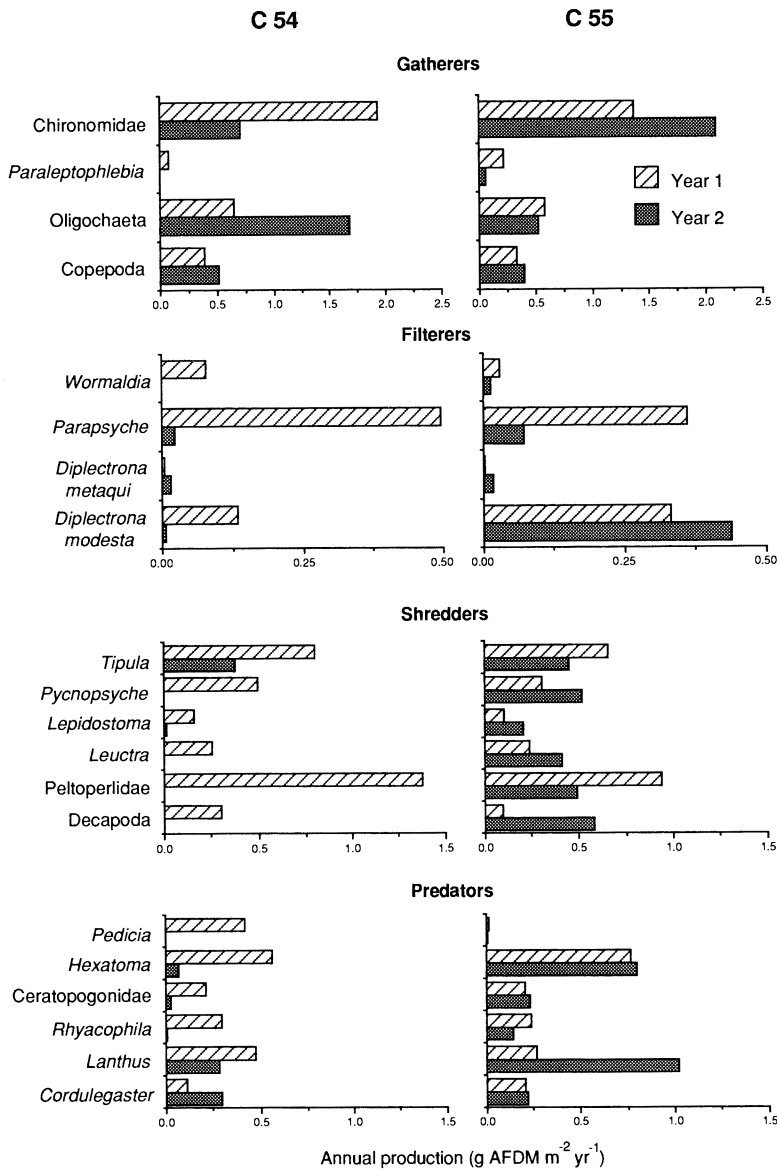


FIG. 4. Annual habitat-weighted production (g AFDM m⁻² yr⁻¹) of the major taxa in C 54 and C 55 during Yr 1 (pre-treatment: October 1984–September 1985) and Yr 2 (January 1986–November 1986) when C 54 received insecticide. Note that scale varies among functional groups.

higher (13×) than the 2× increase in the mixed substrate (Appendix 1).

Production of other functional groups in C 54 during treatment decreased much more than that of gatherers. Within the mixed substrate habitat, functional groups arranged in order of increasing proportional losses of production between years were as follows: gatherers (16%) <

predators (71%) < filterers (77%) < shredders (87%) < scrapers (93%) (Table 4). With the exception of the scraper group, proportional losses of functional group production on the bedrock outcrop in Yr 2 exceeded those in the mixed substrate: gatherers (41%) < predators (78%) < scrapers (82%) < filterers (95%) < shredders (>99%) (Table 4 and Appendix 1). A single fil-

terer species, the hydropsychid *Diplectrona me-taqui* Ross, increased in C 54 during Yr 2. Only early instars of the other filterer taxa were recovered in Yr 2. *Tipula* spp. were the sole substantial contributors to shredder production (> 87%) in mixed substrates in C 54 during treatment. Peltoperlidae, the dominant shredders before treatment, were eliminated from the bedrock outcrop habitat and only a few early instars of this and other shredder taxa were observed in the mixed substrate during treatment. Early instars of *Lepidostoma* and *Leuctra* were the only shredders found on bedrock outcrop during treatment (Appendix 1). The odonates *Lan-thus* and *Cordulegaster* were the predominant predators in C 54 during treatment, accounting for 60% of total predator production (Fig. 4). The only predators to show increases in production during treatment were *Cordulegaster*, Turbellaria, and Acari. Little change in Turbellaria production was measured in the mixed substrate, while on the bedrock outcrop production in Yr 2 was 14× higher than in Yr 1 (Appendix 1).

The similarity in functional structure among mixed substrate and bedrock outcrop communities during treatment of C 54 is evident from the dendrogram in Figure 1B. Both communities were dominated by the gatherer functional group and thus were grouped together and linked only distantly with communities of untreated streams. Cluster analysis of abundance data yielded a very different arrangement of groups; the distances between communities, including those of the treated stream, were small compared with biomass and production clusters (Fig. 1).

Community P/B ratios

Community P/B ratios in Yr 1 ranged between 4.1 (C 54) and 5.0 (C 53) in the mixed substrate habitat and between 4.8 (C 53) and 6.0 (C 54) on the bedrock outcrop (Table 4). The lower P/B in C 54 was partially a consequence of the high standing crop of crayfish which accounted for 23% of total mixed substrate biomass but contributed only 3% to production. Community P/B ratios in C 54 in Yr 2 were higher: 4.9 in the mixed substrate and 6.4 on the bedrock outcrop, indicating a shift to smaller animals with shorter generation times. In contrast, P/Bs decreased in C 55 during the sec-

ond year to 3.5 in the mixed substrate and 3.8 on the bedrock outcrop. Crayfish, with their low P/Bs, again influenced mixed substrate community P/Bs because of their elimination in C 54 and their substantial increase in C 55 (Appendix 1). The decline in bedrock outcrop P/B in C 55 was due largely to the decrease in numbers of *Parapsyche* and *D. modesta*.

Resource ingestion by functional groups

Shredders consumed an estimated 28–47% of average annual standing crop of leaves in the untreated streams, but only 4% of the leaf standing stock in the treated stream (Fig. 5A). Ingestion by gatherers was the highest among the major functional groups in all streams because of their high levels of production and low assimilation efficiencies. Gatherers consumed roughly 34–67% of total annual habitat-weighted FPOM standing stocks in the untreated streams and 26% of FPOM standing stock in the treated stream (Fig. 5B). Secondary consumers ingested a large portion of the animal production in all streams. Approximately 74–83% of total habitat-weighted macrofaunal production was consumed in the untreated streams (Fig. 5C). In the treated stream, an estimated 51% of macrofaunal production was ingested by secondary consumers.

Discussion

Production and functional structure among untreated streams

Total habitat-weighted production estimates in untreated streams during the two study years fell approximately in the middle of the range of values reported from other streams (Table 5). Habitat-weighted production in all three streams exceeded macrofaunal production measured in C 27 (Huryñ and Wallace 1987a), a larger, higher-elevation stream at Coweeta. The higher production in our study streams compared with C 27 was probably in part a consequence of warmer thermal regimes (4500–4700 degree-days/yr in C 53–C 55 vs. 2800–3300 degree-days/yr in C 27) which result in shorter CPIs for some taxa in the warmer streams. Furthermore, the streams in our study had greater standing stocks of organic matter which may have supported higher overall macroinvertebrate abundances. The

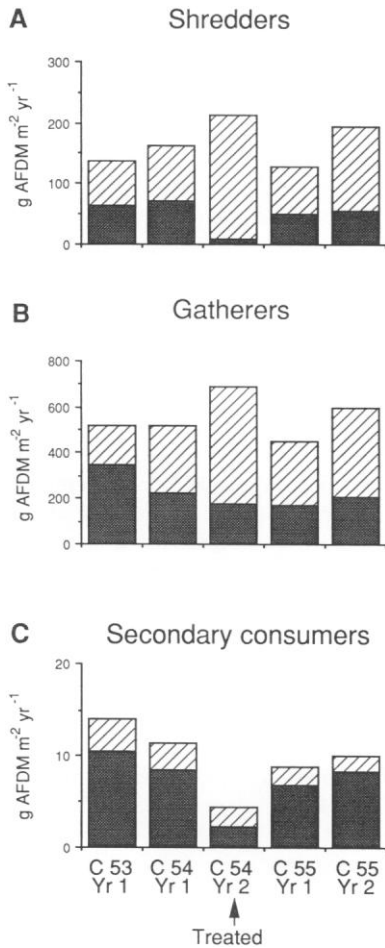


FIG. 5. Comparison of annual habitat-weighted ingestion of (A) shredders, (B) gatherers, and (C) secondary consumers with resource availability in C 53, C 54, and C 55 in Yr 1 (October 1984–September 1985) and in C 54 and C 55 in Yr 2 (January 1986–November 1986) when C 54 received insecticide. The height of each bar = resource availability (leaf litter standing crop in A, FPOM standing crop in B, and total macrofauna production in C) and the darker base of each bar = ingestion.

community P/B ratios observed in our streams were somewhat higher than those of C 27 and other 1st-order streams at higher latitudes, e.g., those studied by Mortensen and Simonsen (1983) and Iversen (1988), while the ratios were lower than those found in a 2nd-order Massachusetts stream and two southern blackwater streams (Table 5). As noted by Iversen (1988),

the relatively low P/B ratios observed in shaded headwater streams reflect the predominance of large-bodied invertebrates with relatively long CPIs, particularly shredders. In both our study and that of Huryn and Wallace (1987a), the abundance of crayfish, with a low P/B ratio, strongly influenced overall community P/B values.

The habitat-weighted and mixed substrate functional composition of the untreated study streams, with the codominance of shredder, gatherer, and predator functional groups, was similar to the functional organization observed in C 27 (Huryn and Wallace 1987a). The large contributions of shredder and gatherer functional groups to total production support predictions of the River Continuum Concept (RCC: Vannote et al. 1980, Minshall et al. 1985). Their importance reflects the predominance of allochthonous energy inputs into these heavily shaded and highly retentive headwater streams. However, in the bedrock outcrop habitat, the erosional characteristics, lack of retention structures, higher velocities, and consequent importance of filter feeders resulted in a functional structure more like that predicted by the RCC for mid-order streams (Huryn and Wallace 1987a).

In a study of recovery of C 53 from insecticide treatment, Wallace et al. (1986) observed that the recovery of functional structure was complete within two years after treatment ceased, yet differences in taxonomic composition still persisted. All taxa occurring in C 53 prior to treatment in 1980 (see Cuffney et al. 1984) had returned by Yr 1 of the present study. However, differences in the relative importance of the shredders *Peltoperlidae*, *Fattigia*, *Lepidostoma*, and *Pycnopsyche*, which were observed in C 53 two years after treatment (Wallace et al. 1986), persisted three years later (Appendix 1). Production of *Peltoperlidae* and *Fattigia* were significantly lower in C 53 than in the other two streams, while production of *Lepidostoma* and *Pycnopsyche* was significantly higher (based on confidence intervals around annual production estimates [95%: Krueger and Martin 1980]).

Production and organic matter relationships

In the untreated streams, organic matter standing crops appeared important in limiting macrofaunal production. For example, C 55, with

TABLE 5. Annual secondary production estimates of lotic macrofaunal communities, and the percent contributions of secondary consumers to total production. Where necessary, units of production were converted to g AFDM using coefficients given in Waters (1977). In the North Carolina streams, larval salamander production is included, whereas only macroinvertebrates are included in other studies.

Stream	Location	Production (g AFDM $m^{-2} yr^{-1}$)	% Sec- ondary con- sumers	Community P/B	Reference
1st order ^a	Minnesota	4.9-19.8	10-16	—	Krueger and Waters (1983)
1st order	Denmark	22.5	5	3.7	Mortensen and Simonsen (1983)
Spring	Denmark	9.6	9	2.7	Iversen (1988)
2nd order ^b	Massachusetts	3.9-4.3	11-14	7.1-7.4	Neves (1979)
1st order (untreated)	North Carolina	8.9-14.0	32-36	4.4-5.0	This study
1st order (treated)	North Carolina	4.3	22	5.1	This study
1st and 2nd order	North Carolina	7.4	28	2.6	Huryn and Wallace (1987)
2nd order (blackwater)	South Carolina	1.8-3.7	16-30	7.5-9.5	Smock et al. (1985)
5th-6th order ^c (blackwater)	Georgia	15.2-30.2	13-16	40.3-84.0	Benke et al. (1984)

^a Riffle habitat only.

^b Cobble habitat only.

^c Main channel.

lowest inputs of leaf litter (Cuffney et al. 1990) had significantly lower standing crops of total CPOM and FPOM in the mixed substrate habitat in Yr 1, and the lowest levels of production of the shredder, gatherer, and predator functional groups. Differences in organic matter standing crop and production levels between C 53 and C 54 were much less than between these two streams and C 55.

Relationships between amount of organic matter and level of functional group production among streams in Yr 1 were even stronger in the bedrock outcrop habitat than in the mixed substrate habitat. Shredder production was positively associated with leaf standing crop. A stronger positive relationship was observed between gatherer production and FPOM standing crop (C 53 > C 54 > C 55). In contrast, filterer production (C 55 > C 54 > C 53) was negatively associated with organic matter standing crop. Relationships between organic matter and production of these functional groups observed on the bedrock outcrop undoubtedly reflect their different food and habitat requirements. Shredders and gatherers are dependent upon retention of organic matter (greatest in C 53). Filterers are dependent upon the entrainment of their food, as well as the availability of suitable attachment sites. Among untreated streams, entrainment of organic matter was lowest in C 53 because of lower water velocities, discharge, and

base-flow FPOM concentrations (Cuffney et al. 1990).

Importance of predators

The large contribution that predators made toward total macrofaunal production in our streams is striking. Considerations of the relationships between stream size and macroinvertebrate functional organization in the RCC have excluded predators, stating that this functional group varies little in dominance with stream order and usually forms about 10% of total invertebrate biomass (Vannote et al. 1980, Cummins 1988). Our findings suggest that invertebrate predators in headwater streams can contribute substantially more than 10% to overall biomass and production. In the untreated streams, invertebrate predators accounted for 33-45% and 26-33% of total annual habitat-weighted biomass and production, respectively. Thus, the contribution of invertebrate predators was roughly equal to, or greater than, that of shredders and gatherers. Predators made up a larger portion of total macrofaunal production than generally observed in other community studies (Table 5). Huryn and Wallace (1987a) observed a similarly high proportion of predators in C 27, and Smock et al. (1985) found that predators formed 30% of macroinvertebrate production in a low-flow swamp site.

The type of vertebrate predators occurring in a stream and their level of production may be important in determining the relative proportion of macroinvertebrate predator production as a whole. No fish occur in these streams or in C 27; salamanders are the major vertebrate predators, and larval salamanders accounted for a small portion of total macrofaunal production. Since production of adult salamanders was not measured in these two studies, these estimates of vertebrate production are conservative. Yet larval salamanders are expected to be of primary importance in terms of predation on aquatic macroinvertebrates because they almost exclusively consume aquatic prey (Lugthart 1991), whereas adults feed heavily on terrestrial insects (Hairston 1949, Krzysik 1979, W. R. Woodall and J. B. Wallace, unpublished data). Other than those in North Carolina, production values cited in Table 5 include only macroinvertebrate communities; although fish were present, their production was not estimated. If fish production were included in these other studies, the proportion of predator production would be higher. However, the extent to which fish use food of aquatic versus terrestrial origin may vary among sites and communities. The higher proportion of macroinvertebrate predator production observed in the low-order, fishless Coweeta streams may reflect less intense predation pressure and competition from vertebrate predators than in most other streams listed in Table 5. There are suggestions from other studies in both lentic (Kajak et al. 1972) and lotic (Schofield et al. 1988) systems that the presence of fish may result in a lower proportion of invertebrate predators in a community. Studies that estimate both vertebrate and invertebrate production together are rare and are needed before we can better understand the interactions between these important components of the stream community (Benke et al. 1988).

The importance of predators in the untreated study streams is indicated clearly by the large proportion of total macrofaunal production estimated to be ingested by secondary consumers. This fairly high level of ingestion, coupled with a strong relationship observed between primary and secondary consumer production in the mixed substrate habitat among the three streams ($r^2 = 0.89$, $p < 0.05$), suggests that secondary consumers may be food-limited in these

streams. Prey availability was undoubtedly underestimated, however, since meiofauna provide energy to higher trophic levels (O'Doherty 1988) and were not thoroughly sampled because of the sieve size we used (P. B. Vila, University of Georgia, personal communication). The relative magnitude of meiofauna production and the size of its contribution to higher trophic levels requires further study.

No significant relationship was observed between the two consumer trophic levels on bedrock outcrops in the three streams, probably because of substantial variation in filter-feeder production in this habitat. A large portion of *Parapsyche* and *Diplectrona* production is derived from ingestion of animals (Ross and Wallace 1983). High secondary consumer/primary consumer ratios on the bedrock outcrop suggest that these filter feeders obtain much of their food not from prey originating within that habitat, but from prey drifting out of the mixed substrate habitat upstream (see Smith-Cuffney and Wallace 1987, Hury and Wallace 1987a).

Neves (1979) noted that trophic level production efficiency (the ratio between secondary consumer production and primary consumer production [Odum 1971]), which he determined in his study to be 13.8%, was similar to that observed in several other studies of benthic invertebrates. Based on this "relative constancy", Neves suggested that a production efficiency of 13% could be assumed and, with the annual production of invertebrate secondary consumers, possibly used to estimate the production of primary consumers. Because of the large contribution to production by invertebrate predators in the present study, much higher trophic level production efficiencies were found, ranging between 47 and 57% in untreated streams. Therefore, our results showed that the 13% production efficiency cannot be applied arbitrarily to different streams. However, the similarity in efficiencies noted among the Coweeta streams and among the larger streams cited by Neves (1979) suggest that, among streams of similar size and functional composition, some consistency in the relationship between trophic levels may exist.

Drought effects

Several taxa in C 55, such as Chironomidae (both Tanypodinae and non-Tanypodinae, see

Lugthart et al. 1990) and *Lanthus*, showed substantial increases in production from Yr 1 to Yr 2 in mixed substrate habitat. These increases may have been related directly or indirectly to severe drought. Wetted channel areas decreased during drought (Wallace et al. 1991a) and may have resulted in the concentration of some invertebrates. Extence (1981) observed this phenomenon in an English river and noted that it may have resulted from active movement of some invertebrates into wetted channel areas. Canton et al. (1984) reported that invertebrate predators, notably the dragonfly *Ophiogomphus severus*, increased during a drought year, presumably because of prey concentration. In addition, they found that a number of chironomid taxa had higher densities in the drought year.

Functional structure of the bedrock outcrop community may be more sensitive to a disturbance such as drought than is the mixed substrate community. Drought reduces flow, and causes a shift in the dominant food source from fine entrained particulates to deposits of CPOM and FPOM. Average discharge in C 55 during Yr 2 was only half that of the previous year and, as a result, leaf standing crop on the bedrock outcrop was almost 6× higher in Yr 2 than in Yr 1. This accumulation of leaves was probably responsible for the higher production of the shredders *Peltoperla* and *Lepidostoma* and the lower production of the filter feeder *Parapsyche cardis* in Yr 2. *Parapsyche*, which typically inhabit areas of high water velocity, would have been adversely affected by the reduction of suitable attachment sites on the bedrock outcrop caused by the higher leaf standing crops and lower flow rates. Furthermore, lower discharge during drought resulted in lower export of seston (Cuffney et al. 1990), and therefore the supply of drifting prey was probably lower.

The greater negative effects of drought observed on the bedrock outcrop communities of the present study contrasted with responses of invertebrates observed following another type of disturbance, clear-cutting. Gurtz and Wallace (1984) found that, in streams in clear-cut catchments, more taxa increased in density in the bedrock outcrop (rock face) than in any other substrate. They suggested that biological stability may be closely related to physical stability of the substrate. It is evident that the nature of disturbance will determine which substrate offers the best refuge. Clear-cutting enhances sed-

imentation and thereby causes habitat loss. The bedrock outcrops, subject to higher current velocities, were less susceptible to the deposition of sediments than other substrates and thus provided a superior habitat. In the present study, bedrock outcrop shifted from a site of entrainment to a site of deposition. This resulted in reduction of filter feeders, a dominant functional group in this habitat.

Decreases in production observed between years in C 55 for a number of taxa, such as *Paraleptophlebia*, *Amphinemura*, and *Peltoperla* (in mixed substrate habitat only), may have been related to drought as well. Specific reasons for such changes are unclear. Canton et al. (1984) noted that Ephemeroptera were affected most severely by reduced discharge in a third-order montane stream. They suggested that lower densities observed for mayflies, as well as other taxa, may have been related to loss of habitat and increased predation pressure.

Production per m² increased in C 55 during the drought of Yr 2; however, when considered on a whole-stream basis, this increase was undoubtedly offset somewhat by loss of wetted perimeter, which varied by about 30% among dry and wet periods in C 55 (Wallace et al. 1991a). Thus, the effects of drought on production in the entire stream versus per m² may give different results depending on severity and the extent to which wetted perimeter is reduced.

Production and functional structure within the treated stream

Insecticide treatments clearly had dramatic effects on secondary production and functional structure in C 54. The observed changes greatly exceeded those that could be expected as a result of drought alone. The shift from co-dominance of gatherer, shredder, and predator functional groups to the dominance of gatherers reflected the loss of many large-bodied, uni- or semi-voltine insect taxa and the increase of smaller animals with shorter life cycles, such as copepods and, potentially, some oligochaetes. Similar shifts in relative abundances and biomass of functional groups were observed in litterbags by Cuffney et al. (1984) during treatment of C 53. It is unlikely that changes in food quality (i.e., microbial conditioning of organic matter) contributed to the reductions in macrofaunal secondary production observed in our

study. Bacterial densities and respiration rates in leaves, wood, and sediments in C 54 during treatment did not differ from those prior to treatment or from those in the other streams (Cuffney et al. 1990). Moreover, hyphomycete fungal activity did not appear to be reduced by insecticide application to C 54 (Suberkropp and Wallace 1992).

The macroinvertebrate community present in C 54 during treatment was primarily composed of organisms that were either tolerant of insecticide or capable of rapid recolonization and growth between treatments. Many taxa, such as *Lepidostoma* and Peltoperlidae, showed recolonization between some treatments that coincided with adult oviposition periods, but they were present only as early instars. Apparently these taxa were unable to survive insecticide treatments (see Wallace et al. 1991b) and contributed little to total production. Odonata were apparently tolerant of insecticide in view of 1) their long life cycles (2–3 yr), 2) the collection of large individuals throughout the treatment year, and 3) the increase in *Cordulegaster* production during treatment. Muirhead-Thompson (1987) reported high degrees of tolerance for four species of dragonfly naiads that were exposed to high concentrations of two chlorinated hydrocarbon insecticides. In their study of insecticide treatment of C 53, Wallace et al. (1987) found that *Lanthis* was a generalist predator which shifted from a diet primarily of insects to one composed mainly of oligochaetes and copepods.

Chironomidae, Copepoda, and Oligochaeta contributed most to production during insecticide treatment. Chironomids and copepods (and possibly oligochaetes) apparently have shorter life cycles than much of the fauna that dominated production prior to treatment. Their capacity for rapid growth between insecticide disturbances provided these animals with resiliency, and was undoubtedly an important factor in their success. Hurny (1990) found that non-Tanypodinae chironomids in C 53 had life cycles ranging from bivoltine to polyvoltine (>12 cohorts per year). Aerial recolonization by adult chironomids could take place rapidly because adults were present almost year-round. Tolerance to insecticide may have been a factor contributing to the success of oligochaetes during treatment. Oligochaete abundances and biomass were disproportionately low in collec-

tions of drift during insecticide applications compared with their standing stocks in the benthos (Wallace et al. 1989). However, other factors, such as their depth in the substratum, may have reduced their propensity to drift.

Although our production estimates for non-Tanypodinae chironomids do account for multiple generations (Lugthart et al. 1990), those of Oligochaeta, and possibly Copepoda, are probably conservative. We estimated copepod production using an annual P:B ratio of 18, which is at the low end of the range (17–30) determined by O'Doherty (1988) in her study of copepods in a Coweeta stream. A P/B of 5 was used for production calculations of oligochaetes because taxa were grouped and voltinism was uncertain. Several studies have reported high reproductive rates for some oligochaete taxa (Brinkhurst and Cook 1980). If oligochaete P/Bs were actually much higher than we assumed, then production of this taxon and the gatherer functional group may have been underestimated considerably in the treated stream. For example, had a P/B of 10 been assumed, habitat-weighted oligochaete production in C 54 would have been >3 g/m² in Yr 2, and total gatherer production would have actually increased over Yr 1 levels.

Primary effects of pesticides have been defined as the direct, toxic effects on growth, survival, or reproduction of animals (Hurlbert 1975). Secondary effects result from changes in community structure and may include population increases due to predator removal (e.g., Ide 1956, Hurlbert et al. 1972) or increased food availability (Hawkes 1955). In the present study, a reduction in predation pressure appeared to play an important role in observed increases of some taxa, such as oligochaetes and copepods. The impact of predation on prey in C 54 is supported by differences in the degree of population changes observed between mixed substrate and bedrock outcrop habitats. The proportion of secondary consumer production within the bedrock outcrop habitat was almost half that found in the mixed substrate habitat. Some predators that had dominated during pretreatment, such as *Isoperla* and *Beloneuria* (Plecoptera), were apparently eliminated, while other important taxa, such as *Rhyacophila* (Trichoptera), Ceratopogonidae, and *Dicranota* (Diptera), were reduced to very low densities. The fact that copepods increased only on bedrock out-

crops, and the much higher proportional increase in oligochaete production in this habitat, suggests that these populations increased as a result of lower predation pressure. It is unlikely that food availability played a role in these increases because the ratio of FPOM to gatherer production in the mixed substrate habitat was approximately 14× higher than in the bedrock outcrop habitat. Macrofaunal inclusion and exclusion caging experiments in another Coweeta stream demonstrated that macrofauna can reduce meiofauna densities, probably by predation (O'Doherty 1988).

Much higher (14×) production of triclads in the bedrock outcrop habitat of C 54 during treatment compared with pre-treatment was probably partially the result of the increase in oligochaetes, their food supply. Food levels influence triclad populations (Boddington and Metrick 1977, Ball and Reynoldson 1981), and oligochaetes are often important prey of triclads (Reynoldson and Young 1965, Reynoldson and Davies 1970, Armitage and Young 1990). However, triclads did not increase in the mixed substrate habitat, despite the >2 fold increase of oligochaete production, suggesting that other mechanisms are also involved. These mechanisms may have included: 1) habitat preferences of triclads; 2) reduced predation pressure on triclad populations on bedrock outcrops as predators are known to influence their distributions (Wright 1975); or, 3) prey size preferences of triclads. Larger sizes of oligochaetes are less susceptible to triclad predation (de Silva 1976), and biomass of oligochaete prey in mixed substrates was 5× greater than on bedrock habitats.

The proportion of total habitat-weighted production contributed by secondary consumers in C 54 during the treatment year was only 22%, compared with their contribution of 32% in the pre-treatment year. As a result of this reduction in secondary consumer production, estimates of secondary consumer ingestion in C 54 were only 51% of total macrofaunal production, much less than the proportion consumed in untreated streams (74–83%).

In addition to treatment effects, C 54 experienced loss in wetted area as a consequence of drought in Yr 2 (Wallace et al. 1991a); however, in contrast to C 55, production per m² in C 54 declined sharply with insecticide treatment and loss of wetted perimeter in Yr 2.

In conclusion, annual benthic production was reasonably similar among untreated streams. Gatherers, shredders, and macroinvertebrate predators were the dominant functional groups. The contribution of macroinvertebrate predators to total annual production was greater than has been reported in most other studies of benthic community production. Organic matter standing crops appeared to play a role in determining levels of production and functional group composition in the untreated streams.

Insecticidal applications severely disturbed the macrofaunal community in C 54, resulting in a large decrease (by 62%) from Yr 1 to Yr 2 in secondary production and a shift in functional structure compared with untreated streams. The impact of this disturbance on leaf litter processing was shown by the large decrease in shredder ingestion during the treatment year. The effects of insecticide applications on functional group structure and production from Yr 1 to Yr 2 in C 54 greatly exceeded those attributable to a record drought in the reference stream, C 55. Although production during Yr 2 decreased by 62% in the treatment stream, overall community production in the reference stream was higher (12%) than that in Yr 1. In summary, both the magnitude and direction of change differed between the natural (drought) and insecticide-induced disturbance.

Our results demonstrate the need for production estimates when assessing resource use by animals and the effects of disturbances on macrofaunal communities. Measures of abundance did not reflect the important roles of shredders and predators in these streams, while biomass measurements underestimated the importance of small bodied gatherers. Furthermore, measurements of abundance greatly underestimated impact of the insecticide treatments on the community.

Macroinvertebrate production formed only a small portion of total energy flow. However, other work in these streams has demonstrated the importance of macroinvertebrates in ecosystem functions and the consequences of loss of macroinvertebrate diversity and production (Wallace et al. 1982, 1991a, Cuffney et al. 1984, 1990). Lower shredder production following insecticide treatment resulted in significant reductions in leaf litter processing rates, the amount of leaf litter processed annually, and

FPOM export (Cuffney et al. 1990). Furthermore, during treatment the decrease in FPOM export was about two-orders-of-magnitude greater than the decrease in secondary production (based on wetted-stream area) and the seasonal relationship of FPOM export to storms was also altered (Wallace et al. 1991a). The ecosystem functions of macroinvertebrates in headwater streams may be important for downstream communities dependent upon delivery of upstream food resources. The value of maintaining faunal diversity extends beyond the conservation of genetic material. Preservation of biodiversity should be an important goal in stream management as invertebrates strongly influence ecosystem function in these headwater streams.

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APPENDIX 1. Annual mean standing stock abundance (A; individuals/m²), ash-free dry biomass (B; mg/m²), and production of ash-free dry biomass (P; mg m⁻² yr⁻¹) of major macrofaunal taxa occurring in the mixed substrate and bedrock-outcrop habitats of C 53, C 54, and C 55 during year 1 (October 1984–September 1985) and year 2 (January 1986–November 1986). The streams are located within the Coweeta Hydrologic Laboratory, Macon County, North Carolina.

Taxon	Insect order ^a	CPI ^b (d)	Site	Year	Mixed substrate			Bedrock outcrop		
					A	B	P	A	B	P
Scrapers										
<i>Baetis</i> spp.	E	120	C 53	1	4	<1	2	13	2	20
			C 54	1	17	<1	2	73	8	114
			C 54	2	0	0	0	0	0	0
			C 55	1	4	<1	<1	7	<1	2
			C 55	2	0	0	0	2	<1	<1
<i>Stenonema</i> spp.	E	340	C 53	1	36	10	41	13	<1	1
			C 54	1	48	14	67	11	1	2
			C 54	2	89	3	15	2	<1	<1
			C 55	1	112	31	138	13	1	3
			C 55	2	24	10	35	5	8	7
<i>Hydroptila coweetensis</i> ^c	T	—	C 53	1	0	0	0	105	4	21
			C 54	1	0	0	0	16	<1	2
			C 54	2	0	0	0	0	0	0
			C 55	1	0	0	0	219	5	23
			C 55	2	0	0	0	108	3	17
<i>Ectopria thoracica</i> ^c	C	365	C 53	1	2	<1	1	0	0	0
			C 54	1	4	<1	1	37	20	63
			C 54	2	0	0	0	15	17	38
			C 55	1	6	1	3	39	13	29
			C 55	2	0	0	0	54	44	163
<i>Oulimnius latiusculus</i> ^c	C	635	C 53	1	0	0	0	0	0	0
			C 54	1	27	1	1	41	1	4
			C 54	2	0	0	0	0	0	0
			C 55	1	277	8	32	68	2	8
			C 55	2	187	5	19	103	3	11
Other taxa ^d	—	—	C 53	1	181	10	64	24	2	3
			C 54	1	69	52	158	126	7	24
			C 54	2	0	0	0	0	0	0
			C 55	1	26	2	7	144	9	35
			C 55	2	10	1	<1	79	13	36
SUM			C 53	1	223	20	108	155	8	45
			C 54	1	165	67	229	304	37	209
			C 54	2	89	3	15	17	17	38
			C 55	1	425	42	180	490	30	100
			C 55	2	221	16	54	351	71	234
Shredders										
<i>Leuctra</i> spp.	P	340	C 53	1	702	40	212	135	6	24
			C 54	1	1345	50	388	103	2	10
			C 54	2	49	1	3	11	<1	<1
			C 55	1	921	38	275	72	3	10
			C 55	2	1366	69	468	271	8	43
Peltoperlidae	P	540	C 53	1	439	84	432	318	96	368
			C 54	1	740	390	1650	753	171	875
			C 54	2	2	4	5	0	0	0

APPENDIX 1. Continued.

Taxon	Insect order ^a	CPI ^b (d)	Site	Year	Mixed substrate			Bedrock outcrop				
					A	B	P	A	B	P		
Shredders (continued)												
Peltoperlidae (cont.)			C 55	1	449	233	1025	913	98	373		
			C 55	2	258	117	446	938	179	799		
<i>Lepidostoma</i> spp.			T	246	C 53	1	848	112	834	201	26	119
					C 54	1	268	34	234	15	2	9
					C 54	2	34	3	16	14	<1	1
					C 55	1	153	20	121	64	2	4
					C 55	2	332	29	234	69	7	44
<i>Pycnopsyche</i> spp.			T	275	C 53	1	487	258	1781	157	91	589
					C 54	1	189	96	748	59	3	18
					C 54	2	75	1	5	0	0	0
					C 55	1	175	51	352	4	1	4
					C 55	2	116	99	592	125	5	26
<i>Molophilus</i> ^c			D	365	C 53	1	289	51	238	0	0	0
					C 54	1	305	58	265	2	<1	1
					C 54	2	35	8	32	0	0	0
					C 55	1	105	15	63	0	0	0
					C 55	2	84	28	129	0	0	0
<i>Tipula</i> spp.			D	310	C 53	1	43	45	336	7	12	22
					C 54	1	46	213	1233	1	2	2
					C 54	2	11	109	587	0	0	0
					C 55	1	34	152	755	3	3	8
					C 55	2	18	126	516	4	8	20
Decapoda ^e			—	—	C 53	1	<1	160	93	0	0	0
					C 54	1	7	404	234	0	0	0
					C 54	2	0	0	0	0	0	0
					C 55	1	2	96	55	0	0	0
					C 55	2	5	676	392	0	0	0
Other taxa ^f			—	—	C 53	1	25	29	91	11	8	15
					C 54	1	78	92	201	15	<1	1
					C 54	2	10	10	20	0	0	0
					C 55	1	102	78	186	1	<1	<1
					C 55	2	134	90	250	0	0	0
SUM					C 53	1	2833	779	4017	829	239	1137
					C 54	1	2978	1337	4953	948	180	916
					C 54	2	216	136	668	25	<1	1
					C 55	1	1941	683	2832	1057	107	399
					C 55	2	2313	1234	3027	1407	207	932
Collector-gatherers												
<i>Paraleptophlebia</i> spp.			E	340	C 53	1	492	23	140	134	6	30
					C 54	1	134	17	109	70	5	11
					C 54	2	26	5	8	37	<1	<1
					C 55	1	427	42	254	77	2	7
					C 55	2	69	17	69	48	2	9
<i>Serratella</i> sp.			E	330	C 53	1	42	2	9	671	81	552
					C 54	1	122	38	78	566	169	899
					C 54	2	0	0	0	30	2	7
					C 55	1	176	12	72	218	61	271
					C 55	2	1	2	3	68	20	82

APPENDIX 1. Continued.

Taxon	Insect order ^a	CPI ^b (d)	Site	Year	Mixed substrate			Bedrock outcrop		
					A	B	P	A	B	P
Collector-gatherers (continued)										
<i>Amphinemura wui</i>	P	300	C 53	1	33	4	17	678	51	386
			C 54	1	118	13	61	612	45	281
			C 54	2	10	1	1	37	<1	<1
			C 55	1	103	7	53	602	45	280
			C 55	2	52	1	2	265	22	107
Chironomidae ^{s,h}	D	—	C 53	1	40,685	233	4583	20,074	52	1172
			C 54	1	35,135	137	2524	10,743	41	813
			C 54	2	9868	47	927	5582	11	290
			C 55	1	16,366	62	1398	20,500	44	1161
			C 55	2	27,592	100	2216	17,000	50	1211
Copepoda ⁱ	—	—	C 53	1	77,163	77	1390	8919	9	160
			C 54	1	32,119	32	578	1503	2	27
			C 54	2	32,786	33	590	20,157	22	389
			C 55	1	20,736	21	373	2484	3	45
			C 55	2	24,699	25	445	4695	5	85
Nematoda ⁱ	—	—	C 53	1	22,105	17	84	832	1	3
			C 54	1	7363	6	28	306	<1	1
			C 54	2	13,615	10	52	1167	1	5
			C 55	1	6293	5	24	703	1	3
			C 55	2	10,580	8	40	784	1	3
Oligochaeta ⁱ	—	—	C 53	1	11,656	135	677	890	15	77
			C 54	1	7097	196	978	1208	8	41
			C 54	2	9268	462	2309	10,061	107	533
			C 55	1	3268	133	666	1332	7	36
			C 55	2	3270	119	593	1693	9	45
Other taxa ^k	—	—	C 53	1	1057	105	182	75	2	9
			C 54	1	795	248	332	97	3	16
			C 54	2	782	6	30	58	1	2
			C 55	1	607	78	182	88	<1	1
			C 55	2	527	369	346	42	2	8
SUM			C 53	1	153,233	596	7082	32,273	217	2389
			C 54	1	82,883	687	4688	15,105	273	2089
			C 54	2	66,355	564	3917	37,129	144	1226
			C 55	1	47,976	360	3022	26,004	163	1804
			C 55	2	66,790	641	3714	24,595	111	1550
Collector-filterers										
<i>Diplectrona metaqui</i>	T	332	C 53	1	53	26	135	33	17	75
			C 54	1	0	0	0	7	4	11
			C 54	2	0	0	0	15	11	43
			C 55	1	1	1	2	7	3	7
			C 55	2	10	4	7	45	24	98
<i>D. modesta</i>	T	332	C 53	1	185	45	275	63	16	67
			C 54	1	92	9	74	70	67	240
			C 54	2	38	4	5	15	4	12
			C 55	1	232	65	362	72	25	132
			C 55	2	573	55	473	80	72	215
<i>Parapsyche cardis</i>	T	332	C 53	1	10	1	5	164	70	435
			C 54	1	35	9	25	339	206	1361

APPENDIX 1. Continued.

Taxon	Insect order ^a	CPI ^b (d)	Site	Year	Mixed substrate			Bedrock outcrop		
					A	B	P	A	B	P
Collector-filterers (continued)										
<i>Parapsyche</i>			C 54	2	12	8	20	47	6	29
<i>cardis</i> (cont.)			C 55	1	0	0	0	530	385	2735
			C 55	2	0	0	0	112	159	547
<i>Polycentropus</i>	T	332	C 53	1	24	1	3	0	0	0
sp.			C 54	1	4	1	1	0	0	0
			C 54	2	0	0	0	0	0	0
			C 55	1	2	1	2	0	0	0
			C 55	2	2	1	2	0	0	0
<i>Wormaldia</i>	T	63	C 53	1	21	3	83	10	4	51
<i>moesta</i> ¹			C 54	1	10	<1	2	33	10	191
			C 54	2	0	0	0	0	0	0
			C 55	1	2	1	8	26	4	75
			C 55	2	0	0	0	0	0	0
<i>W. moesta</i> ^m	T	269	C 53	1	33	4	25	17	4	20
			C 54	1	15	2	7	27	3	15
			C 54	2	0	0	0	0	0	0
			C 55	1	21	2	13	18	3	15
			C 55	2	10	3	11	56	6	27
Simuliidae	D	180	C 53	1	0	0	0	83	2	10
			C 54	1	41	1	4	12	<1	2
			C 54	2	0	0	0	3	<1	<1
			C 55	1	10	1	4	68	1	6
			C 55	2	0	0	0	2	<1	1
SUM			C 53	1	326	80	526	370	113	658
			C 54	1	197	22	113	488	290	1820
			C 54	2	50	12	25	80	21	84
			C 55	1	268	71	391	721	421	2970
			C 55	2	595	63	493	295	261	888
Predators										
1) Invertebrata										
<i>Cordulegaster</i>	O	1140	C 53	1	98	244	675	0	0	0
sp.			C 54	1	68	81	170	0	0	0
			C 54	2	80	161	451	0	0	0
			C 55	1	21	95	235	0	0	0
			C 55	2	46	142	255	0	0	0
<i>Lanthus</i>	O	660	C 53	1	163	365	1040	10	13	14
<i>vernalis</i>			C 54	1	109	205	715	1	14	18
			C 54	2	70	171	423	12	23	21
			C 55	1	77	89	284	5	52	158
			C 55	2	85	338	1171	5	18	23
<i>Beloneuria</i>	P	660	C 53	1	67	138	351	25	22	38
spp.			C 54	1	31	91	266	8	20	23
			C 54	2	0	0	0	0	0	0
			C 55	1	35	114	335	80	51	134
			C 55	2	32	43	104	68	58	154
<i>Isoperla</i> spp.	P	300	C 53	1	154	13	77	99	17	123
			C 54	1	101	15	83	226	52	334
			C 54	2	0	0	0	0	0	0

APPENDIX 1. Continued.

Taxon	Insect order ^a	CPI ^b (d)	Site	Year	Mixed substrate			Bedrock outcrop		
					A	B	P	A	B	P
Predators (continued)										
<i>Isoperla</i> (cont.)			C 55	1	70	8	57	126	16	99
			C 55	2	46	2	13	54	10	49
<i>Rhyacophila</i> spp.	T	340	C 53	1	56	30	188	102	41	170
			C 54	1	122	49	340	138	35	213
			C 54	2	6	1	5	14	1	2
			C 55	1	123	32	238	136	47	262
			C 55	2	44	26	139	67	48	197
<i>Ceratopogonidae</i> ^c	D	365	C 53	1	5534	121	653	681	20	74
			C 54	1	2808	65	314	179	4	16
			C 54	2	537	10	42	55	2	2
			C 55	1	2245	41	238	124	2	9
			C 55	2	2670	52	268	265	4	19
<i>Glutops</i> sp. ^c	D	365	C 53	1	19	49	253	1	3	4
			C 54	1	5	19	94	0	0	0
			C 54	2	6	18	75	0	0	0
			C 55	1	4	30	109	0	0	0
			C 55	2	11	60	243	0	0	0
<i>Hexatoma</i> sp. ^c	D	365	C 53	1	323	71	365	20	15	19
			C 54	1	523	199	853	19	4	10
			C 54	2	86	102	91	6	1	1
			C 55	1	343	884	884	4	1	2
			C 55	2	478	906	906	35	3	4
<i>Pedicia</i> spp. ^c	D	365	C 53	1	112	48	273	23	2	6
			C 54	1	20	85	650	3	<1	<1
			C 54	2	0	0	0	0	0	0
			C 55	1	10	3	14	18	1	1
			C 55	2	9	3	7	0	0	0
<i>Tanypodinae</i>	D	340	C 53	1	3162	17	127	1904	12	87
			C 54	1	2921	22	130	566	3	19
			C 54	2	664	8	47	325	1	3
			C 55	1	1511	7	52	707	3	23
			C 55	2	3198	18	127	990	2	13
<i>Acari</i> ⁱ	—	—	C 53	1	7076	19	95	2462	7	33
			C 54	1	3134	8	42	1747	5	24
			C 54	2	4928	13	66	2782	7	37
			C 55	1	2877	8	39	2484	7	33
			C 55	2	4152	11	56	2770	7	37
<i>Turbellaria</i> ⁱ	—	—	C 53	1	606	16	78	79	3	14
			C 54	1	221	5	26	46	1	7
			C 54	2	245	6	30	770	20	102
			C 55	1	142	3	15	95	4	21
			C 55	2	60	1	5	129	4	22
<i>Other taxa</i> ⁿ	—	—	C 53	1	520	167	480	573	29	159
			C 54	1	710	330	635	377	11	41
			C 54	2	21	10	24	31	1	3
			C 55	1	268	101	166	216	18	80
			C 55	2	417	406	462	261	18	69
SUM:			C 53	1	17,890	1298	4655	5979	184	741
Invertebrata			C 54	1	10,783	1174	4318	3310	149	705
			C 54	2	6643	430	1265	3995	56	171

APPENDIX 1. Continued.

Taxon	Insect order ^a	CPI ^b (d)	Site	Year	Mixed substrate			Bedrock outcrop		
					A	B	P	A	B	P
Predators (continued)										
Invertebrata (SUM)			C 55	1	7726	723	2666	4165	202	822
(cont.)			C 55	2	11,248	1317	3756	4644	172	587
SUM:			C 53	1	41	629	982	10	301	119
Vertebrata			C 54	1	14	300	277	2	42	52
(Salamander			C 54	2	6	55	79	0	0	0
larvae)			C 55	1	9	99	181	3	133	42
			C 55	2	7	62	36	11	323	117

^a E = Ephemeroptera, P = Plecoptera, O = Odonata, T = Trichoptera, D = Diptera, C = Coleoptera.

^b CPI = Cohort Production Interval.

^c Life history unclear; CPI of 365 assumed.

^d *Epeorus (Iron) sp.*, *Stenacron sp.*, *Molanna blenda*, *Neophylax mitchelli*, *Thaumalea thornburghae*, *Optioservus immunis*.

^e Assuming P/B = 0.58 (Huryn and Wallace 1987c).

^f *Fattigia pele*, *Pseudostenophylax uniformis*, *Psilotreta spp.*, *Theliopsyche sp.*, *Limonia sp.*, *Anchytarsus bicolor*.

^g Exclusive of Tanypodinae.

^h Production estimated by the method of Huryn and Wallace (1986).

ⁱ Assuming P/B = 18 (O'Doherty 1988).

^j Assuming P/B = 5 (Benke 1984).

^k *Habrophlebia vibrans*, *Soyedina carolinensis*, *Lype diversa*, *Dixa sp.*, *Leptotarsus sp.*, Nymphomyiidae, *Ormosia sp.*, *Sciara sp.*, Cladocera, Decapoda.

^l Summer cohort.

^m Winter cohort.

ⁿ *Sweltsa lateralis*, *Pseudogoera singularis*, *Dicranota spp.*, Dolichopodidae, Empididae, nr. *Pedicia*, *Pilaria spp.*, *Pseudolimnophila spp.*, Decapoda.