Effects of Resource Limitation on a Detrital-Based Ecosystem

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EFFECTS OF RESOURCE LIMITATION ON A
DETRITAL-BASED ECOSYSTEM

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Abstract. We examined the importance of terrestrial detrital inputs to secondary productivity of a headwater stream. Following a year of pretreatment studies on two headwater streams, we excluded terrestrial litter inputs (=treatment) to one stream while using the other as a reference. We excluded litter for 3 yr followed by 1 yr of small woody debris (≤10 cm diameter) removal and litter exclusion. Monthly benthic samples were collected from dominant mixed substrate (cobble, pebble, and sand-silt) as well as from moss-covered bedrock outcrop substrates. We used randomized intervention analysis (RIA) to test the null hypotheses that no change in abundance or biomass of functional feeding groups or specific taxa occurred in the treatment stream relative to the reference stream.

Benthic organic matter was significantly lower in mixed substrate habitats of the treatment stream; however, small woody debris did not show a significant reduction prior to manual removal during year 4. At the end of the treatment period, total benthic invertebrate abundance in mixed substrates in the treatment stream was less than one-tenth of that in the reference stream, and biomass in the treatment stream was one-sixth of that in the reference stream. Biomass and abundance of shredders, gatherers, total primary consumers, and predators displayed significant treatment effects ($P < 0.012$–0.00001, RIA) in the mixed substrate habitats during the 4-yr treatment. Only scraper and filterer functional groups failed to show differences between streams during the 4-yr treatment. Twenty of the 30 taxa comprising >90% of total secondary production displayed a significant decrease in abundance, biomass, or both, in the treatment stream relative to the reference stream ($P < 0.05$, RIA). Total secondary production in mixed substrate habitats declined to 22% of pretreatment values by the fourth year of treatment and is among the lowest reported for streams. Removal of small woody debris resulted in an additional 47–50% decrease in abundance, biomass, and production of the benthic fauna compared to the third year of litter exclusion.

In contrast, fauna of moss-covered bedrock substrates displayed no significant differences between streams in terms of any functional group, or in terms of abundance and biomass of individual taxa. Furthermore, secondary production on bedrock outcrops remained similar between streams. Results strongly suggest that food webs of bedrock habitats are not as closely linked to immediate allochthonous inputs from the surrounding forest as those of mixed substrates, although they may be linked in the long term.

Using a 9-yr record, we determined the relationship between organic matter standing crop and invertebrate abundance, biomass, and production in the treatment stream. There is a strong relationship between leaf litter standing crops and secondary productivity in mixed substrate habitats. In contrast, bedrock outcrop fauna showed a stronger relationship to fine benthic organic matter (FBOM) standing crop than to leaf litter. Despite a large residual mass of organic matter in the treatment stream, as well as other ongoing sources of input (dissolved organic matter, soil organic matter, and throughfall), litter exclusion clearly shows strong bottom-up effects extending from primary consumers to predators.

Abundance, biomass, and production of predators in the treatment stream were also strongly related to that of their prey throughout all pretreatment and treatment years. Our results suggest that, owing to simple bioenergetic efficiencies, production of predators is constrained by productivity of their prey. Although our results clearly show strong bottom-up effects, the importance of predators (top-down) can not be ignored, as available data suggest that predators consume most benthic invertebrate production. Our study underscores the importance of terrestrial–aquatic linkages in maintaining productivity of headwater streams draining forested catchments.

Key words: bottom-up regulation, benthos; detritus; food webs; functional groups; land–water interface; resource limitation; secondary production; stream; stream insects; top-down; woody debris.

INTRODUCTION

Detritus has been recognized as an important component of both terrestrial and aquatic systems (e.g., Odum and de la Cruz 1963). About 70 to 80% of all primary production from forest (O'Neill and Reichle 1980) and stream (Wetzel and Ward 1992) ecosystems eventually enters the detrital food web. In most streams draining forested headwater catchments in eastern North America, allochthonous inputs from the surrounding forest far exceed those of within-stream primary production (Webster et al. 1995). Furthermore, with the exception of tundra and arid land streams, allochthonous inputs to streams exceed those of autochthonous sources for most streams that have been studied (Webster and Meyer 1997).

Detritus is pervasive throughout most ecosystems, and many animal populations rely on it as a food resource. For example, soil invertebrate abundance and biomass display positive relationships with soil organic matter in agroecosystems (Hendrix et al. 1986, 1992, Roper and Gupta 1995) as well as in forests (Blair et al. 1994). Small plot manipulations of litter supplies to the forest floor also indicate an important linkage between organic matter and nematode populations (Arpin et al. 1995). Large pools of dissolved and particulate organic detritus may be much more important in lakes than generally acknowledged (Wetzel 1995). In some regions, high biomass of intertidal grazers and filter feeders is maintained by subsidies of detritus from offshore kelp beds (Bustamante et al. 1995, Bustamante and Branch 1996). Detritus and its infusion into many classic food webs are often-ignored but very important parts of food web complexity (Polis and Strong 1996, Polis et al. 1997). Furthermore, detrital subsidies from one habitat may contribute substantially to productivity of other habitats (Polis at el. 1997).

Since the first half of the 20th century, it has been known that many stream-dwelling invertebrates consume detritus of terrestrial origin (e.g., Lloyd 1921, Hynes 1941, Brinck 1949), and productivity of some invertebrate assemblages in some headwater streams relies on detrital inputs from the surrounding forest (Hynes 1963, Ross 1963). Thus, widely accepted linkages exist between detritivores, detritus, and detritus processing in streams (Fisher and Likens 1973, Cummins 1974, Hynes 1975, Anderson and Sedell 1979, Webster and Benfield 1986, Cushing et al. 1995, and Wallace and Webster 1996).

Detritivores held in artificial streamside channels were food limited (Richardson 1991), and higher levels of coarse particulate organic matter (CPOM) loading resulted in higher densities of collectors feeding on fine particulate organic matter (FPOM, Richardson and Neill 1991). Significant increases were observed only for pooled gatherers and filterers and not for individual taxa. Moderate, nonsignificant increases in predatory

invertebrates were found in the high CPOM channels (Richardson and Neill 1991). In an ecosystem-level study, we excluded leaf litter inputs to a headwater stream for 3 yr and found significant decreases in abundance or biomass of CPOM- and FPOM-feeding detritivores as well as predators compared to populations in a nearby reference stream (Wallace et al. 1997). In this manipulation of detrital inputs we noted that, despite litter exclusion, a large residual mass of woody debris and FBOM remained in the treated stream.

Woody debris in streams influences a wide array of abiotic features as well as biotic community structure and function (Harmon et al. 1986). These include (1) rapid dissipation of stream energy in high-gradient systems (Heede 1972, Bilby and Likens 1980, Smith et al. 1993a, b), (2) reduced current velocities (Trotter 1990), (3) increased retention of particulate organic matter, which may also provide food for invertebrates (e.g., Bilby and Likens 1980, Speaker et al. 1984, Smock et al 1989, Trotter 1990, Wallace et al. 1995a), (4) substrate for invertebrates (Nilson and Larimore 1973, Benke et al. 1984, Smock et al. 1989), and (5) modification of stream habitat and benthic community structure (Molles 1982, Huryn and Wallace 1987a, Smock et al. 1989, Wallace et al. 1995a).

In addition to providing substrate and habitat, woody debris also provides food for some xylophagous invertebrates (Pereira et al. 1982) as well as enhances availability of FPOM by particle retention. During a 3-yr litter exclusion study, several invertebrate populations that showed no reductions in abundance or biomass represented taxa known to feed to some extent on woody debris or woody particles buried in the stream bed (Wallace et al. 1997). Epixylic biofilms—organic layers consisting of microbiota, extracellular polysacccharides, trapped FPOM, and dissolved organic materials—also represent a potential food resource for invertebrates (Couch and Meyer 1992, Tank and Webster 1998). Therefore, woody debris represents an additional terrestrial–aquatic linkage not directly addressed by Wallace et al. (1997) or other studies.

Many studies have examined the effects of adding resources such as nutrients to lakes (e.g., Schindler et al. 1978, Edmondson and Lehman 1981) and streams (Elwood et al. 1981, Peterson et al. 1985, Hart and Robinson 1990, Rosemond et al. 1993), or organic matter to streams (Warren et al. 1964). However, ecosystem-level studies that examine the effects of resource depression on stream invertebrate assemblages such as leaf litter reduction (Reice 1991, Richardson 1991, Wallace et al. 1997) or light reduction (Fuller et al. 1986, Steinman et al. 1990) are rare.

Most of the studies that examined the influence of resources on stream communities were conducted over relatively short time periods (weeks to <1 yr) and examined changes in either abundance or biomass. Indirect effects associated with food limitation in detrital

TABLE 1. Physical parameters of streams draining catchments C 53 (reference) and C 55 (treatment = litter exclusion) at the Coweeta Hydrologic Laboratory. Elevations were measured at the gauging flumes.

Variable	C 53	C 55
Catchment		
Area (ha)	5.2	7.5
Elevation (m asl)	829	810
Channel length (m)	135	170
Wetted width (m)†	0.7–1.2	1.2–1.6
Bankful channel area (m²)	327	373
Bedrock outcrop, % composition	27	13
Mixed substrates, % composition	73	87
Discharge (L/s)		
Average (5-yr avg.)	1.85	2.39
Maximum (5-yr)	34.0	40.2
Temperature (for 1985–1997, °C)		
Annual average (12-yr avg.)	12.2	12.2
Annual degree-days (12-yr avg.)	4485	4512
Maximum (12 yr)	20.3	20.1
Minimum (12 yr)	0.7	0.7
Chemistry (1985–1993)		
pH	6.8	6.7
HCO₃ (mg/L as CaCO₃)	4.38	3.6
NO₃-N (µg/L)	3	4
NH₄-N (µg/L)	2	2
SRP (µg/L)	3	2

† Average wetted widths as measured during dry and wet periods.

food webs probably require several generations of invertebrate consumers to detect significant changes (Richardson and Neill 1991). Multi-year manipulations of entire ecosystems are important tools to assess environmental change and the physical, chemical, and biotic factors controlling ecosystem-level processes (Carpenter et al. 1995). Therefore, experimental manipulation of terrestrial detrital inputs over multiple years represents an approach that allows assessment of terrestrial–aquatic linkages between allochthonous detritus and animal communities at the ecosystem level. However, few studies have examined the influence of resource manipulation on secondary production, which provides a better understanding of energy flow through the animal community than either abundance or biomass (e.g., Benke 1993).

In this paper, we report on a two-stage detritus manipulation that includes three years of leaf litter exclusion and a fourth year of litter exclusion combined with small woody debris removal. The objectives of this study were to assess the impact of this detritus manipulation on the following: (1) stream organic matter inputs and standing crops, (2) benthic animal abundance and biomass on two distinct types of substrates, and (3) secondary production, the flow (or flux) of mass·area⁻¹·time⁻¹, which incorporates abundance, biomass, individual growth rates, survivorship, and development times into a single value (Benke 1993). Finally, we provide long-term data including 5 yr of pretreatment and 4 yr of treatment (3 yr of litter exclusion and 1 yr of litter exclusion combined with small woody debris removal) linking benthic pro-

ductivity with inputs of organic matter from the surrounding forest. Our broad objective is to assess the effects of an ecosystem-level resource reduction on animal community structure.

STUDY SITES

The two streams examined in this study are within the Coweeta Hydrologic Laboratory (U.S. 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 were given by Swank and Crossley (1988). The study streams are first order, and drain catchments (C) 53 (reference) and 55 (treatment). Vegetation consists of mixed hardwoods, dominated by oaks and hickories. Dense growths of understory rhododendron (*Rhododendron maximum*) 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 two streams (Table 1). Streams are fishless, and salamanders are the only vertebrates. Discharge was gauged continuously using FW-1 stage and ISCO 3230 Bubble Flow Meter (ISCO, Inc., Lincoln, Nebraska USA) recorders attached to 30-cm H-flumes at the base of each catchment.

The substrate particle size distribution was assessed visually at 1-m intervals along the entire length of each stream (Table 1). In the two streams, 73% (reference) to 87% (treatment) of the substrate consisted of a heterogeneous mixture of cobbles, pebbles, gravel, sand, and silt, which we term mixed substrate habitat. The remaining substrate was composed of stretches of bed-

rock outcrop with growths of moss. The overall rough-
ness of the stream bed topography, including woody
debris, results in high retention, with abundant accu-
mulations of leaves and wood. Cuffney et al. (1990)
and Wallace et al. (1991) reported additional infor-
mation about the study streams.

Precipitation during our study was usually above the
long-term average of 182 cm/yr. When expressed as a
percentage of the long-term average, year 1 (pretreat-
ment) = 106%, year 2 = 124%, year 3 = 97%, year
4 = 111%, and year 5 = 114% (based on a 64-yr record
from the Coweeta Hydrologic Laboratory data files).

METHODS

Benthic sampling

Invertebrates and benthic organic matter were sam-
pled randomly by two methods (Lugthart and Wallace
1992). The mixed substrate habitats were sampled with
a 400-cm^2 corer. Material within the corer was removed
by hand and with a cup (to ≈10-cm depth or bedrock).
After removal, water depths in the corer were measured
for volume estimates, and following agitation, a sub-
sample of the water in the corer was removed for later
organic matter quantification using the methods de-
scribed by Lugthart and Wallace (1992). Bedrock out-
crops were sampled by scraping and brushing moss and
associated particles from a 15 × 15 cm area into a
plastic bag that was pressed to the rock surface. From
September 1993 to August 1997 samples were col-
lected monthly from each stream. Seven benthic sam-
ples, four from mixed substrates and three from bed-
rock outcrops, were collected from each stream on each
sampling date.

Organic matter in samples, including invertebrates
and salamanders, was elutriated from the inorganic sub-
strate, passed through nested 1-mm and 250-μm sieves,
and preserved in a 6–8% formalin solution containing
Phloxine B dye to facilitate sorting. Animals were re-
moved from the CPOM on the 1-mm sieve by hand
picking under 15× magnification and preserved in 6–
8% formalin solution. CPOM and FBOM in the sam-
ples were processed, weighed, ashed, and re-weighed
to obtain ash free dry mass (AFDM) of different cat-
egories following the procedures of Lugthart and Wal-
lace (1992). Material on the 250-μm sieve was sub-
sampled (1/8–1/64 of the whole sample) using a sample
splitter (Waters 1969) following Lugthart and Wallace
(1992). Invertebrates in the subsample were removed
by hand using a stereomicroscope (15× magnification).
Invertebrates and larval salamanders were identified
and counted. Identifications of 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 mea-
sured to the nearest mm using 12× magnification and
a graduated stage or an ocular micrometer. We mea-

sured snout–vent lengths of salamanders. For Cope-
poda, Hydracarina, Nematoda, and Cladocera, biomass
(AFDM) was obtained from mean mass of >50 indi-
viduals 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 for most taxa was estimated using
the size–frequency method (Hamilton 1969) and was
corrected for the cohort production interval (CPI, Ben-
ke 1979). Invertebrate CPIs were the same as those
used by Lugthart and Wallace (1992) and were esti-
mated using length–frequency histograms constructed
from monthly samples of each taxon in either the study
streams or another Coweeta stream (Huryn and Wallace
1987a, b). For salamanders, we used larval develop-
ment periods from Lugthart (1991).

Production of non-Tanypodinae chironomids was es-
timated using the community-level method of Huryn
(1990). An empirically derived production/biomass
(P/B) value of 18 for Copepoda (O'Doherty 1985) was
assumed. The product of standing stock biomass and
annual P/B ratio was used to estimate production for
the remaining taxa. Theoretical P/B values of 5 and 10
were used for several taxa considered to be univoltine
and bivoltine, respectively (Waters 1977, Lugthart and
Wallace 1992). With the exception of oligochaetes,
these taxa comprised a very small portion of total bio-
mass. Oligochaete taxa were grouped, and voltinism
was uncertain; thus production was estimated using a
P/B value of 5. These estimates may be conservative,
since higher reproductive rates have been reported for
some oligochaetes (Brinkhurst and Cook 1980).

Production was estimated separately for the mixed
substrate and bedrock outcrop substrate. Habitat-
weighted production for the entire stream can be cal-
culated using the proportion of bedrock outcrop and
mixed substrates (Table 1).

Animals were assigned to the following functional
feeding groups: shredder, collector-gatherer (=gath-
erers), scraper, collector-filterer (=filterers), or preda-
tor. Designations were made following Merritt and
Cummins (1996) or based on our knowledge of the
local fauna. Generally these followed those of Lugthart
and Wallace (1992) and Whiles and Wallace (1995),
the one exception being Stenonema sp. Extensive gut
analysis of Stenonema specimens revealed little evi-
dence of diatom feeding in these streams, and they were
transferred from scrapers to collectors (S. L. Eggert, J.
B. Wallace, and J. L. Meyer, unpublished data). For
between-stream analysis of total primary consumers,
we summed shredders, gatherers, scrapers, and filterers.
For long-term (9 yr) measurements of production, we
used previous measurements from 1985 and 1986 (Lug-

TABLE 2. Direct leaf-fall (g AFDM·m^{-2}·yr^{-1}) and lateral movement (= blow-in) of leaves (g AFDM·linear m^{-1}·yr^{-1}) for the reference stream (C 53) and the treatment stream (C 55) during pretreatment and treatment (litter exclusion) years.

Stream	Measurement	n	Mean ($\pm$1 SD)
C 53	Direct fall	6	387 ($\pm$25.1)
C 55	Direct fall†	6	338 ($\pm$55.0)
C 55	Direct fall (treatment)‡	3	18.0 ($\pm$11.1)
C 53	Lateral movement	6	472 ($\pm$190.4)
C 55	Lateral movement§	6	293 ($\pm$103.1)
C 55	Lateral movement (treatment)‖	3	18.1 ($\pm$8.2)

Note: During treatment periods in C 55, direct litterfall and lateral movement traps were located inside and outside the exclusion canopy and the lateral movement fence.
    † Includes 3-yr pretreatment and 3 yr of measurement outside exclusion canopy.
    ‡ Includes 3-yr of measurements made inside litter exclusion canopy.
    § Includes 3-yr of pretreatment and 3 yr of measurements outside lateral movement fence.
    ‖ Includes 3 yr of measurements made inside lateral movement fence.

thart and Wallace 1992) and 1989 and 1990 (Whiles and Wallace 1995) from C 55. *Stenonema* sp. was reassigned as a gatherer group for these multi-year comparisons.

Functional feeding groups are based primarily on mode of feeding. This is not entirely satisfactory for filter-feeding hydropsychid caddisflies, which are omnivorous in these streams; a portion of their food is derived from animal consumption. For long-term comparison of predator–prey relationships, we assigned a portion of filterer abundance and biomass to predators (30% for *Parapsyche cardis* and 15% for *Diplectrona* spp.) based on the animal consumption values of these taxa in a nearby Coweeta stream (Ross and Wallace 1983). Our values for total primary consumers and predators differ slightly from those reported by Wallace et al. (1997) because they include another year of data and because filterers were recognized as omnivores.

Following a year of pretreatment study on C 55 and the reference stream (C 53), a litter exclusion canopy was constructed in August 1993 on C 55. The canopy, made from gill netting (1.2-cm mesh), was constructed over the bankful channel width and below the rhododendron understory to exclude falling leaves and small woody debris. Along each side of the 180-m canopy, we erected a fence 20 cm high to exclude blow-in and lateral movement of litter. The canopy was open at the sides to allow aerial insect colonization. Any accumulated leaf litter on the canopy was removed at regular intervals using a leaf blower. Light attenuation by the canopy is <1%. In late summer 1996, following 3 yr of litter exclusion, we removed all small (≤10 cm diameter) woody debris on the stream bed surface by hand. All woody debris removed from the stream bed was measured (length and diameter) and subsampled to obtain mass per unit volume. Subsamples of known volume and surface area were also collected and preserved in formalin to assess invertebrate populations associated with removed wood. On 12 November 1996 and 10 April 1997 we removed small woody debris appearing on the stream bed, because buried wood surfaced during storm flows.

Pretreatment litterfall inputs were assessed from the period of winter 1985 through autumn 1988 using eighteen 0.25-m^2 traps placed every 10 m along or above each stream. Lateral litter inputs were estimated using 12 traps (0.5 m long) placed along the banks of each stream (Wallace et al. 1995b). Following canopy construction, direct litterfall was measured using the same type direct-fall traps inside ($n = 16$) and outside ($n = 6$) the canopy, as well as lateral movement traps inside ($n = 16$) and outside ($n = 6$) the lateral movement fence of C55. Concurrently, direct ($n = 6$) and lateral movement ($n = 6$) traps were placed along the reference stream (C 53). Collecting and processing litter inputs followed the procedure described by Wallace et al. (1995b).

This ecosystem-level study is unreplicated, employing one treatment and one reference stream. We used Randomized Intervention Analysis (RIA, Carpenter et al. 1989) for comparing before- and after-treatment changes in C 55 relative to C 53 for benthic detritus and abundance and biomass of specific animal taxa and functional feeding groups. RIA tests the null hypothesis that no change in the variable of interest occurred in the treatment stream relative to the reference stream following treatment. Rejection of the null hypothesis of no change, combined with divergent trends between reference and treatment following manipulation, implies a treatment effect.

RESULTS

Leaf litter inputs

Direct and lateral movement traps showed that leaf litter inputs to C 55 were reduced by 95% for direct leaf-fall and 94% for lateral movement by the exclusion canopy and lateral movement fence (Table 2). Direct leaf-fall into the treatment stream was 338 g AFDM·m^{-2}·yr^{-1} during pretreatment and outside the canopy during treatment, compared to 18 g·m^{-2}·yr^{-1} for traps under the canopy. Lateral movement declined from 293 g AFDM·linear m^{-1}·yr^{-1} outside the lateral movement fence to 18 g inside the fence. RIA indicated

TABLE 3. Organic matter standing crops (g AFDM/m²) for mixed substrate and bedrock outcrop habitats before treatment (before) and following treatment (after = litter exclusion) of C 55. C 53 is the reference stream.

Habitat	C 53, before	C 55, before	C 53, after	C 55, after	RIA probability	n
Mixed substrates						
Total FBOM	1081.2	772.5	1535.8	584.7	<0.000001	72
Total CBOM	1057.9	704.7	1387.2	527.6	0.010	72
Leaf detritus	149.4	111.1	258.9	7.1	<0.000001	72
Small woody debris†	690.9	443.6	735.9	434.1	0.709†	72
Small woody debris‡	690.9	443.6	844.6	121.5	0.037‡	36
Bedrock outcrop						
Total FBOM	16.0	14.8	19.9	18.0	0.833	60
Total CBOM	34.3	31.1	29.9	17.0	0.395	60
Moss	9.2	14.7	9.8	9.6	0.102	60

Notes: Results of the RIA are based on monthly samples with "before" data from 1984–1985 and 1992–1993 and "after" data from September 1993 to August 1997. RIA tests the null hypothesis that no change occurred for each type of organic matter in the treatment stream (C 55) relative to the reference stream (C 53), with n = total number of months included in test. Monthly data for bedrock outcrop samples in 1984–1985 were not available. CBOM = coarse benthic organic matter (>1 mm), FBOM = fine benthic organic matter (<1 mm).

† Includes entire litter exclusion period plus small wood removal year for the treatment stream.

‡ Includes only last year (small woody debris removal) for the treatment stream.

a significant difference in leaf-fall between the reference stream and measurements made under the canopy of the treatment stream ($P = 0.021$), but not outside the canopy ($P = 0.271$). Lateral movement measures indicated very significant differences in litter input between reference and treatment streams during the exclusion period ($P < 0.0001$), but no difference between streams outside the fence ($P = 0.115$).

Organic matter standing crop

Benthic organic matter standing crop displayed significant changes between streams only in the mixed substrate habitats. Three categories of benthic organic matter (leaf detritus, fine benthic organic matter [FBOM], and total coarse benthic organic matter [CBOM]) showed significant between-stream differences during the litter exclusion and the small woody debris removal period (Table 3). Changes in leaf detritus and FBOM were highly significant between streams ($P < 0.000001$), whereas the change in CBOM

was marginally significant ($P = 0.010$). Despite small woody debris removal during the fourth year of litter exclusion, the overall decrease in small woody debris throughout the period was not significantly different between streams ($P = 0.709$ for mixed substrates). However, following small wood removal, i.e., comparing only the fourth year of treatment (litter exclusion and small woody debris removal) with pretreatment, there was a significant difference in small woody debris between streams ($P = 0.037$, Table 3). In contrast to mixed substrates, moss and FBOM stored on bedrock substrates showed no significant difference between streams during the 4-yr treatment period (Table 3).

Temporal differences between streams in average benthic organic matter (BOM) standing crop were evident in mixed substrate habitats. Over the 4-yr period of litter exclusion, BOM declined in the litter exclusion stream and increased in the reference stream (Fig. 1 and Table 4). During the entire treatment period, BOM standing crop in mixed substrates of the exclusion
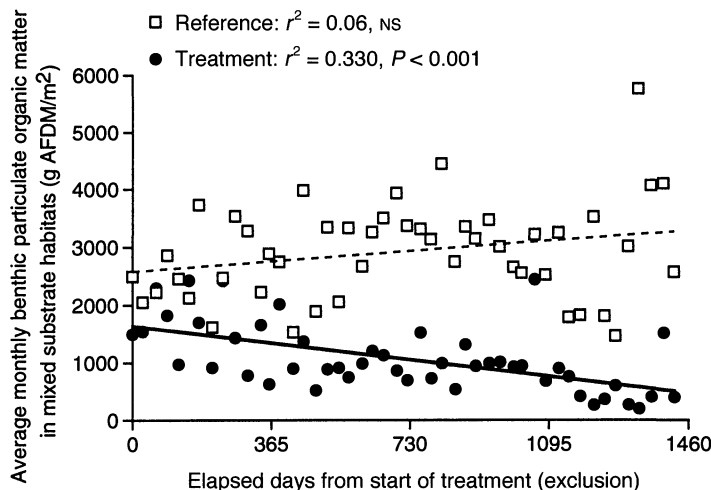

FIG. 1. Average monthly standing crop of benthic particulate organic matter in mixed substrate habitats of the reference (C 53) and treatment (C 55) streams vs. elapsed days from start of pretreatment. Data include the 4-yr period of litter exclusion and 1 yr of small woody debris removal (C 55) starting in September 1993 and ending in August 1997. See Table 4 for regression statistics.

TABLE 4. The top part of the table reports the coefficient of determination (r^2) between time (elapsed days, independent variable) from start of litter exclusion in September 1993 and monthly average standing crop of benthic organic matter (g AFDM/m^2, dependent variable), including total benthic organic matter (BOM), coarse benthic organic matter (CBOM), and fine benthic organic matter (FBOM), in mixed substrate habitats of the treatment stream (C 55, litter exclusion) and the reference stream (C 53). The bottom part of the table gives the same information for total invertebrate abundance (individuals/m^2) and invertebrate biomass (mg AFDM/m^2).

Stream	Dependent variable	r^2	P	Slope	95% CI (for slope)
Benthic organic matter					
C 53	Total BOM	0.059	>0.05	NS	
C 55	Total BOM	0.330	<0.001	−0.795	± 0.336
C 53	Total CBOM	0.037	>0.1	NS	
C 55	Total CBOM	0.243	<0.001	−0.517	± 0.271
C 53	Total FBOM	0.038	>0.1	NS	
C 55	Total FBOM	0.211	<0.001	−0.278	± 0.159
Invertebrates					
C 53	Total invertebrate abundance	0.025	>0.2	NS	
C 55	Total invertebrate abundance	0.400	<0.001	−17.55	± 6.4
C 53	Total invertebrate biomass	0.002	>0.5	NS	
C 55	Total invertebrate biomass	0.333	<0.001	−0.442	± 0.19

Notes: P = significance level of regression; slope (coefficient) has units of g AFDM·m^{-2}·d^{-1} for organic matter, individuals·m^{-2}·d^{-1} for invertebrate abundance, and mg AFDM·m^{-2}·d^{-1} for invertebrate biomass. In each case, n = 48 and df = 46; NS = nonsignificant relationship.

stream declined at an average rate of 0.795 ± 0.336 g AFDM·m^{-2}·d^{-1} (mean ± 95% CI, Table 4). This decline includes both CBOM and FBOM (0.517 ± 271, 0.278 ± 0.159 g AFDM·m^{-2}·d^{-1}, respectively [mean ± 95% CI, Table 4]).

Invertebrate response

Total invertebrate abundance in mixed substrate habitats of the treatment stream and reference stream displayed different trends during the treatment period. Invertebrate abundance decreased in the exclusion stream during the treatment period, while increasing in the reference stream, resulting in a very significant treatment effect between streams (P < 0.000001, RIA; Table 5). Invertebrate biomass in the mixed substrate habitats of the treatment stream at the end of the 4-yr treatment was 21% of the pretreatment year, while that of the reference stream exhibited little change (<6%)

between pretreatment and treatment periods (P < 0.001, RIA; Table 5).

Total invertebrate abundance in the mixed substrates of the treatment stream decreased during each successive year (Table 5 and Appendix). The loss of invertebrates in mixed substrate habitats of the treatment stream was 17.5 ± 6.4 individuals·m^{-2}·d^{-1} (mean ± 95% CI) during the 4-yr treatment. Average invertebrate biomass loss during the treatment was 0.44 ± 0.19 mg AFDM·m^{-2}·d^{-1} (Table 4). Although overall abundance of invertebrates in mixed substrate habitats of the reference stream increased during the study, they displayed no distinct relationship with elapsed days, as did those of the treatment stream (Table 4).

In sharp contrast to mixed substrates, invertebrate abundance and biomass in moss-covered bedrock habitats exhibited little change between pretreatment and treatment periods. Average total abundance of inver-

TABLE 5. Average annual standing stock abundance and biomass of total invertebrates in mixed substrates and moss-covered bedrock substrates in the reference (C 53) and treatment (C 55) streams for the pretreatment year, each of the three years of litter exclusion (LE), and litter exclusion plus small woody debris removal (year 4).

Stream and substrate	Pretreatment	LE, yr 1	LE, yr 2	LE, yr 3	LE + wood removal, yr 4	RIA probability
Abundance (individuals/m^2)						
C 53, mixed	62 252	82 749	106 361	93 949	110 083	
C 55, mixed	37 670	27 570	21 800	16 663	8 803	<0.000001
C 53, bedrock	20 477	15 642	20 090	15 015	13 869	
C 55, bedrock	16 514	8537	15 507	22 079	14 776	0.998
Biomass (mg AFDM/m^2)						
C 53, mixed	1 815	1 685	2 082	2 289	1 707	
C 55, mixed	1 002	684	450	426	212	<0.001
C 53, bedrock	870	384	478	589	518	
C 55, bedrock	611	172	345	400	289	0.545

Note: Randomized intervention analyses (RIA) are probabilities of no change (log[x + 1]-transformed data) in benthic abundance and biomass between the reference and treatment streams for each of the substrate types following treatment of C 55.

TABLE 6. Average abundance and standing stock biomass for invertebrate functional feeding groups in mixed substrate habitats of the reference (C 53) and treatment (C 55) streams during the pretreatment period (before = September 1992 to August 1993) and treatment period (leaf litter exclusion and small wood removal [C 55], September 1993 to August 1997).

Functional group	C 53, before	C 53, after	C 55, before	C 55, after	RIA probability
Abundance (individuals/m²)					
Scrapers	44	23	562	387	0.408
Shredders	1 360	2 849	954	506	<0.000001
Gatherers	53 733	85 722	30 940	15 144	<0.000001
Filterers	288	402	323	176	0.174
Total primary consumers	55 425	88 995	32 778	16 214	<0.000001
Predators	6 827	9 291	4 892	2 496	<0.000001
Biomass (mg AFDM/m²)					
Scrapers	2	3	6	7	0.670
Shredders	700	726	401	187	0.012
Gatherers	339	283	158	63	0.001
Filterers	102	38	35	25	0.326
Total primary consumers	1 143	1 050	600	282	0.006
Predators	672	891	403	161	<0.000001

Note: Randomized intervention analyses (RIA) are probabilities of no change (log $[x + 1]$-transformed data) in benthic abundance and biomass of each functional group between reference and treatment stream following treatment of C 55.

tebrates declined from the pretreatment to treatment period in bedrock habitats of both streams, i.e., by ~10% in the manipulated stream and 32% in the reference stream ($P = 0.998$, RIA, Table 5). Invertebrate biomass on bedrock outcrops also decreased, exhibiting a 53% decline during the treatment period in the treatment stream and a 40% decline in the reference stream ($P = 0.545$, RIA, Table 5). Furthermore, abundance and biomass of invertebrate populations on bedrock substrates tended to fluctuate in a similar manner over the 5 yr of the study (Table 5 and Appendix). Thus, invertebrate populations in moss-covered bedrock habitats in the two streams exhibited similar fluctuations throughout the 5-yr study, whereas those in mixed substrate habitats showed opposite trends.

Functional group changes

Abundance of shredders, gatherers, predators, and total primary consumers in mixed substrate habitats changed significantly after litter was excluded ($P < 0.000001$, RIA; Table 6). In the treatment stream, each of these four groups averaged a 47 to 51% decrease in abundance in mixed substrate habitats during the 4-yr treatment, compared to pretreatment values. Conversely, the abundance of shredders, gatherers, total primary consumers, and invertebrate predators increased in the reference stream during this same interval (Table 6 and Appendix). In addition to invertebrate predators, salamander abundance exhibited a significant treatment effect ($P = 0.009$, RIA). Annual values for most shredders, gatherers, predators, and total primary consumers tended to decrease in the treatment stream during each successive year (Appendix).

Invertebrate predator ($P < 0.000001$, RIA) and gatherer ($P < 0.001$, RIA) biomass changed significantly following litter exclusion. Biomass of shredders ($P < 0.012$, RIA), total primary consumers ($P < 0.006$, RIA), and salamanders ($P < 0.01$, RIA) also decreased

significantly following treatment. Although the increase in scrapers in the treatment stream was not significant ($P = 0.670$, RIA), this was the only functional group that did not show a decrease in biomass in mixed substrate habitats of the treatment stream following litter exclusion (Appendix).

In sharp contrast to mixed substrate habitats, no functional group displayed significant between-stream differences for either abundance ($P = 0.22–0.863$, RIA) or biomass ($P = 0.39–0.994$, RIA) in the bedrock outcrop substrates following litter exclusion and wood removal (Table 7). Salamanders also exhibited no change in bedrock outcrop habitats ($P = 1.0$ for abundance and $P = 0.863$ for salamander biomass). However, we caution that salamander abundance and biomass in bedrock habitats was very low and variable.

Individual taxa

At least 18 of the major taxa, which contributed >90% of total benthic production in mixed substrates, had either reduced abundance, biomass, or both, in the treatment relative to the reference (Table 8). Among the shredders displaying significant changes were plecopterans (Peltoperlidae and *Leuctra* spp.) and trichopterans (*Lepidostoma* spp. and *Pycnopsyche* spp.). One trichopteran shredder (*Fattigia pele*) exhibited no significant change following treatment. Although no dipteran shredders exhibited significant changes, three taxa of Tipulidae, *Tipula* spp., *Molophilus* sp., and *Lipsothrix* sp., approached significance ($P < 0.10$) in either abundance or biomass (Table 8). When only the fourth year of treatment (wood removal and litter exclusion) was compared with pretreatment, there was a significant difference (RIA) between streams for abundance ($P = 0.013$) and biomass ($P = 0.04$) of *Tipula* and *Molophilus* ($P = 0.024$). However, *Lipsothrix* biomass did not differ significantly between streams for pretreatment and fourth year of treatment ($P = 0.069$).

TABLE 7. Average abundance and standing stock biomass for invertebrate functional feeding groups in bedrock outcrop habitats of the reference (C 53) and treatment (C 55) streams during the pretreatment period (before = September 1992 to August 1993) and treatment period (litter exclusion and small wood removal [C 55], September 1993 to August 1997).

Functional group	C 53, before	C 53, after	C 55, before	C 55, after	RIA probability
Abundance (individuals/m^2)					
Scrapers	174	266	262	379	0.782
Shredders	578	786	622	520	0.400
Gatherers	15 554	11 296	12 191	11 631	0.752
Filterers	1 125	1 125	906	761	0.227
Total primary consumers	17 434	13 473	13 982	13 290	0.863
Predators	3 043	2 681	2 532	1 934	0.317
Biomass (mg AFDM/m^2)					
Scrapers	59	23	36	27	0.822
Shredders	82	64	52	35	0.574
Gatherers	186	92	90	61	0.994
Filterers	429	258	337	140	0.916
Total primary consumers	757	436	514	263	0.612
Predators	113	56	97	38	0.686

Note: Randomized intervention analyses (RIA) are probabilities of no change (log[x + 1]-transformed data) in benthic abundance and biomass for each functional group between reference and treatment stream.

Among gatherer taxa, the decrease in abundance of copepods and chironomids were especially striking, declining 78% and 57%, respectively, between pretreatment and the third year of litter exclusion. Following small wood removal, copepods and chironomids declined by 95% and 76%, respectively, of pretreatment values. The wood-associated larvae of Sciaridae (Diptera) showed a significant decrease in the treatment stream (P = 0.004 for abundance and 0.006 for biomass, RIA) when only the fourth year of treatment was compared with pretreatment. Three taxa, *Neophylax* sp, a scraper; *Seratella* sp., a gatherer; and *Diplectrona modesta,* a filterer, increased significantly in the mixed substrate habitat of the treatment stream relative to the reference stream (Table 8).

Invertebrate predators in four orders exhibited a change between streams in mixed substrate habitats following treatment. These changes include decreases in abundance and biomass of two odonates, *Lanthus* sp. and *Cordulegaster* sp. The perlid stonefly, *Beloneuria* sp., decreased in biomass in the treatment stream by 95% in this period. Dipteran predators were also affected, with abundance declining by 6–81% for Ceratopogonidae, Tanypodinae, and *Hexatoma* spp. in mixed substrate habitats of the treatment stream (Table 8 and Appendix.).

Functional group production

By the fourth year of resource reduction, total secondary production in mixed substrate habitats of the treatment stream had declined by 78% from pretreatment values (5.01 g vs. 1.1 g AFDM·m^{-2}·yr^{-1}), while increasing by 6% in the reference stream (9.28 vs. 9.91 g AFDM·m^{-2}·yr^{-1}; Table 9). The decrease in production in the litter exclusion stream was more pronounced for predators than gatherers, gatherers than shredders, and shredders than filterers. However, one functional group, scrapers, displayed an average yearly increase of ~13% in production from the pretreatment year in the mixed

substrate habitats of the treatment stream (Table 9 and Appendix.). Total secondary production of invertebrates declined during each successive year of treatment in the mixed substrate habitat of the treatment stream. In contrast, that of the reference stream increased somewhat during the same period (Table 9).

In distinct contrast to mixed substrates, total secondary production of invertebrates in bedrock habitats of both streams fluctuated in a similar pattern during each year of the study (Table 9). Except for scrapers, each functional feeding group displayed similar fluctuations or reductions in bedrock outcrops of the reference stream during this same period (Table 9). As observed for mixed substrate habitats, scraper production in bedrock outcrops during the last two years of treatment of the treatment stream was higher than that of the pretreatment year.

Temporal trends in invertebrate populations

Trends in total primary consumer, invertebrate predator, gatherer, and shredder abundance or biomass in mixed substrate habitats of the reference and litter-excluded stream over the 1825-d study are shown in Fig. 2. Each of these groups decreased significantly through time in the litter-exclusion stream relative to the reference stream. Plots of monthly abundance indicate that the significant between-stream difference was due to a slight increase in the reference stream during years 2 through 5 and a consistent decrease in the treatment stream (Fig. 2). Annual cycles of abundance (peaks in autumn/winter of each year) were evident in the treatment stream even following litter exclusion, but total numbers of individuals declined each successive year. The increased downward trends in abundance and biomass following removal of small woody debris (~day 1460, in Fig. 2) are evident for most groups.

Invertebrates in bedrock outcrop habitats showed very different patterns from those of mixed substrate habitats. Primary consumer and predator populations

TABLE 8. Randomized intervention analysis of probability of no change in abundance and biomass of functional groups and specific taxa between the reference stream and the treatment stream for four years of litter exclusion and including one year of small woody debris removal.

Functional group and taxon	Order	Mixed substrates		Bedrock substrates	
		Probability, abundance	Probability, biomass	Probability, abundance	Probability, biomass
Scrapers					
Epeorus sp.	E	0.409	0.528	0.142	0.085
Baetis sp.	E	0.428	0.213	0.017	0.221
Ectopria sp.	C	0.859	0.785	0.487	0.063
Neophylax sp.	T	**<0.000001**	**0.015**	0.344	**0.042**
Shredders					
Peltoperlidae	P	0.089	0.003	0.816	0.762
Leuctra spp.	P	0.011	0.001	0.118	0.191
Lepidostoma spp.	T	<0.000001	<0.000001	0.359	0.424
Pycnopsyche spp.	T	0.004	0.003	0.214	0.125
Fattigia pele	T	0.266	0.160	1.000	0.976
Tipula spp.	D	0.069	0.422	0.769	0.781
Molophilus spp.	D	0.222	0.060	1.000	1.000
Lipsothrix sp.	D	0.934	0.062	1.000	0.823
Gatherers					
Nematoda	NI	0.018	0.059	0.938	0.682
Oligochaeta	NI	.17	0.816	0.514	0.089
Copepoda	NI	<0.000001	<0.000001	0.992	0.616
Paraleptophlebia sp.	E	0.217	0.494	0.481	0.577
Stenonema spp.†	E	<0.000001	<0.000001	**0.028**	0.280
Seratella sp.	E	**0.010**	0.137	0.822	0.250
Lype diversa	T	0.972	0.988	0.558	0.844
Sciaridae (*Bradysia* sp.)	D	0.175	0.179	0.752	0.703
Chironomidae‡	D	0.001	<0.000001	0.601	0.610
Filterers					
Diplectrona modesta	T	**0.022**	0.116	0.434	0.163
Parapsyche cardis	T	0.516	0.126	0.827	0.911
Invertebrate predators					
Lanthus sp.	O	<0.000001	0.001	0.922	0.755
Cordulegaster sp.	O	<0.000001	0.004		
Beloneuria sp.	P	0.006	0.004	0.309	0.968
Isoperla spp.	P	0.516	0.244	0.472	0.194
Sweltsa lateralis	P	0.542	0.393	0.264	1.000
Rhyacophila spp.	T	0.982	0.021	0.246	0.413
Pseudogoera sp.	T	0.414	0.701	0.212	**0.025**
Tanypodinae	D	<0.000001	<0.000001	0.186	0.084
Ceratopogoniidae	D	<0.000001	0.001	0.954	0.186
Hexatoma spp.	D	<0.000001	<0.000001	0.646	0.788
Dicranota spp.	D	0.212	0.872	0.090	0.285
Pedicia sp.	D	0.064	0.100	0.136	0.489
Empididae	D	0.262	0.486	0.805	0.771
Vertebrate predators					
Salamanders		0.009	0.010	1.000	0.863

Notes: All analyses were run on log (*x* + 1)-transformed data based on monthly means from both mixed substrate and bedrock habitats (*n* = 60 for each habitat). Insect orders as follows: D = Diptera, E = Ephemeroptera, NI = Noninsect, O = Odonata, P = Plecoptera, and T = Trichoptera. Bold type denotes those taxa whose abundance or biomass increased in a particular habitat in the treatment stream relative to the reference stream. All other significant changes were decreases in the treatment stream.
† Functional feeding group based on absence of significant diatoms in gut content analysis.
‡ Non-Tanypodinae Chironomidae.

in the moss-covered bedrock habitat showed similar monthly trends in both streams, with abundance and biomass declining during year 2 of the study and increasing to year 1 levels during the final two years (Fig. 3).

Additive effects of wood removal

The additive effects of wood removal were examined using RIA comparisons between streams for abundance and biomass of each functional feeding group for the last year of exclusion along with that of litter exclusion plus small woody debris removal. Invertebrate biomass of functional groups of shredders, gatherers, and total primary consumers differed significantly between streams for the mixed substrates (RIA, *P* < 0.05, Table 10). However, biomass did not differ significantly between streams for bedrock substrates following small

TABLE 9. Annual secondary production (mg AFDM·m^{-2}·yr^{-1}) of invertebrates by functional feeding group in mixed substrate and bedrock habitats of the reference (C 53) and treatment (C 55) streams.

Functional group	Stream	Year 1	Year 2	Year 3	Year 4	Year 5
Mixed substrates						
Scrapers	C 53	13	16	10	2	24
	C 55	33	35	26	51	37
Shredders	C 53	3 851	3 625	3 646	5 443	2 774
	C 55	1 810	1 718	545	1 003	242
Gatherers	C 53	2 586	2 524	3 114	2 908	4 302
	C 55	1 356	760	835	619	327
Filterers	C 53	473	171	268	209	173
	C 55	256	133	118	173	112
Predators	C 53	2 357	3 106	3 661	4 706	2 639
	C 55	1 629	1 237	630	279	386
Sum	C 53	9 280	9 442	10 699	13 267	9 912
	C 55	5 014	3 884	2 154	2 125	1 104
Bedrock outcrop						
Scrapers	C 53	202	54	142	110	193
	C 55	137	32	45	213	176
Shredders	C 53	387	512	411	637	218
	C 55	412	382	190	420	144
Gatherers	C 53	1 520	799	1 258	839	849
	C 55	918	378	865	934	805
Filterers	C 53	3 704	1 099	1 414	2 211	2 399
	C 55	3 202	404	957	1 265	1 552
Predators	C 53	722	382	363	367	284
	C 55	446	136	202	362	149
Sum	C 53	6 535	2 846	3 588	4 163	3 943
	C 55	5 115	1 332	2 259	3 193	2 826

Note: Year 1 is the pretreatment year (September 1992–August 1993) for C 55, years 2–4 (September 1993–August 1997) are the years of litter exclusion, and year 5 is the year of litter exclusion and small woody debris removal for C 55.

wood removal. Comparison of abundance of invertebrates between these two periods revealed no significant differences between streams for any functional group in either mixed substrate or bedrock substrate (RIA, $P > 0.05$, Table 10).

Relationships between primary consumers and predators

Is there any evidence that predator abundance and biomass track that of their prey, and do similar relationships exist for the treatment and reference stream? During the 5-yr period, monthly benthic samples displayed a significant positive relationship between predator and primary consumer abundance and in some cases also biomass. For example, in mixed substrate habitats of both reference and treatment streams, there were significant relationships between monthly ($n = 60$) abundance of predators and that of primary consumers (reference stream, $r^2 = 0.545, P < 0.001$; treatment stream, $r^2 = 0.728, P < 0.001$; Table 11). The mixed substrates of the treatment stream also displayed a significant relationship ($r^2 = 0.292, P < 0.001$) between predator and primary consumer biomass, whereas the reference did not (Table 11). Gatherers constitute the most important component of the prey items in guts of predators, and predator abundance and biomass were generally positively related to that of gatherers (Table 11).

In bedrock outcrop habitats of both streams, there was a significant relationship between predator and primary consumer abundance and biomass. Predator

abundance in monthly ($n = 60$) bedrock samples was strongly related to that of primary consumer abundance in both streams (reference stream, $r^2 = 0.56, P < 0.001$; treatment stream, $r^2 = 0.68, P < 0.001$). Predator biomass and primary consumer biomass on bedrock outcrop substrates were also strongly related (reference stream, $r^2 = 0.63, P < 0.001$; treatment stream, $r^2 = 0.649, P < 0.001$; Table 11). However, predator biomass in bedrock habitats of both streams was not as strongly related to gatherer biomass as was predator and gatherer abundance (Table 11).

Long-term relationships between resources and primary and secondary consumers

The five years of pretreatment studies of C 55 encompassed extreme drought and wet periods at Coweeta. During these five years, there were vast differences in leaf litter standing crop among years. Quite apart from the timing of storms, there was a significant negative relationship between maximum annual instantaneous discharge and annual average leaf litter standing crop (Fig. 4A).

Annual invertebrate abundance, biomass, and production data in mixed substrate habitats from 1985 and 1986 (Lugthart and Wallace 1992), 1989, and 1990 (Whiles and Wallace 1995), and the current study were plotted with standing crop of leaf litter for each year. Over nine years of study, there was a strong positive relationship between leaf litter standing crop in mixed substrates and primary consumer abundance as well as predator abundance (Table 12, Fig. 4B). There were

FIG. 2. Temporal patterns of abundance (no. individuals/m²) and biomass (mg AFDM/m²) for primary consumers, invertebrate predators, shredders, and collectors in mixed substrate habitats of the reference stream (C 53, open squares) and litter exclusion stream (C 55, solid circles) from September 1992 to August 1997. Each value represents the mean monthly abundance or biomass. Litter exclusion (C 55) started in September 1993, and the 1-yr pretreatment and treatment periods are separated by the first vertical line; the second vertical line denotes the final year (litter exclusion and small woody debris removal). Broken (C 53) and unbroken (C 55) horizontal lines indicate means of the pretreatment and 4-yr treatment period.
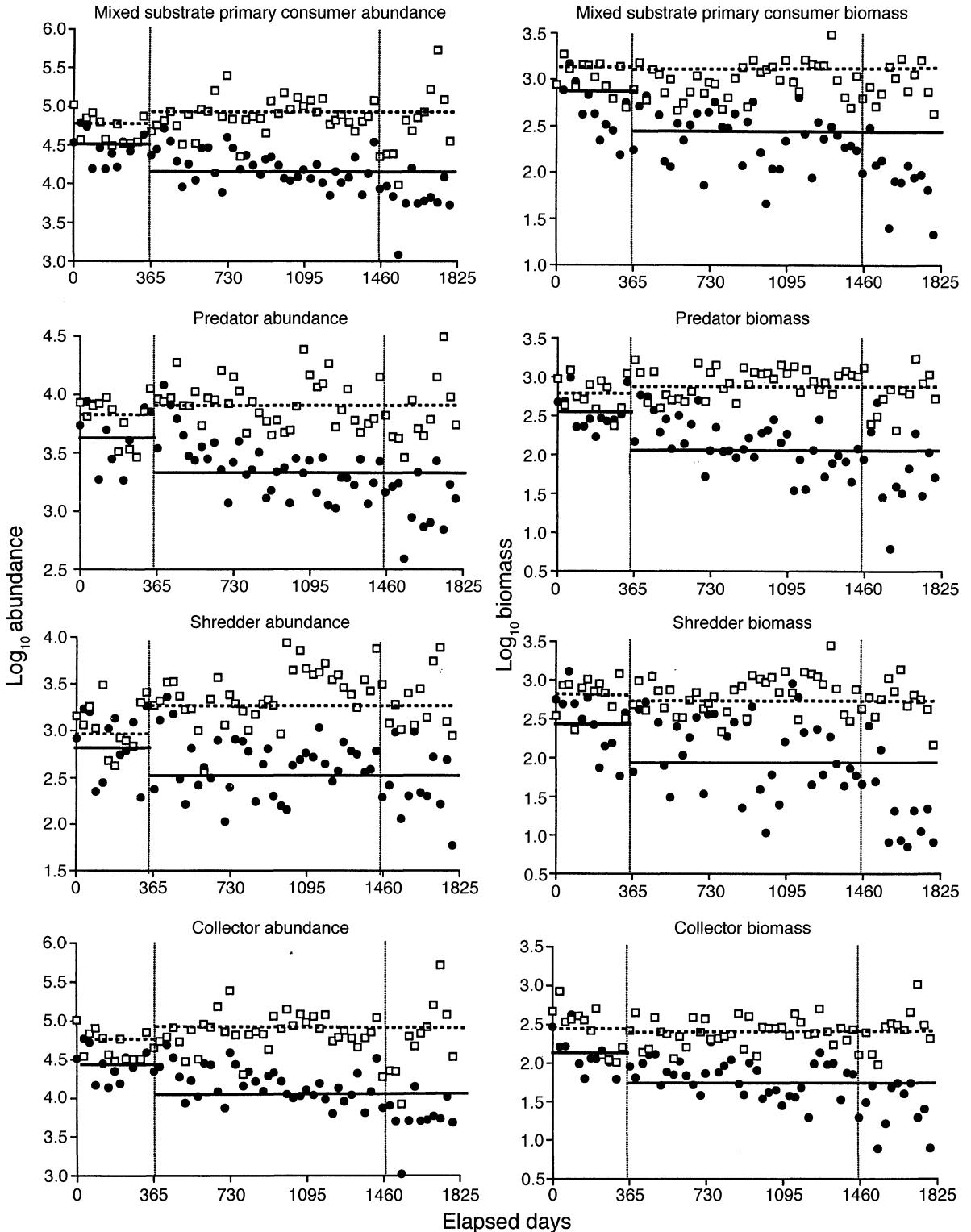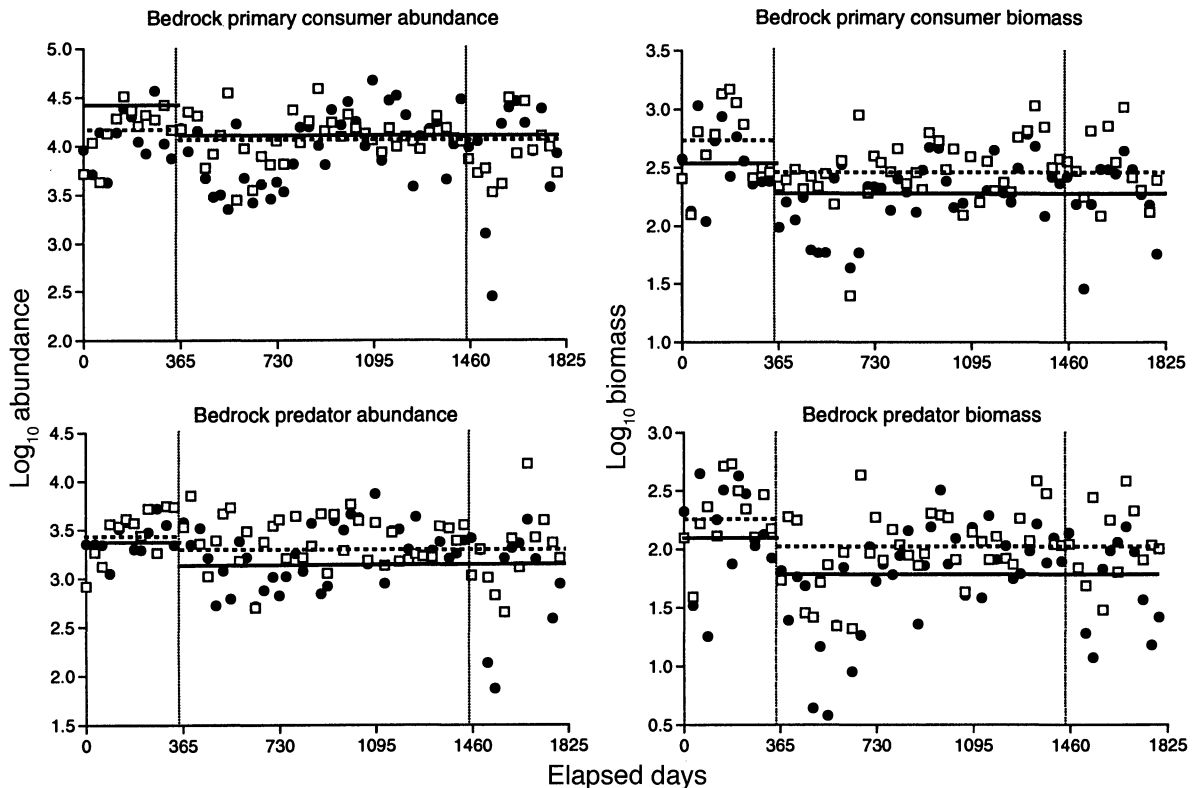
FIG. 3. Temporal patterns of abundance (no. individuals/m^2) and biomass (mg AFDM/m^2) for primary consumers and invertebrate predators on moss-covered bedrock substrates of the reference stream (C 53, open squares) and litter-exclusion stream (C 55, solid circles) from September 1992 to August 1997. Each value represents the mean monthly abundance or biomass. Litter exclusion (C 55) started in September 1993, and the 1-yr pretreatment and treatment periods are separated by the first vertical line; the second vertical line denotes the last year (litter exclusion and small woody debris removal). Broken (C 53) and unbroken (C 55) horizontal lines indicate means of the pretreatment and 4-yr treatment period.

also very significant relationships between annual leaf litter standing crop and secondary production of shredders, collectors, total primary consumers, predators, and total invertebrates (Table 12, Fig. 4C) in mixed substrates over the 9-yr period. Only filterer and scraper

TABLE 10. Randomized intervention analysis testing the null hypothesis of no change in abundance and biomass of each functional feeding group between the reference and treatment stream between year 3 (litter exclusion) and year 4 (litter exclusion plus small woody debris removal).

Functional or trophic group	Mixed substrates		Bedrock substrates	
	Abundance	Biomass	Abundance	Biomass
Scrapers	0.109	0.066	0.969	0.671
Shredders	0.626	0.027	0.794	0.562
Gatherers	0.154	0.022	0.668	0.455
Filterers	0.998	0.120	0.276	0.618
Total primary consumers	0.172	0.012	0.874	0.946
Invertebrate predators	0.230	0.976	0.183	0.432
Salamanders	0.272	0.223	0.859	0.954

Notes: All analyses were run on log(x + 1)-transformed data based on monthly means from both mixed substrate and bedrock habitats (n = 24 for each habitat). See Appendix for average abundance and biomass for each habitat.

functional groups showed no relationship between secondary production and standing crop of leaf litter for the mixed substrates (Table 12). Neither abundance, biomass, nor production of invertebrates in mixed substrate habitats displayed a significant relationship with annual FBOM standing crop in mixed substrates over the 9-yr period (Table 12).

There were strong relationships between predators and prey over the 9-yr period. Predator abundance was strongly related to prey abundance (r^2 = 0.96, P < 0.001, Fig. 4D) in mixed substrate habitats. The lowest predator abundance measured during untreated years occurred during 1990 (asterisk, Fig. 4D), which was the year of greatest stream discharge. The poorest relationship between predators and primary consumers was for biomass (r^2 = 0.751, P < 0.005). Secondary production of predators was strongly related to both primary consumer production (r^2 = 0.916, P < 0.001) and total production (r^2 = 0.964, P < 0.001) in mixed substrates. The relationship between predators and total production is strong, in part because predators are included in both variables.

In bedrock habitats, only abundance of shredders and predators and biomass of shredders displayed a sig-

TABLE 11. Relationship between benthic abundance and biomass for primary consumers or gatherers alone (independent variable) and invertebrate predator abundance and biomass (dependent variable).

Stream	Independent variable	Dependent variable	r^2	Slope	95% CI (for slope)
Mixed substrate					
C 53	Primary consumer abundance	Predator abundance	0.545	0.577	±0.138
C 55	Primary consumer abundance	Predator abundance	0.728	0.817	±0.131
C 53	Primary consumer biomass	Predator biomass	0.031	NS	
C 55	Primary consumer biomass	Predator biomass	0.292	0.564	±0.231
C 53	Gatherer abundance	Predator abundance	0.532	0.555	±0.137
C 55	Gatherer abundance	Predator abundance	0.711	0.781	±0.131
C 53	Gatherer biomass	Predator biomass	0.042	NS	
C 55	Gatherer biomass	Predator biomass	0.296	0.676	±0.274
Bedrock substrates					
C 53	Primary consumer abundance	Predator abundance	0.560	0.809	±0.189
C 55	Primary consumer abundance	Predator abundance	0.681	0.740	±0.133
C 53	Primary consumer biomass	Predator biomass	0.630	0.861	±0.173
C 55	Primary consumer biomass	Predator biomass	0.649	1.147	±0.222
C 53	Gatherer abundance	Predator abundance	0.477	0.681	±0.188
C 55	Gatherer abundance	Predator abundance	0.642	0.636	±0.125
C 53	Gatherer biomass	Predator biomass	0.151	0.315	±0.196
C 55	Gatherer biomass	Predator biomass	0.226	0.514	±0.250

Notes: Regressions were based on $\log_{10}$-transformed monthly means for abundance (individuals/m²) or biomass (mg AFDM/ m²) for mixed substrate and bedrock substrate ($n = 60$ for each comparison). C 53 is the reference stream, and C 55 is the treatment (litter exclusion) stream; NS = not significant.

nificant ($P < 0.05$) relationship with leaf litter standing crop over the 9-yr period of study (Table 13), which is in sharp contrast to the pattern just described for mixed substrates. There were no significant relationships between annual leaf litter standing crops and secondary production for any invertebrate group in bedrock habitats, which was different from the pattern for mixed substrates. In contrast with leaf litter, there were numerous significant relationships between invertebrates and FBOM standing crop on bedrock outcrops (Table 13). Production of collectors and total primary consumers, as well as total production, displayed significant positive relationships with mean annual FBOM standing crops on the bedrock outcrop substrates (Table 13). There was no significant association between annual moss standing crop and production of invertebrates ($P > 0.05$) on bedrock outcrops. However, production of gatherers, shredders, and total primary consumers was significantly ($P < 0.05$ to <0.02) related to total organic matter standing crop (FBOM and CBOM, including moss, leaf litter, and woody debris) on bedrock substrates.

Predator abundance on bedrock substrates was also strongly associated with that of prey ($r^2 = 0.876$, $P < 0.001$) over the 9-yr period, as was observed for mixed substrate habitats. There was no successive decline of predators and primary consumers with litter exclusion; predator and primary consumer abundance on bedrock substrates was lowest during the first year of exclusion (Fig. 5A). There was also a significant relationship between biomass of predators and that of primary consumers on bedrock substrates ($r^2 = 0.798$, $P < 0.002$) over the 9-yr period. Although the fourth year of treatment exhibited the lowest predator and primary consumer biomass, the pattern did not follow that exhibited

by mixed substrate habitat, as biomass was lowest for each group during the first year of exclusion and fluctuated thereafter (Fig. 5B). Annual secondary production of predators also displayed a significant relationship with both primary consumer ($r^2 = 0.68$, $P = 0.01$) and total production ($r^2 = 0.806$, $P < 0.002$) over the 9-yr period on bedrock substrates (Fig. 5C). However, these latter two variables are not completely independent (see *Discussion: Predator–prey relationships*).

DISCUSSION

The diversion of most of the energy fixed by autotrophs to the detrital food web obfuscates classical plant–herbivore–predator food chains (Polis 1994, Polis and Strong 1996). Detritus is also not incorporated into the "green world hypothesis" of Hairston et al. (1960) and Fretwell (1977). Others have suggested that decomposers as a group must be food-limited (Hairston et al. 1960, Pomeroy 1991). Furthermore, organic energy flows up the food chain and at some point must determine biomass and production of higher trophic levels (Carpenter et al. 1991). As previously reported, ecosystem-level manipulations of detrital inputs are rare (Wallace et al. 1997); however, our manipulation clearly shows bottom-up effects that were propagated through primary consumers and top carnivores. In addition, our results are undoubtedly conservative, as we only succeeded in partially severing the linkage between these headwater streams and the surrounding forest (see *Discussion: Predator–prey relationships*).

Detrital resources and productivity of headwater streams

Throughout forested regions, headwater streams such as those we studied receive a significant amount
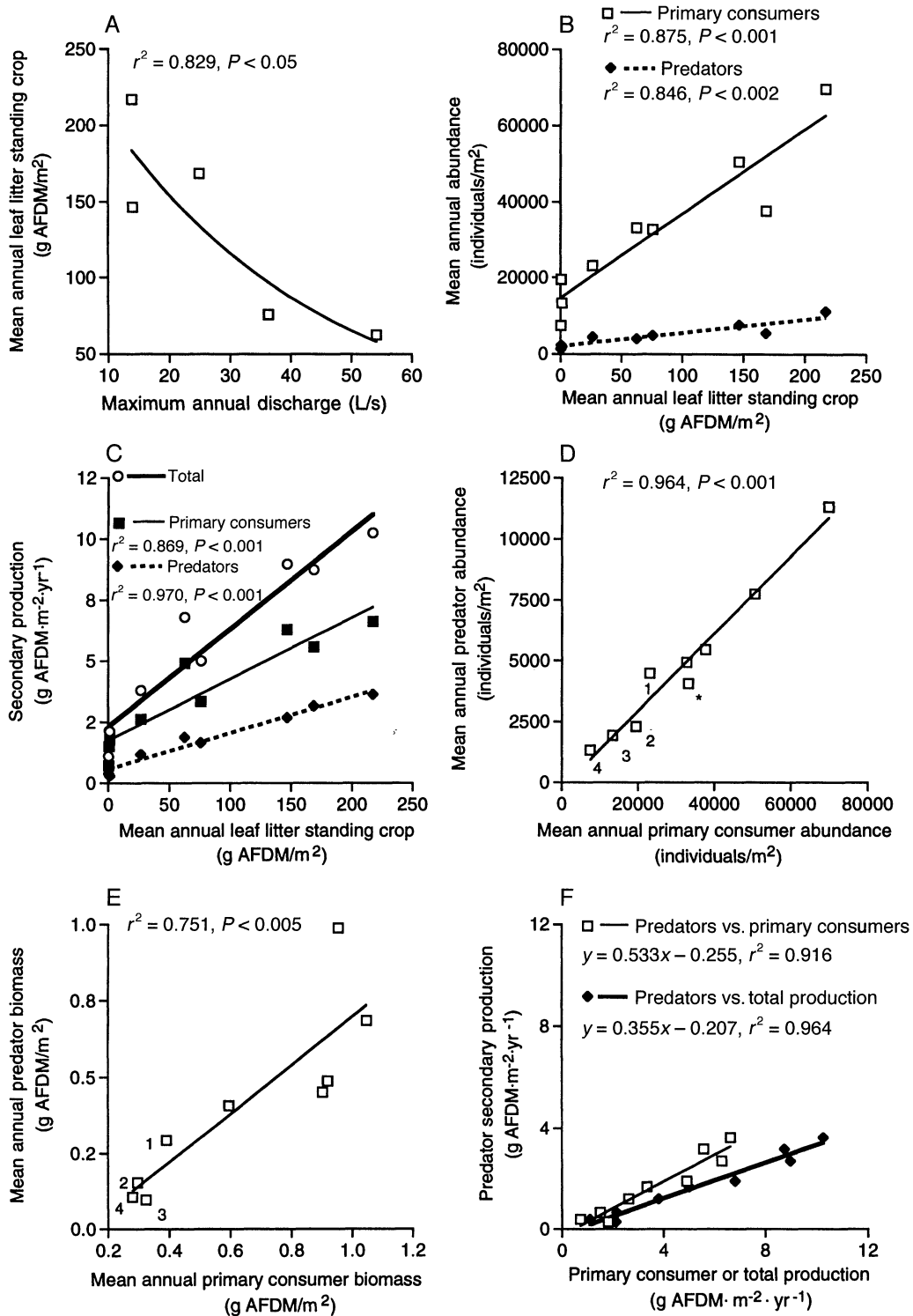
FIG. 4. Long-term relationships in mixed substrates of the treatment stream (C 55). Data are for 1985, 1986, 1989, and 1990, in addition to the 5 yr of the present study. (A) Relationship between annual leaf litter standing crop in mixed substrates and annual maximum instantaneous discharge during each of the five pretreatment years for C 55. (B) Relationship between annual leaf litter standing crop and abundance of primary consumers and predators in C 55 (the four litter-exclusion years, including small woody debris removal, are the four points in the lower left for each group). (C) Relationship between annual leaf litter standing crop and total, primary consumer, and predator secondary production. (D) Relationship between mean annual primary consumer and predator abundance (numbers 1–4 designate the four litter-exclusion years; the asterisk indicates a pretreatment year with record high discharge). (E) Relationship between annual predator and primary consumer biomass (1–4, as above). (F) Relationship between primary consumer production or total production and predator production.

TABLE 12. Long-term relationships between annual leaf litter standing crop (g AFDM/m^2) and fine benthic organic matter (FBOM; g AFDM/m^2) in mixed substrates and annual mean abundance, mean biomass, and production of invertebrates in C 55 for the years 1985, 1986, 1989, 1990, and September 1992 to August 1997.

Functional feeding group	Abundance		Biomass		Production	
	r^2	P	r^2	P	r^2	P
Leaf litter standing crop						
Scrapers	0.423	NS	0.005	NS	0.058	NS
Shredders	0.922	***	0.722	*	0.794	*
Collectors	0.875	***	0.836	***	0.883	***
Filterers	0.433	NS	0.475	*	0.307	NS
Total primary consumers	0.875	***	0.754	*	0.868	***
Predators	0.844	***	0.884	***	0.971	***
Total invertebrates	0.875	***	0.874	***	0.922	***
FBOM standing crop						
Scrapers	0.170	NS	0.315	NS	0.216	NS
Shredders	0.001	NS	0.004	NS	0.001	NS
Collectors	0.010	NS	0.014	NS	0.014	NS
Filterers	0.051	NS	0.175	NS	0.134	NS
Total primary consumers	0.011	NS	0.016	NS	0.007	NS
Predators	0.034	NS	0.006	NS	0.000	NS
Total invertebrates	0.013	NS	0.001	NS	0.003	NS

Notes: The coefficient of determination (r^2) and probability values (P) of linear regressions were obtained by regressing annual mean abundance (individuals/m^2), biomass (g AFDM/m^2), or secondary production (g AFDM·m^{-2}·yr^{-1}) (dependent variables) on leaf litter or FBOM standing crop (g AFDM/m^2) (independent variables). These data include 5 yr of pretreatment and 4 yr of treatment (3 yr of litter exclusion plus 1 yr of small wood removal and litter exclusion) ($n = 9$).

* $P < 0.05$; *** $P < 0.001$; NS = not significant.

of energy from a variety of allochthonous sources (Webster et al. 1995). Although examples of terrestrial-to-aquatic subsidies are best known (i.e., Strong 1992), examples of aquatic-to-terrestrial energy flow are also known (Polis and Hurd 1995, Polis and Strong 1996). Primary consumers in these detritus-based streams at Coweeta do not influence the rate of supply of their resources; however, they can influence standing crop of resources (Cuffney et al. 1990). Litter exclusion

(Wallace et al. 1997) clearly showed that these forest streams are subsidized, donor-controlled systems. Nonetheless, we undoubtedly underestimated the extent of the stream's dependence on allochthonous inputs in our initial 3-yr exclusion and to a somewhat smaller extent by the present small woody debris removal. Our litter exclusion reduced inputs to ~5% of pretreatment values, which resulted in much lower standing crops of leaf litter in the treatment stream relative to that of

TABLE 13. Long-term relationships between standing crop of leaf litter (g AFDM/m^2) and fine benthic organic matter (FBOM; g AFDM/m^2) in bedrock outcrop habitats and annual mean abundance, mean biomass, and production of invertebrates in C 55 for the years 1985, 1986, 1989, 1990, and September 1992 to August 1997.

Functional feeding group	Abundance		Biomass		Production	
	r^2	P	r^2	P	r^2	P
Leaf litter standing crop						
Scrapers	0.019	NS	0.359	NS	0.299	NS
Shredders	0.530	*	0.526	*	0.307	NS
Collectors	0.258	NS	0.065	NS	0.290	NS
Filterers	0.215	NS	0.083	NS	0.007	NS
Total primary consumers	0.262	NS	0.352	NS	0.161	NS
Predators	0.500	*	0.178	NS	0.010	NS
Total invertebrates	0.292	NS	0.302	NS	0.115	NS
FBOM standing crop						
Scrapers	0.006	NS	0.112	NS	0.187	NS
Shredders	0.652	*	0.602	*	0.441	NS
Collectors	0.510	*	0.221	NS	0.627	*
Filterers	0.022	NS	0.125	NS	0.103	NS
Total primary consumers	0.524	*	0.475	*	0.524	*
Predators	0.500	*	0.410	NS	0.193	NS
Total invertebrates	0.528	*	0.475	*	0.457	*

Notes: The coefficient of determination (r^2) and probability values (P) of linear regressions were obtained by regressing annual mean abundance (individuals/m^2), biomass (g AFDM/m^2), and secondary production (g AFDM·m^{-2}·yr^{-1}) (dependent variables) on leaf litter or FBOM standing crop (independent variables). These data include 5 yr of pretreatment and 4 yr of treatment (3 yr of litter exclusion plus 1 yr of small wood removal and litter exclusion) ($n = 9$).

* $P < 0.05$; NS = not significant.
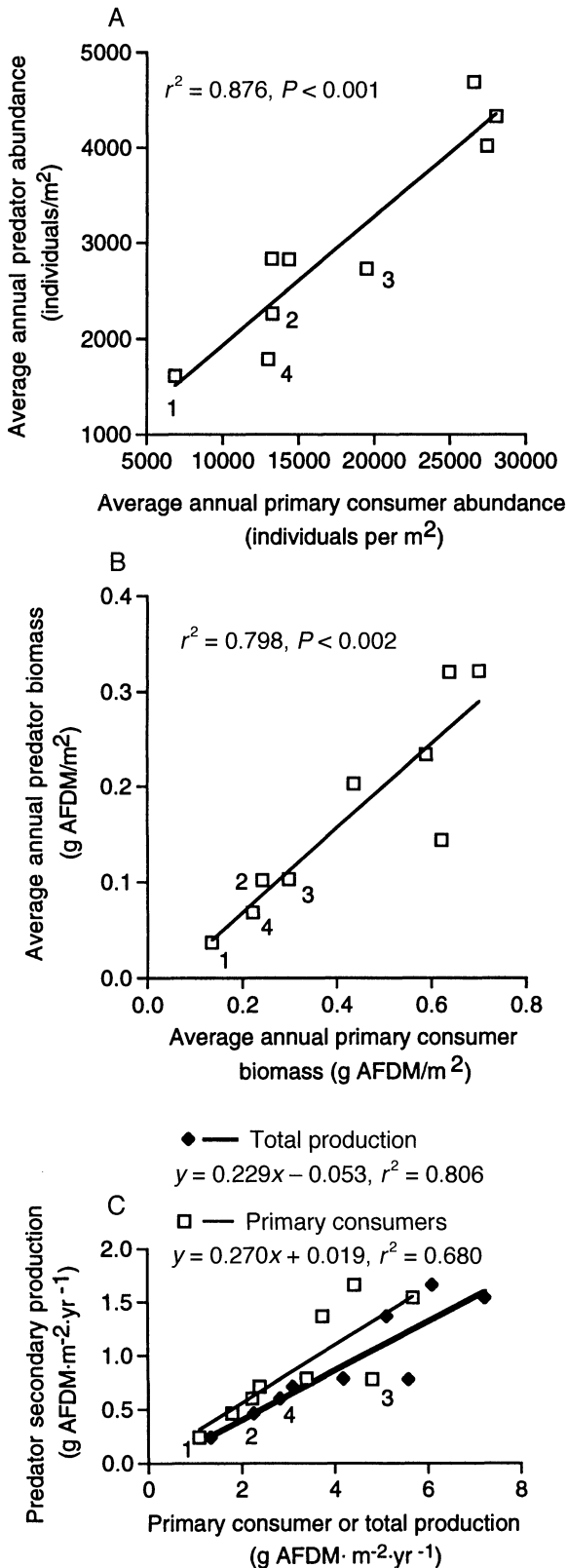
FIG. 5. Long-term relationships on bedrock outcrop substrates of the litter-excluded stream. Data are for 1985, 1986, 1989, and 1990, in addition to the 5 yr of the present study.

the reference. A large mass of FBOM and CPOM (primarily woody debris) remained in the exclusion stream following the initial 3 yr of litter exclusion. Despite small wood removal at the start of the fourth year of exclusion, buried small woody debris amounting to several kg continued to resurface following storms and was removed by hand. Additional sources of terrestrially derived nutrients and organic matter also remained throughout our experiment and include the following. First, nutrients and dissolved organic carbon (DOC) continued to enter the stream by soil water as well as throughfall. Our manipulation did not curtail DOC inputs, although it reduced in-stream DOC generation (Meyer et al. 1998). Second, particulate organic matter from soils, and from throughfall, not only remained, but continued to enter. Bank runoff, measured for the past 2 yr, contributes an average 22.8 g AFDM of particulate organic matter/m^2 of wetted stream area each year (J. B. Wallace, E. R. Siler, and S. L. Eggert, *unpublished data*). Third, BOM existing in the stream prior to exclusion, as well as large woody debris (>10 cm diameter), remained in the stream bed. A significant decrease in small woody debris was found only following manual removal of small wood after 3 yr of exclusion (Table 3). Last, primary production is another obvious source of organic matter; however, in Coweeta headwater streams such production is very low and light-limited even during winter months by dense growths of riparian rhododendron (Webster et al. 1983, Lowe et al. 1986, Mulholland et al. 1997). Despite our efforts at eliminating or reducing stored organic particles within the treatment stream, >1 kg AFDM/m^2 remained during the fourth year of exclusion following small woody debris removal (Table 3). Thus, the actual importance of the terrestrial–aquatic linkages to aquatic productivity is undoubtedly greater than shown by our experiment. Complete severing of detrital inputs from the catchment will undoubtedly be very difficult, if not impossible.

It has been suggested that the ability of an ecosystem to resist displacement after disturbance is due in part to accumulated structure such as large organic matter storage in an ecosystem (Webster et al. 1975). A large standing crop of relatively resistant, organic matter that is slow to turn over can also enhance ecosystem stability by retaining and recycling nutrients and buffering against short-term environmental changes (O'Neill and Reichle 1980). Fisher and Likens (1973) also suggested

←

(A) Relationship between mean annual primary consumer abundance and predator abundance (the data points marked by numbers indicate litter-exclusion years 1, 2, 3, and 4, and woody debris removal [year 4]). (B) Relationship between annual primary consumer and predator biomass (data points 1–4, as above). (C) Relationship between primary consumer production or total production and predator production (1–4, as above).

that accumulated detritus in streams confers stability on them, such that streams are directly dependent on the surrounding forest for functional integrity as well as for reduced erodibility. Our results clearly support the concept that invertebrate community structure in these headwater streams is maintained to a large degree by accumulated organic matter. For example, after terrestrial litter inputs were curtailed, the reduction in abundance and biomass of most of the invertebrate community of mixed substrate habitats was a long, slow, continual process (Fig. 2). This is undoubtedly due in part to the relatively large store of organic matter in mixed substrates of the exclusion stream (Table 3), as well as to ongoing inputs not curtailed by litter exclusion. This reinforces the suggestion that several generations of invertebrate consumers may be required to detect food limitation in detrital food webs (Richardson and Neill 1991). However, despite the large residual sources of organic matter in mixed substrate habitats, most aquatic invertebrates displayed significant reductions in abundance or biomass, or both, in mixed substrates of the exclusion stream relative to the reference stream.

How important is terrestrially derived detritus to abundance, biomass, and secondary productivity of benthos in these Coweeta streams? In a nearby Coweeta stream that was subjected to four seasonal treatments with an insecticide, invertebrate abundance declined by 25% and biomass by ~79%, while secondary production was reduced 60% (Lugthart and Wallace 1992). By the fourth year of litter exclusion and small wood removal, invertebrates in the treatment stream were reduced 76% in abundance, 78% in biomass, and 78% in productivity from pretreatment values. Thus, the effects of reduction in allochthonous resources on invertebrate populations were at least as severe as seasonal treatments with an insecticide. In fact, other than the riffle habitat of a South Pacific Island stream, productivity after 4 yr of treatment in the mixed substrate habitats is lower than that of some 40 streams worldwide (Benke 1993). This underscores the importance of terrestrial detritus to invertebrate productivity of small, forested headwater streams such as those at Coweeta.

Stream geomorphology and effects of litter exclusion

If residual detritus buffers the system against change, why did bedrock-outcrop fauna exhibit no significant change during the 4-yr manipulation despite little stored organic matter in bedrock outcrop habitats (Fig. 3)? Steeper-gradient reaches of southern Appalachian streams are generally dominated by moss-covered bedrock substrate. Higher current velocities, less particle retention, and low standing crops of CPOM and FPOM (e.g., Table 3) generally characterize these bedrock outcrops (Gurtz and Wallace 1984, Huryn and Wallace 1987a). Benthic community structure on this bedrock is more characteristic of that downstream and is dominated by filterers, gatherers, and predators (Huryn and

Wallace 1987a). Most of these animal groups rely primarily on transported organic matter and FPOM trapped within the moss and are less dependent on CPOM. During pretreatment and the first 2 yr of litter exclusion, FPOM export (seston) from the treatment stream exceeded that of the reference stream. However, by the third year of litter exclusion, total seston export from the treatment stream dropped to 81% of that from the reference stream and displayed a further decline to 73% of the reference levels during the first year of wood removal (J. B. Wallace, S. L. Eggert, J. R. Webster, and J. L. Meyer, *unpublished data*). Hence, there was sufficient material in transport to replenish FPOM associated with these bedrock habitats. Clearly, taxa associated with moss-covered bedrock habitats were less directly dependent on allochthonous resources, because no taxon on moss-covered bedrock showed a significant decrease in abundance or biomass during the 4-yr litter exclusion (Table 8). However, we anticipate that extension of litter exclusion for a longer period, e.g., a decade, would deplete both stored and transported FPOM. Eventually, long-term depletion of stored and transported FPOM would result in bedrock outcrop communities which could not sustain present levels of benthic abundance and biomass, as was observed for mixed substrates. Resources used by bedrock fauna are more displaced in time and by antecedent processes than those used by mixed substrate fauna; this is consistent with the functional similarity between bedrock reaches in headwaters and larger downstream segments.

Why do shredders display differences in response among mixed substrate and bedrock habitats in the litter exclusion stream (cf. Tables 6 and 7)? Total shredder biomass/m^2 of stream bottom was 6.1 (treatment) to >10 times (reference) greater for mixed substrates than moss-covered bedrock habitats. Plecopteran shredders, primarily Peltoperlidae and *Leuctra* spp., comprised 91 (treatment) to 92% (reference) of total shredder biomass on moss-covered bedrock substrates of these streams, vs. 20% of shredder biomass in the mixed substrate habitats. It has been suggested that early instars of plecopteran shredders such as *Leuctra* spp. are primarily collectors (Dobson and Hildrew 1992), which is consistent with the primary food resource available in the moss-covered bedrock habitat, FPOM. Unlike mixed substrate habitat, bedrock outcrop FPOM did not show a significant difference among the reference and treatment streams during the experiment (Table 3).

Based on mean monthly individual biomass, shredders on bedrock substrates of both streams were significantly smaller that those found in mixed substrates ($P < 0.001$, Mann-Whitney Rank Sum Test, $n = 60$, for each stream). Moss-covered bedrock substrates at Coweeta support primarily early instars of stonefly shredders. Average monthly mass per individual *Leuctra* on bedrock substrates in both streams was significantly smaller than that in mixed substrates ($P < 0.004$ for the reference stream and $P < 0.02$ for the treatment

stream). Between-stream comparisons of monthly individual mass of peltoperlids in similar habitats were not significantly different for bedrock substrates ($P > 0.05$); however, peltoperlids in mixed substrates were significantly larger in the reference stream ($P < 0.001$, Mann-Whitney Rank Sum Test). This suggests either increased mortality in later instars and/or decreased growth in mixed substrate habitats of the treatment stream.

Taxa showing no effects or delayed effects of resource exclusion

Scrapers were the only functional group that a showed a tendency to increase in production in mixed substrate habitats over the 4-yr treatment (Table 9). However, production of scrapers was low at the start (0.6% of total production) of the experiment and throughout the 4 yr of treatment (3.3% of total production). If primary production had not been limited by light, we would have anticipated a greater shift toward increased grazer production.

Filterers in mixed substrate habitats exhibited some decrease in abundance and biomass in the treatment stream, but these decreases were not significant (Table 6). Following 4 yr of treatment, productivity of filterers in the treatment and reference streams remained similar to that of the pretreatment year in mixed substrate habitats (Table 9). One filtering species, *Diplectrona modesta,* significantly increased in abundance in mixed substrate habitats of the treatment stream (Table 8). The failure of filterers to display a significant decrease during litter exclusion is undoubtedly related to increased concentrations of suspended organic matter, which increased during the initial years of treatment (J. B. Wallace and S. L. Eggert, *unpublished data*). The flushing of FBOM stored in the stream bed decreased during later years of exclusion. We anticipate that with continued depletion of FPOM, filterers will decline significantly.

Several taxa of detritus-feeding invertebrates that failed to show any significant decrease in abundance or biomass during the initial 3 yr of litter exclusion are those known to feed on woody debris or FBOM retained within the stream bed. Taxa known to feed on buried materials include sericostomatid caddisfly larvae, *Fattigia pele* (Wagner 1991), Diptera such as *Molophilus,* (Merritt and Cummins 1996), and Oligochaeta. Such residual organic matter was present throughout the 3-yr litter exclusion. Also, the standing crop of small woody debris in the treatment stream only became significantly different from the reference stream following its removal (Table 3). Other studies have noted that woody tissue is common in guts of a number of taxa for which we found no significant reductions during treatment. These include: *Lipsothrix,* which inhabit woody debris (Dudley and Anderson 1987), *Paraleptophlebia, Lype, Tipula,* and Sciaridae (Pereira et al. 1982).

There was also a change in the relative abundance of taxonomic groups of shredders during the 3-yr litter exclusion prior to removal of small woody debris. At the ordinal level, the major shredders in both streams were dipterans, trichopterans, and plecopterans. The proportion of shredder biomass in each of these groups changed more in the treatment than in the reference stream. Dipteran shredders (all Tipulidae) increased from 63 to 89% of total shredder biomass, trichopteran shredders decreased from 27 to 3%, and plecopteran shredders decreased somewhat less during the first 3 yr of litter exclusion. This shift toward a dominance of dipteran shredders (i.e., *Lipsothrix* and *Tipula*) during the first 3 yr of litter exclusion in the treatment stream is consistent with a shift toward wood-consuming taxa.

We collected subsamples of woody debris removed from the stream to measure invertebrates associated with wood substrates. Based on the total amount of wood removed and invertebrate abundance on these subsamples, we calculated abundance of animals on wood as a proportion of those collected in benthic core sampling during year 3 of litter exclusion. Invertebrates removed with wood averaged 11.5% of benthic abundance measured with the benthic corer during year 3. This estimate varied by functional group, as follows: scrapers = <0.02%, shredders = 43%, gatherers = 8%, filterers = 8%, and predators = 29% of average benthic abundance. Acari, predaceous water mites, accounted for 65% of predators removed with wood and 19% of total invertebrates removed. The wood boring tipulid, *Lipsothrix,* represented 83% of the total shredders removed with woody debris. In fact, our estimates of *Lipsothrix* abundance in the small woody debris subsamples exceeded those measured with the benthic corer. In the benthic corer samples, *Lipsothrix* abundance was 51 individuals/m^2 (Appendix) vs. estimates of 209/m^2 with removed wood. These results are not surprising, since the larger pieces of small woody debris, i.e., >6–10 cm diameter, are not sampled effectively with the benthic coring device. Estimates of standing crop of small woody debris made with the benthic corer were only 28% of the small woody debris removed (Wallace et al., *in press*).

Wood is well known as a poor food resource for freshwater organisms. Lignins, complex aromatic polymers formed from phenyl propanoid units, comprise 20–30% of woody tissue and serve as a barrier that protects cellulose and hemicellulose against degradative microbial enzymes (Shearer 1992). Dipteran shredders such as *Tipula* have been reported to assimilate up to 18–19% of the cellulose they ingest (Sinsabaugh et al. 1985), which is apparently mediated by bacteria in the rectal caecum rather than ingested microbial enzymes. Tipulids have an exceptionally alkaline gut (pH > 11.0), which has high proteolytic activity and would destroy ingested microbial cellulases and hemicellulases (Martin et al. 1980, Sharma et al. 1984, Suberkropp 1992). Some guts of invertebrates such as *Tipula*

in the exclusion stream contained >60% woody tissue (S. L. Eggert and J. B. Wallace, *unpublished data*). Highly alkaline guts have also been reported for a number of terrestrial insects that feed on woody and humic-rich materials. These include some Lepidoptera (Mishra 1991), wood-feeding beetles (Scarabaeidae and Passalidae, Terra and Ferreira 1994), and soil-feeding termites (Brune and Kuhl 1996). Highly alkaline conditions promote degradation and hydrolysis of lignocellulose, humic residues, and polyphenolic constituents of woody debris (Mishra 1991, Brune and Kuhl 1996). Hence, the greater persistence of dipteran shredders during the initial 3-yr litter exclusion may be due, in part, to their greater ability to utilize wood. Following removal of small woody debris in the fourth year of litter exclusion, all tipulids (*Tipula, Lipsothrix,* and *Molophilus*) decreased in mixed substrates of the treatment stream (Appendix). However, over the 4-yr treatment the decrease in either abundance or biomass for these shredders only approached significance ($0.05 < P < 0.10$, Table 8). Some small woody debris (121 g AFDM/m^2, Table 3) remained buried in the stream bed following removal, providing a limited energy source.

Leaf litter is more labile and has a higher breakdown rate than woody debris (e.g., Golladay and Webster 1988, Maharning and Bärlocher 1996). Furthermore, aquatic hyphomycetes are more abundant on leaf litter than woody debris (Maharning and Bärlocher 1996). However, available data do not suggest that, apart from the absence of leaf litter from the treatment stream, residual organic matter remaining in the channel of the treatment stream was poorer in nutritional quality than similar material in the reference stream (Meyer et al., *in press*). Although the standing crop of bacterial exopolymers was lower in the treatment stream, invertebrates in both streams derived a similar and significant portion of their carbon from bacteria or exopolymers (Hall and Meyer 1998). Additional evidence suggests that nutritional quality of residual organic matter was enhanced on epixylic biofilms in the treatment stream. Microbial activities (i.e., respiration, fungal biomass, extracellular enzyme activity) and decomposition of woody substrates were much higher in the exclusion stream than in the reference stream (Tank 1996, Tank and Webster 1998). The absence of leaf litter in C 55 apparently released epixylic microbes from competition for nutrients with microbes normally associated with decomposing leaves (Tank 1996, Tank and Webster 1998).

Long-term relationship between allochthonous detritus and production

During a 9.5-yr period of continuous organic matter export measurement made prior to exclusion of litter in C 55, there was a strong relationship between leaf litter export and maximum storm discharge ($P < 0.001$, Wallace et al. 1995b). Furthermore, most leaf litter removed from the wetted perimeter of the stream was retained in the narrow riparian zone, rather than exported to downstream reaches during storms (Wallace et al. 1995b). Prior to treatment, storms resulted in large annual fluctuations in organic matter standing crop in C 55. Wallace et al. (1995b) suggested that such fluctuations could potentially produce "bottlenecks" on benthic communities, especially leaf-shredding insects. The present study suggests that such effects extend well beyond leaf-shredding taxa and include many primary consumers and predators (Fig. 4A–F). Our long-term studies of C 55 suggest that even during untreated or "normal" periods, large differences in storm flows among years may influence secondary productivity of benthic communities within Coweeta streams (Fig. 4C). In addition to physical removal of invertebrates from substrate during high flow, abiotic forces such as storms may disrupt food resources, i.e., leaf litter, with consequences for invertebrate survival and growth. Hence, storms that remove organic matter may induce indirect long-term effects on abundance, biomass, and productivity of the benthic community (Fig. 4A–F). Human activities that alter stormflow frequency and intensity (e.g., impervious surfaces in the watershed, Dunne and Leopold 1978) would have a similar effect. The effect of drought and wet years on aquatic productivity is not limited to streams. For example, long-term productivity and trophic structure of a Gulf Coast estuary in Florida have been linked to freshwater inputs and alluvial river flow. River flow was strongly associated with annual rainfall in Georgia, well >100 km from the estuary (Livingston et al. 1997).

Predator–prey relationships

In both mixed substrate and bedrock substrates of the treatment stream, there was a significant relationship between abundance and biomass of predators and primary consumers, as well as with gatherers that constitute the majority of prey (R. O. Hall, J. B. Wallace, and S. L. Eggert, *unpublished manuscript*; Table 11). For each comparison of relationships between predators and their prey, the treatment stream displayed a higher r^2 than the reference stream (Table 11). In mixed substrate habitats, slopes for predator–prey relationships were also consistently higher in the treatment stream than the reference. The higher slope values indicate somewhat greater predator abundance and biomass per unit prey in the treatment stream compared with that of the reference stream. The difference in slopes between the exclusion and reference stream may reflect differences in intraguild predation in the two streams. R. O. Hall, J. B. Wallace, and S. L. Eggert (*unpublished manuscript*) found evidence that some of the largest biomass flows during winter in the litter excluded stream were predators consuming other predators, which was not observed in the reference stream. Slopes may also be steeper in the exclusion stream because its predators consume proportionally more prey per unit predator biomass than those of the ref-

erence stream. There is evidence that predators in the exclusion stream were consuming more of three common prey taxa than those in the reference stream (R. O. Hall, J. B. Wallace, and S. L. Eggert, *unpublished manuscript*).

If the linkage between predators and prey is strong, manipulation of the food base should produce a strong, measurable response in both primary and secondary consumers. This was observed following litter exclusion. Total abundance and biomass of predators decreased in mixed substrate habitats of the treatment stream following litter exclusion (Table 6), as did most major taxa of predators (Table 8). Total secondary production of predators declined by 76% of pretreatment values in the mixed substrates, which was very similar to the decrease in total invertebrate production (78% decrease).

Our data show a strong bottom-up effect of leaf litter on abundance and production of primary consumers that is propagated through secondary consumers. There was a positive relationship between primary consumer and predator production in both mixed substrate ($r^2 = 0.916$, $P < 0.0001$) and bedrock habitats ($r^2 = 0.68$, $P = 0.0062$) over a 9-yr period in the treatment stream. The strong positive relationship between predator and primary consumer production implies that predator production is closely linked with that of prey. There is an obvious statistical problem associated with the relationship between total production and predator production (i.e., nonindependence, because predators are in both variables). However, the inclusion of predators in both variables makes sense from a biological standpoint, as predators do eat other predators in these two streams (R. O. Hall, J. B. Wallace, and S. L. Eggert, *unpublished manuscript*). The slope of the relationship between total secondary production and predator production is ~0.35 (Fig. 4F) for the predominant mixed substrate habitats (=87% of stream area). The additional year of data for small woody debris removal did not change this slope from that reported previously by Wallace et al. (1997). This slope is in close agreement with known bioenergetic efficiencies reported for invertebrate predators (production/ingestion ≈ 33–39%, Slanksy and Scriber 1982). The slope between total production and that of predators for bedrock outcrop habitats (0.23) is somewhat lower than that for mixed substrates; however, the slope values for the two habitats do not differ significantly (Zar 1984, test for difference among slopes).

The close agreement between general bioenergetic efficiencies reported for predators and the slope (0.35) for the relationship of predator production to total production over a 9-yr period has two major implications for mixed substrate habitats in this stream. First, predator production is apparently limited by that of prey, and, second, invertebrate predators growing at 35% efficiency would have to ingest most of the macroinvertebrate production to achieve measured rates of production. Thus, our results clearly show bottom-up effects demonstrated by litter exclusion; however, results also suggest the potential for top-down (predatory) effects (Wallace et al. 1997).

In natural environments, most prey are consumed by many species of predators. Most predator–prey-interaction studies suffer from a number of problems. These include concentrating on only one or two predators, limiting time scales to one generation or less, failing to consider multiple predators, and rarely accounting for intraguild predation (Sih et al. 1998). Most invertebrate predators consume multiple prey taxa (e.g., Allan 1983; R. O. Hall, J. B. Wallace, and S. L. Eggert, *unpublished manuscript*). In fact, many invertebrate predators feed at multiple trophic levels, including other predators (i.e., intraguild predation, sensu Polis and Holt 1992), which complicates conventional food chain theory (Polis 1994, Polis and Strong 1996; R. O. Hall, J. B. Wallace, and S. L. Eggert, *unpublished manuscript*). Intraguild predation on other invertebrate predators accounts for 16–27% of all predator ingestion in our study streams; hence, this predation is diffusely distributed among multiple taxa (R. O. Hall, J. B. Wallace, and S. L. Eggert, *unpublished manuscript*).

Diffuse predation may be an important reason why the effects of predators are often difficult to show at larger scales in many streams (however, see Power 1992, Huryn 1998). Hildrew (1992:317), reviewing stream food webs, described a difficulty in studies of predators: "The inference is that either predation is really dynamically trivial in running waters or the experiments are unable to detect the effects through some details of scale, timing, or design." In contrast to such diffuse predation is the specialized predation of a parasitic microsporidian on a dominant grazing caddisfly, which produced pronounced effects in Michigan streams (Kohler and Wiley 1997). However, diffuse consumption by predators, including intraguild predation and multiple prey, undoubtedly obscures the potential importance of predation. Detecting the potential importance of such diffuse predation in this detritus-based stream would probably be impossible without multi-year studies that assessed secondary production while simultaneously curtailing the detritus food base.

Although our litter exclusion clearly shows bottom-up effects, our results suggest a ratio-dependent positive correlation that is consistent with conditions where both bottom-up and top-down forces co-limit populations (Power 1992). Such models of predator and prey abundance and biomass over gradients of productivity are the subject of considerable debate (cf. Berryman 1992, Ginzburg and Akcakaya 1992, Slobodkin 1992, Abrams 1994, Gleeson 1994; see also Rosenzweig 1973, Oksanen et al. 1981, Diehl et al. 1993). Power (1992) succinctly summarized these views with respect to top-down and bottom-up forces in food webs. However, such models are generally for single-predator and single-prey systems and are not amenable to multiple predators and prey at the ecosystem level. Spatial scales also influence such studies as models of algae–snail

responses to nutrient additions in streams, which have noted local prey-dependent functional responses that gave results similar to ratio-dependent responses when integrated over large areas and times (Blaine and DeAngelis 1997). Although they were not analyzing production data, Warren and Gaston (1992) suggested that such ratio dependency between predators and prey might be linked to energy flow. From a larger ecosystem perspective, production of prey, as well as production of predators falling victim to intraguild predation (sensu Polis and Holt 1992) limits energy available to secondary consumers. Thus, ecosystem-level production and bioenergetics may constrain energy available to secondary consumers. As noted above, bioenergetic efficiencies reported for invertebrate predators appear to be the best explanation for the 9-yr relationship between secondary production and predator production. In a larger, more productive stream than the headwater streams at Coweeta, it was shown that most (>80%) of the benthic invertebrate productivity is required to support observed fish production (Huryn 1996). Thus, consumption of most benthic production by predators is not unrealistic.

Previously, we suggested that litter exclusion avoided the vast array of indirect effects often associated with curtailing litter inputs to streams, i.e., logging and land-use changes, and showed that allochthonous detritus alone plays a major role in productivity of headwater stream communities (Wallace et al. 1997). However, this previous analysis underestimated the importance of terrestrial–stream linkages. Consumption of woody debris increased in the treatment stream during litter exclusion (R. O. Hall, J. B. Wallace, and S. L. Eggert, *unpublished manuscript*). Removal of small woody debris during the fourth year of the study resulted in an additional 47% decrease in abundance and 50% decline in biomass of benthic invertebrates compared to the third year of litter exclusion. Significant ($P < 0.05$, RIA) declines in biomass of shredders, collectors, and total primary consumers occurred in mixed substrate habitats between year 3 (litter exclusion alone) and year 4 (litter exclusion coupled with small woody debris removal). During this same period, total secondary production decreased by 48%. In general, the changes in benthic abundance, biomass, and production in mixed substrate habitats following removal of small woody debris exceeded those observed between successive years of litter exclusion. Most studies have focused on the role of large woody debris in stream ecosystems. The present study shows that small woody debris alone plays an important role as a food resource.

In summary, our results clearly demonstrate the importance of food web subsidies from one ecosystem to another. This study strongly supports bottom-up regulation of the benthos in detrital-based streams and links predator production to that of prey. Furthermore, this study has underestimated the impact of bottom-up regulation of forested headwater streams, as we have

ongoing sources of inputs, i.e., nutrients, DOC, throughfall, and soil organic matter, as well as large woody debris and retained organic matter. It may be impossible effectively to curtail all detrital inputs into an ecosystem that is situated lower in the landscape than the donor ecosystem. Despite C 55's large in situ storage of organic matter, as well as the ongoing "leakage" from the surrounding forest, our study demonstrates the importance of terrestrial–aquatic linkages to maintaining productivity of headwater streams.

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APPENDIX

Abundance, A (individuals/m²), mean annual standing stock biomass, B (mg AFDM/m²), and secondary production, P (mg AFDM·m⁻²·yr⁻¹), for major taxa in each functional feeding group found in the mixed substrate and moss-covered bedrock substrate of Catchment 53 (C 53 = reference stream) and Catchment 55 (C 55 = treatment stream). Order = noninsects (NI), or insect orders, where C = Coleoptera, D = Diptera, E = Ephemeroptera, O = Odonata, P = Plecoptera, and T = Trichoptera. CPI = cohort production interval in days or, where noted, the assumed annual P/B that was used for production calculations. Years are as follows: PreTmt = pretreatment year (September 1992 to August 1993); LE-1, LE-2, LE-3 = litter exclusion years 1 through 3 for C 55 (September 1993 to August 1996); WR-1 = small wood removal combined with ongoing litter exclusion for C 55 (September 1996 to August 1997).

Taxon	Order	CPI	Site	Year	Mixed substrates			Bedrock substrates		
					A	B	P	A	B	P
Scrapers										
Epeorus sp.	E	340	C 53	PreTmt	0	0	0	23	48	137
				LE-1	0	0	0	15	1	17
				LE-2	1	2	7	13	13	56
				LE-3	1	0	0	7	3	26
				WR-1	2	3	16	28	26	102
			C 55	PreTmt	8	0	2	11	15	69
				LE-1	2	0	0	4	0	1
				LE-2	8	0	3	11	2	3
				LE-3	0	0	0	15	26	99
				WR-1	2	2	11	20	19	104
Baetis sp.	E	120	C 53	PreTmt	5	0	3	64	2	25
				LE-1	0	0	0	25	0	5
				LE-2	0	0	0	200	3	58
				LE-3	2	0	0	165	2	43
				WR-1	2	0	1	236	2	63
			C 55	PreTmt	1	0	0	60	2	28
				LE-1	4	0	1	4	0	2
				LE-2	8	0	1	35	0	4
				LE-3	2	0	1	27	1	12
				WR-1	0	0	0	44	2	28
Neophylax sp.	T	213	C 53	PreTmt	22	1	8	27	4	23
				LE-1	6	0	2	65	1	13
				LE-2	0	0	0	36	0	4
				LE-3	0	0	0	14	1	7
				WR-1	28	0	3	14	1	3
			C 55	PreTmt	2	0	2	43	1	7
				LE-1	4	0	1	36	1	8
				LE-2	70	1	10	68	2	15
				LE-3	30	2	20	214	2	39
				WR-1	30	0	4	146	1	15
Other scrapers‡			C 53	PreTmt	17	0	2	60	6	18
				LE-1	36	3	14	52	7	20
				LE-2	3	2	3	34	7	24
				LE-3	3	1	2	93	15	34
				WR-1	11	1	3	70	11	25
			C 55	PreTmt	551	5	29	148	18	33
				LE-1	367	5	33	107	7	21
				LE-2	215	3	12	191	9	23
				LE-3	392	8	31	437	26	63
				WR-1	414	5	23	155	12	29
Total scrapers			C 53	PreTmt	44	2	13	174	59	202
				LE-1	42	3	16	157	9	54
				LE-2	4	4	10	283	24	142
				LE-3	5	1	2	279	20	110
				WR-1	43	5	24	347	39	193
			C 55	PreTmt	562	6	33	263	36	137
				LE-1	377	5	35	151	8	32
				LE-2	302	4	26	304	13	45
				LE-3	423	10	51	693	55	213
				WR-1	447	8	37	366	33	176

APPENDIX. Continued.

Taxon	Order	CPI	Site	Year	Mixed substrates			Bedrock substrates		
					A	B	P	A	B	P
Shredders										
Leuctra spp.	P	340	C 53	PreTmt	495	20	110	74	4	20
				LE-1	599	40	204	88	3	15
				LE-2	1009	60	292	58	2	12
				LE-3	993	29	196	114	3	16
				WR-1	1634	34	252	35	1	5
			C 55	PreTmt	464	16	103	72	4	20
				LE-1	157	5	33	14	0	2
				LE-2	240	9	24	40	1	5
				LE-3	229	7	43	60	1	7
				WR-1	223	3	29	42	0	3
Peltoperlidae	P	540	C 53	PreTmt	416	71	273	476	78	353
				LE-1	425	117	520	532	70	384
				LE-2	309	102	354	589	41	290
				LE-3	723	87	425	1066	82	543
				WR-1	132	42	149	386	33	204
			C 55	PreTmt	220	24	112	541	39	306
				LE-1	277	28	169	583	37	285
				LE-2	116	19	94	341	26	185
				LE-3	131	5	54	716	37	339
				WR-1	86	6	40	202	18	121
Lepidostoma spp.	T	246	C 53	PreTmt	18	5	350	26	0	7
				LE-1	499	43	383	14	0	1
				LE-2	864	54	445	33	1	7
				LE-3	1320	66	708	76	2	29
				WR-1	273	14	139	21	1	7
			C 55	PreTmt	4	1	115	4	0	1
				LE-1	106	11	103	14	0	2
				LE-2	3	0	0	6	0	0
				LE-3	11	0	4	30	0	5
				WR-1	9	0	4	9	0	1
Pycnopsyche sp.	T	275	C 53	PreTmt	63	242	980	1	0	0
				LE-1	286	95	853	68	7	112
				LE-2	158	152	882	5	0	7
				LE-3	182	131	852	18	2	40
				WR-1	88	122	757	0	0	0
			C 55	PreTmt	66	77	255	1	0	3
				LE-1	43	3	50	0	0	0
				LE-2	13	1	2	0	0	0
				LE-3	0	0	0	1	0	1
				WR-1	1	0	1	0	0	0
Fattigia pele	T	664	C 53	PreTmt	72	59	129	0	0	0
				LE-1	43	55	129	0	0	0
				LE-2	42	37	69	0	0	0
				LE-3	91	108	221	4	0	1
				WR-1	126	108	239	0	0	0
			C 55	PreTmt	23	24	59	0	0	0
				LE-1	18	21	55	0	0	0
				LE-2	9	4	9	0	0	0
				LE-3	28	5	17	0	0	0
				WR-1	9	6	15	1	0	1
Molophilus sp.	D	365	C 53	PreTmt	220	47	272	0	0	0
				LE-1	140	39	208	0	0	0
				LE-2	458	53	292	0	0	0
				LE-3	364	75	383	1	0	1
				WR-1	228	48	234	0	0	0
			C 55	PreTmt	128	19	121	0	0	0
				LE-1	48	14	82	0	0	0
				LE-2	22	3	10	0	0	0
				LE-3	66	11	60	0	0	0
				WR-1	28	3	21	0	0	0

APPENDIX. Continued.

Taxon	Order	CPI	Site	Year	Mixed substrates			Bedrock substrates		
					A	B	P	A	B	P
Tipula sp.	D	310	C 53	PreTmt	34	246	1706	1	0	7
				LE-1	39	178	1188	0	0	0
				LE-2	63	197	1054	1	0	90
				LE-3	81	385	2252	0	0	0
				WR-1	34	230	964	0	0	0
			C 55	PreTmt	40	226	996	4	8	83
				LE-1	21	193	1189	2	9	88
				LE-2	8	153	397	0	0	0
				LE-3	10	154	653	2	5	55
				WR-1	3	29	129	1	1	16
Lipsothrix sp.	D	5†	C 53	PreTmt	10	0	0	0	0	0
				LE-1	6	15	77	0	0	0
				LE-2	3	6	31	0	0	0
				LE-3	15	44	222	0	0	0
				WR-1	3	5	24	0	0	0
			C 55	PreTmt	1	7	35	0	0	0
				LE-1	2	2	11	0	0	0
				LE-2	2	1	5	0	0	0
				LE-3	51	30	148	4	3	13
				WR-1	0	0	0	0	0	0
Other shredders§			C 53	PreTmt	31	11	31	0	0	0
				LE-1	13	18	64	0	0	0
				LE-2	54	52	229	9	2	6
				LE-3	74	56	185	25	3	7
				WR-1	23	7	18	1	1	2
			C 55	PreTmt	8	8	15	1	0	0
				LE-1	19	9	26	12	2	5
				LE-2	13	3	4	0	0	0
				LE-3	20	9	25	1	0	0
				WR-1	5	2	4	1	1	2
Total shredders			C 53	PreTmt	1360	700	3851	578	82	387
				LE-1	2052	600	3625	702	80	512
				LE-2	2960	713	3646	695	46	411
				LE-3	3843	980	5443	1305	92	637
				WR-1	2541	611	2774	443	35	218
			C 55	PreTmt	954	401	1810	622	52	412
				LE-1	692	287	1718	625	49	382
				LE-2	425	193	545	387	27	190
				LE-3	545	222	1003	814	44	420
				WR-1	363	48	242	255	21	144
Gatherers										
Paraleptophlebia sp.	E	340	C 53	PreTmt	66	9	37	6	1	4
				LE-1	100	11	51	5	0	1
				LE-2	179	8	62	8	0	0
				LE-3	53	8	27	6	0	1
				WR-1	51	10	63	1	0	0
			C 55	PreTmt	134	5	32	69	0	7
				LE-1	54	3	18	6	0	1
				LE-2	158	3	17	9	1	3
				LE-3	36	2	12	6	0	1
				WR-1	52	1	14	5	0	2
Serratella sp.	E	330	C 53	PreTmt	9	7	41	374	129	711
				LE-1	20	12	51	484	37	284
				LE-2	0	0	0	340	48	306
				LE-3	2	0	1	220	47	250
				WR-1	4	0	2	128	47	179
			C 55	PreTmt	14	6	36	133	34	230
				LE-1	8	0	2	46	7	47
				LE-2	73	5	45	140	26	151
				LE-3	37	6	43	90	18	111
				WR-1	79	6	43	34	6	36

APPENDIX. Continued.

Taxon	Order	CPI	Site	Year	Mixed substrates			Bedrock substrates		
					A	B	P	A	B	P
Stenonema sp.	E	340	C 53	PreTmt	12	23	79	1	0	0
				LE-1	47	27	117	4	1	6
				LE-2	103	34	216	6	0	2
				LE-3	72	29	155	1	0	2
				WR-1	71	26	120	4	1	5
			C 55	PreTmt	14	22	87	19	1	9
				LE-1	13	3	18	2	0	1
				LE-2	10	2	14	4	5	13
				LE-3	6	1	4	1	0	1
				WR-1	0	0	0	1	0	0
Amphinemura sp.	P	300	C 53	PreTmt	12	4	18	585	22	183
				LE-1	34	2	14	616	20	189
				LE-2	58	4	25	849	36	274
				LE-3	165	7	42	808	18	146
				WR-1	143	5	35	1138	17	239
			C 55	PreTmt	23	2	13	458	32	236
				LE-1	23	1	8	203	10	90
				LE-2	34	1	9	938	21	210
				LE-3	62	2	13	941	34	219
				WR-1	56	1	15	778	30	273
Lype diversa	T	332	C 53	PreTmt	72	8	38	0	0	0
				LE-1	76	7	39	3	0	0
				LE-2	96	5	27	0	0	0
				LE-3	76	7	44	1	0	0
				WR-1	137	16	109	0	0	0
			C 55	PreTmt	41	5	26	1	0	0
				LE-1	47	4	21	0	0	0
				LE-2	77	4	24	0	0	0
				LE-3	244	14	109	4	0	1
				WR-1	12	1	9	0	0	0
Chironomidae (= non-Tanypodinae)	D	‖	C 53	PreTmt	23 789	84	1169	12 755	32	592
				LE-1	25 923	59	1234	7967	11	283
				LE-2	39 105	98	1694	11 942	31	648
				LE-3	30 747	99	1570	7547	23	422
				WR-1	35 666	139	2901	7675	21	420
			C 55	PreTmt	16 448	57	780	10 282	20	418
				LE-1	9466	26	410	4363	10	221
				LE-2	13 288	21	515	8873	18	460
				LE-3	7024	15	304	14 066	26	569
				WR-1	3874	9	184	10 302	19	486
Sciaridae	D	365	C 53	PreTmt	64	5	16	2	0	1
				LE-1	70	3	11	5	0	0
				LE-2	331	21	83	3	0	0
				LE-3	635	19	83	12	0	2
				WR-1	228	5	33	0	0	0
			C 55	PreTmt	95	4	14	1	0	0
				LE-1	83	4	18	0	0	0
				LE-2	102	6	22	1	0	0
				LE-3	21	2	6	0	0	0
				WR-1	15	1	3	0	0	0
Copepoda	NI	18†	C 53	PreTmt	14 418	14	260	1086	1	20
				LE-1	26 430	26	475	1588	2	29
				LE-2	39 525	40	711	1400	1	25
				LE-3	29 431	29	529	719	1	13
				WR-1	33 507	34	603	207	0	4
			C 55	PreTmt	5942	6	107	490	1	9
				LE-1	5000	5	90	528	1	9
				LE-2	1454	2	25	618	1	11
				LE-3	1272	1	23	466	1	9
				WR-1	320	0	5	155	0	4

APPENDIX. Continued.

Taxon	Order	CPI	Site	Year	Mixed substrates			Bedrock substrates		
					A	B	P	A	B	P
Nematoda	NI	5†	C 53	PreTmt	11 371	9	43	294	0	1
				LE-1	13 111	10	50	250	0	1
				LE-2	11 204	9	43	250	0	1
				LE-3	14 792	14	69	252	0	1
				WR-1	17 899	15	75	196	0	1
			C 55	PreTmt	6927	5	26	252	0	1
				LE-1	5876	5	23	97	0	0
				LE-2	2516	2	10	264	0	1
				LE-3	3897	4	19	172	0	1
				WR-1	1498	2	8	131	0	1
Oligochaeta	NI	5†	C 53	PreTmt	3906	177	883	431	1	6
				LE-1	4268	81	404	176	1	7
				LE-2	3780	50	251	188	0	2
				LE-3	3801	78	389	128	0	2
				WR-1	10 817	69	347	49	0	1
			C 55	PreTmt	1281	45	223	465	1	7
				LE-1	1308	30	149	581	2	7
				LE-2	851	31	154	880	3	16
				LE-3	937	17	86	1450	4	19
				WR-1	596	9	46	234	1	3
Other gatherers¶			C 53	PreTmt	17	0	2	21	0	1
				LE-1	114	14	77	0	0	0
				LE-2	1	1	3	0	0	0
				LE-3	9	0	1	9	0	0
				WR-1	4	2	14	0	0	0
			C 55	PreTmt	21	2	11	21	0	1
				LE-1	13	1	4	30	0	1
				LE-2	33	0	1	10	0	0
				LE-3	33	0	1	50	0	2
				WR-1	20	0	1	44	0	2
Total gatherers			C 53	PreTmt	53 734	339	2586	15 555	187	1520
				LE-1	70 194	252	2524	11 096	72	799
				LE-2	94 383	269	3114	14 986	118	1258
				LE-3	79 783	289	2908	9704	90	839
				WR-1	98 527	320	4302	9397	87	849
			C 55	PreTmt	30 940	158	1356	12 191	90	918
				LE-1	21 893	81	760	5856	30	378
				LE-2	18 595	77	835	11 736	74	865
				LE-3	13 569	65	619	17 246	82	934
				WR-1	6521	31	327	11 684	56	805
Filterers										
Diplectrona modesta	T	332	C 53	PreTmt	167	57	315	273	18	190
				LE-1	166	14	88	321	17	151
				LE-2	64	19	109	406	17	186
				LE-3	42	10	43	71	13	90
				WR-1	85	24	98	161	6	56
			C 55	PreTmt	271	33	236	157	24	182
				LE-1	95	20	116	80	14	71
				LE-2	157	19	90	663	14	142
				LE-3	192	29	152	57	11	74
				WR-1	119	14	92	89	9	40
Parapsyche cardis	T	332	C 53	PreTmt	2	20	51	741	403	3464
				LE-1	0	0	0	372	144	925
				LE-2	1	0	2	406	211	1184
				LE-3	1	3	16	823	295	1900
				WR-1	10	1	14	475	295	2281
			C 55	PreTmt	1	0	2	595	310	2985
				LE-1	6	0	2	237	48	312
				LE-2	3	4	10	288	166	802
				LE-3	1	0	0	593	146	1112
				WR-1	4	1	11	690	140	1491

APPENDIX. Continued.

Taxon	Order	CPI	Site	Year	Mixed substrates			Bedrock substrates		
					A	B	P	A	B	P
Other filterers#			C53	PreTmt	120	25	107	114	8	49
				LE-1	204	14	83	63	4	24
				LE-2	302	31	157	399	5	44
				LE-3	461	23	149	683	18	221
				WR-1	272	11	60	321	8	62
			C 55	PreTmt	51	2	18	155	3	36
				LE-1	38	1	15	40	3	21
				LE-2	43	4	18	54	1	13
				LE-3	30	4	21	134	6	80
				WR-1	16	4	10	119	5	21
Total filterers			C 53	PreTmt	288	102	473	1127	429	3704
				LE-1	370	29	171	756	164	1099
				LE-2	367	50	268	1211	233	1414
				LE-3	504	36	209	1576	326	2211
				WR-1	367	36	173	957	309	2399
			C 55	PreTmt	323	35	256	906	337	3202
				LE-1	139	21	133	356	65	404
				LE-2	203	26	118	1006	180	957
				LE-3	222	33	173	784	162	1265
				WR-1	139	19	112	898	154	1552
Predators										
Cordulegaster sp.	O	1140	C 53	PreTmt	37	96	207	0	0	0
				LE-1	95	236	359	0	0	0
				LE-2	16	85	87	0	0	0
				LE-3	27	184	356	0	0	0
				WR-1	18	145	235	0	0	0
			C 55	PreTmt	40	72	133	0	0	0
				LE-1	23	52	70	0	0	0
				LE-2	4	27	24	0	0	0
				LE-3	3	24	30	0	0	0
				WR-1	12	42	95	0	0	0
Lanthus sp.	O	660	C 53	PreTmt	26	148	281	0	0	0
				LE-1	55	177	455	0	0	0
				LE-2	67	252	612	1	3	14
				LE-3	98	178	439	3	0	0
				WR-1	35	132	307	1	0	3
			C 55	PreTmt	30	86	258	1	16	38
				LE-1	24	70	224	0	0	0
				LE-2	8	6	23	1	16	14
				LE-3	10	19	42	5	12	39
				WR-1	15	18	50	0	0	0
Sweltsa sp.	P	630	C 53	PreTmt	57	2	10	3	0	0
				LE-1	16	0	2	0	0	0
				LE-2	13	1	1	0	0	0
				LE-3	9	2	5	0	0	0
				WR-1	16	1	3	2	1	2
			C 55	PreTmt	73	8	26	0	0	0
				LE-1	66	5	14	0	0	0
				LE-2	95	7	19	4	0	0
				LE-3	46	3	9	0	0	0
				WR-1	37	2	6	0	0	0
Beloneuria sp.	P	660	C 53	PreTmt	50	94	216	18	15	60
				LE-1	91	89	318	33	13	64
				LE-2	124	229	600	12	10	44
				LE-3	145	150	411	43	13	58
				WR-1	31	108	286	16	9	57
			C 55	PreTmt	11	22	67	6	19	32
				LE-1	10	18	58	15	3	15
				LE-2	9	8	16	19	8	24
				LE-3	16	3	16	48	10	54
				WR-1	5	1	8	16	3	12

APPENDIX.   Continued.

Taxon	Order	CPI	Site	Year	Mixed substrates			Bedrock substrates		
					A	B	P	A	B	P
Isoperla spp.	P	300	C 53	PreTmt	39	10	47	130	45	252
				LE-1	189	13	140	102	6	66
				LE-2	82	20	108	98	18	102
				LE-3	134	6	48	66	8	49
				WR-1	136	8	73	75	16	83
			C 55	PreTmt	40	6	32	55	12	78
				LE-1	53	8	77	48	3	32
				LE-2	38	3	19	53	6	47
				LE-3	34	1	11	16	0	4
				WR-1	32	1	10	69	3	34
Rhyacophila spp.	T	340	C 53	PreTmt	97	10	55	141	23	202
				LE-1	58	31	164	84	21	139
				LE-2	36	16	67	98	11	84
				LE-3	88	19	105	57	22	138
				WR-1	62	16	82	43	7	41
			C 55	PreTmt	31	8	37	155	29	160
				LE-1	84	4	39	31	7	43
				LE-2	85	5	43	57	9	55
				LE-3	34	6	28	45	11	68
				WR-1	10	2	12	34	8	12
Pseudogoera singularis	T	365	C 53	PreTmt	21	3	12	109	7	58
				LE-1	13	3	10	169	3	25
				LE-2	42	15	29	69	2	14
				LE-3	56	1	6	196	5	29
				WR-1	12	3	6	52	1	17
			C 55	PreTmt	4	0	1	76	0	7
				LE-1	2	0	2	44	1	6
				LE-2	1	0	0	60	2	8
				LE-3	5	0	0	190	2	25
				WR-1	0	.0	0	76	3	39
Ceratopogonidae	D	365	C 53	PreTmt	2106	100	447	244	9	49
				LE-1	3606	113	673	163	5	26
				LE-2	3679	162	757	68	3	16
				LE-3	4861	181	1681	78	5	40
				WR-1	2196	104	511	48	1	9
			C 55	PreTmt	1633	62	314	77	4	18
				LE-1	1226	48	259	88	2	13
				LE-2	941	38	195	37	2	11
				LE-3	916	27	61	358	4	61
				WR-1	378	14	69	20	2	8
Hexatoma spp.	D	365	C 53	PreTmt	352	84	566	9	1	5
				LE-1	558	61	571	2	1	3
				LE-2	621	122	604	2	0	1
				LE-3	1091	131	789	4	0	2
				WR-1	585	100	546	6	1	6
			C 55	PreTmt	510	75	508	5	1	11
				LE-1	210	33	247	0	0	0
				LE-2	121	41	233	1	0	1
				LE-3	29	3	18	57	1	8
				WR-1	95	13	65	12	2	10
nr. *Pedicia* sp.	D	340	C 53	PreTmt	40	24	132	0	0	0
				LE-1	65	27	186	0	0	0
				LE-2	32	79	439	0	0	0
				LE-3	117	49	259	0	0	0
				WR-1	69	54	296	0	0	0
			C 55	PreTmt	18	19	106	0	0	0
				LE-1	22	12	67	0	0	0
				LE-2	1	1	2	0	0	0
				LE-3	6	3	11	8	1	8
				WR-1	2	0	2	0	0	0

APPENDIX. Continued.

Taxon	Order	CPI	Site	Year	Mixed substrates			Bedrock substrates		
					A	B	P	A	B	P
Dicranota spp.	D	310	C 53	PreTmt	70	6	28	137	3	28
				LE-1	114	5	23	70	2	15
				LE-2	101	12	96	126	2	35
				LE-3	82	16	116	111	3	27
				WR-1	45	16	82	67	1	11
			C 55	PreTmt	16	1	5	94	3	26
				LE-1	19	0	3	37	0	3
				LE-2	29	1	9	52	1	5
				LE-3	32	1	10	77	6	52
				WR-1	33	3	18	27	2	12
Glutops sp.	D	365	C 53	PreTmt	9	63	199	0	0	0
				LE-1	6	15	51	0	0	0
				LE-2	4	22	62	0	0	0
				LE-3	13	10	76	0	0	0
				WR-1	2	12	24	0	0	0
			C 55	PreTmt	4	29	61	0	0	0
				LE-1	5	27	91	0	0	0
				LE-2	2	8	16	0	0	0
				LE-3	2	4	19	0	0	0
				WR-1	1	3	8	0	0	0
Tanypodinae	D	340	C 53	PreTmt	1195	5	43	231	1	6
				LE-1	1884	9	71	189	0	3
				LE-2	2129	10	73	407	1	12
				LE-3	955	6	42	61	0	2
				WR-1	1705	13	91	926	1	21
			C 55	PreTmt	710	2	19	175	1	7
				LE-1	807	1	14	133	0	2
				LE-2	417	1	6	155	1	4
				LE-3	94	0	2	58	0	1
				WR-1	247	0	6	255	0	6
Empididae	D	340	C 53	PreTmt	260	9	59	241	4	32
				LE-1	583	3	28	102	2	12
				LE-2	112	2	16	147	2	15
				LE-3	69	1	4	27	0	2
				WR-1	45	1	5	98	3	12
			C 55	PreTmt	222	3	26	260	6	35
				LE-1	320	2	16	77	1	4
				LE-2	16	0	1	103	2	11
				LE-3	19	0	1	66	2	8
				WR-1	10	0	1	28	0	3
Acari	NI	5†	C 53	PreTmt	2415	6	32	1737	5	24
				LE-1	2707	7	36	1974	5	26
				LE-2	1463	4	20	1877	5	25
				LE-3	1934	5	26	1486	4	20
				WR-1	3250	9	43	1336	4	18
			C 55	PreTmt	1539	4	21	1600	4	22
				LE-1	1583	4	21	1054	3	14
				LE-2	493	1	7	1487	4	20
				LE-3	643	2	9	1557	4	21
				WR-1	387	1	5	984	3	13
Other invertebrate predators††			C 53	PreTmt	54	12	23	43	1	6
				LE-1	52	12	20	44	1	4
				LE-2	130	17	92	11	0	1
				LE-3	136	45	344	19	0	1
				WR-1	399	13	51	55	2	5
			C 55	PreTmt	11	7	16	27	2	12
				LE-1	14	7	35	23	1	4
				LE-2	18	5	19	45	0	2
				LE-3	15	3	12	58	4	13
				WR-1	72	7	33	53	1	2

APPENDIX. Continued.

Taxon	Order	CPI	Site	Year	Mixed substrates			Bedrock substrates		
					A	B	P	A	B	P
Total invertebrate predators			C 53	PreTmt	6827	672	2357	3043	113	722
				LE-1	10 092	801	3106	2932	58	382
				LE-2	8650	1046	3661	2915	57	363
				LE-3	9815	983	4706	2152	61	367
				WR-1	8606	734	2639	2726	48	284
			C 55	PreTmt	4892	403	1629	2532	97	446
				LE-1	4469	291	1237	1549	20	136
				LE-2	2277	151	630	2074	50	202
				LE-3	1905	97	279	2542	56	362
				WR-1	1333	107	386	1572	25	149
Salamanders‡‡			C 53	PreTmt	5	58	93	0	0	0
				LE-1	9	59	113	0	0	0
				LE-2	16	181	336	1	29	29
				LE-3	7	69	153	2	22	43
				WR-1	4	53	134	1	38	67
			C 55	PreTmt	4	29	62	0	0	0
				LE-1	1	4	13	0	0	0
				LE-2	0	0	0	0	0	0
				LE-3	1	11	26	3	36	60
				WR-1	1	26	32	1	18	34

† Assumed annual P/B.

‡ Other scrapers = *Ectopria* sp. (C), Elmidae (C), and *Hydroptila* sp. (T).

§ Other shredders = *Psilotieta* sp. (T), *Limonia* sp. (D), and *Anchytarsus* sp. (C).

‖ Chironomidae production measured using community growth are from Huryn (1990).

¶ Other gatherers = *Soyedina* sp. (P), Nymphomyiidae (D), *Ormosia* sp. (D), and Syrphidae (D).

Other filterers = *Diplectrona metaqui* (T), *Wormaldia* spp. (T), *Dolophilodes distinctus* (T), *Dixa* sp. (D), *Simulium* sp. (D), and Sphaeridae (NI).

†† Otherinvertebrate predators = *Malirekus hastatus* (P), *Molanna blenda* (T), *Pedicia* sp. (D), *Pilaria* sp. (D), *Pseudolimnophila* sp. (D), *Rhabdomastix* sp. (D), and Dolichopodidae (D), and Turbellaria (NI).

‡‡ Salamanders = *Desmognathus* spp. (average CPI_r = 880) and *Eurycea* sp. (average CPI = 365).