

ORGANIC MATTER FLOW IN STREAM FOOD WEBS WITH REDUCED DETRITAL RESOURCE BASE

ROBERT O. HALL, JR.,^{1,4} J. BRUCE WALLACE,² AND SUSAN L. EGGERT³

¹*Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA*

²*Department of Entomology, University of Georgia, Athens, Georgia 30602 USA and*

Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA

³*Department of Entomology, University of Georgia, Athens, GA 30602 USA*

Abstract. Food webs based on flows of organic matter were developed for two small streams to examine food web response to a large reduction in detrital inputs. At the study site, Coweeta Hydrologic Laboratory in the southern Appalachians, leaf litter inputs and associated microbial assemblages are the main energy source for food webs in headwater streams. We eliminated leaf litter inputs to one stream using a net placed over the first 180 m of stream from its origin. Food webs based on flow of organic matter were developed for a reference stream and the litter-excluded stream for two months, July and December of year 1 of the litter exclusion, to examine effects of leaf litter exclusion on the trophic base of the food web, size distribution of flows, predator–prey interactions, and trophic structure. Flows ($\text{mg AFDM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$; AFDM = ash-free dry mass) were estimated using gut content analyses for detritus and prey items, coupled with secondary production estimates. We used a whole-stream ^{13}C tracer method to estimate assimilation of bacteria by invertebrates. The food webs encompassed most (84–91%) of invertebrate secondary production, but <30% of the estimated total links. The primary sources of organic matter for the food web in the reference stream were leaf tissue, bacterial carbon, and animal prey, with ~25–30% of total secondary production derived from each. In-stream primary production led to <1% of invertebrate secondary production. A higher fraction of food web production in the litter-excluded stream was derived from wood. Magnitudes of detrital flows were lower in the litter-excluded stream, and some taxa were missing compared to the reference stream. The fraction of predator ingestion approached 100% of total secondary production for both streams, but this predation was distributed diffusely among several taxa. Flows to predators were fewer and smaller in the litter-excluded stream, yet these flows had higher per-biomass consumption coefficients, suggesting stronger interactions among the remaining common taxa. These food webs enabled us to examine interactions among taxa in the streams; hence, we found responses of the stream ecosystem to litter-exclusion that we would not have considered had we only measured changes in invertebrate population sizes or system-level changes in organic matter flow.

Key words: *bacteria; Coweeta Hydrologic Laboratory, North Carolina; detritus; detritivory; food webs; macroinvertebrates; organic matter flow; predation; resource reduction; streams.*

INTRODUCTION

Food webs provide a means to examine a role of a species in ecosystem processes and have historically been used to understand community and ecosystem function. Food web analyses have been used to examine trophic structure (Hairston et al. 1960), flow of energy or nutrients (Baird and Ulanowicz 1989), and consumer control of populations (Paine 1992). Food web approaches have been central to the description of ecological processes, such as community assembly (Cohen and Newman 1985), competition (Paine 1966), and consumer regulation of ecosystem processes (Carpenter et al. 1985, Power 1990).

Manuscript received 8 April 1999; 4 October 1999; accepted 11 November 1999.

⁴ Present address: Department of Zoology and Physiology, University of Wyoming, Laramie, Wyoming 82071-3166 USA. E-mail: bhall@uwo.edu

There are at least two disparate approaches to describe food webs. These are binary food webs and food webs based on energy flow. The first, described by Elton (1927), links species together based on observed feeding interactions without any quantification of the links (binary food webs). Food webs of this sort from many ecosystems were compared for common patterns in connectance, predator-prey ratios, and community assembly (Cohen 1978, Pimm 1982, Briand and Cohen 1987). This approach has been criticized because much of the raw food web data were not complete. Lower trophic levels were highly aggregated, many species in the web were ignored, and feeding interactions were arbitrarily defined (Paine 1988, Winemiller 1990, Martinez 1991, Polis 1991). These webs also contained sampling errors and uneven taxonomic aggregation that may affect the patterns found in webs with few species (Kenny and Loehle 1991, Martinez 1991). Recently, researchers have described binary food webs that con-

tain more detail in order to combat such criticisms (Martinez 1991, Closs and Lake 1994, Tavares-Cromar and Williams 1996). It also has been suggested that highly resolved binary food webs will provide insight into ecosystem function (Bengtsson and Martinez 1996). A more fundamental problem with these food webs is that all links were considered equal, because links were not quantified in terms of energy flow or interaction strength (Polis 1994, Benke and Wallace 1997). Furthermore, because these webs were designed to examine patterns in communities, completeness may be important; if most species are not included in the food web, then we can say little about the community. In theory, data for these webs are the easiest to collect; one simply needs to know the diets of all the taxa considered. However, to know all food web links in an ecosystem is likely impossible; indeed, identification of a large fraction of the links in a food web is a formidable task (Polis 1991).

A second approach, taken by Lindeman (1942), is based on energy flow. Lindeman grouped taxa by trophic levels, groups of organisms that feed upon a group that is closer to the abiotic energy source. Lindeman's focus was to quantify energy flow between trophic levels and to examine efficiency of that energy transfer, rather than identifying all links between individual species. Many studies used his approach to analyze energy flow through ecosystems (e.g., Odum and Odum 1955, Teal 1957, 1962), with some later studies resolving the food web well beyond trophic levels (e.g., Baird and Ulanowicz 1989). Ulanowicz (1986, 1997) has developed a method to examine ecosystem organization based on material flows. The energetic approach has often aggregated taxa into somewhat arbitrary trophic levels or functional groups, obscuring species' population dynamics. Flow webs are more difficult to construct than binary webs, because it is more difficult to quantify rates of material flow than the presence/absence of a link. This is why previous studies (e.g., Teal 1962, deRuiter et al. 1995) used trophic levels or functional groups.

One pervasive weakness in the analysis of ecosystem food webs is not including or quantifying the role of heterotrophic microbes, even though microbes often dominate secondary production and respiration in an ecosystem. Although our understanding of microbial food webs is advancing (Pace et al. 1990, Meyer 1994, Sherr and Sherr 1994, Borchardt and Bott 1995, Porter 1996), the role of microbes is often not quantified in food webs. Allochthonous litter inputs support much of the secondary production in shaded headwater streams. Microbial conditioning of leaf litter and consumption of microbes and associated detritus by macroinvertebrates may represent strong links in the food web by regulating leaf decomposition (Cuffney et al. 1990) and energy flow (Teal 1957).

By constructing a highly detailed food web that measures flows between consumers and resources, we have

a new perspective by which we can examine controls of food web structure. In this study we experimentally decreased the detrital resource base in a stream and examined change in food web structure relative to a reference stream. The role of productivity in structuring food webs has been well studied, both theoretically (Oksanen et al. 1981, Sterner et al. 1997) and empirically (Hairston and Hairston 1993, Rosemond et al. 1993, Wootton and Power 1993). Changes in basal resources (e.g., plants or detritus) can alter secondary production (Wallace et al. 1997b, 1999) and maximum food chain length (Jenkins et al. 1992). Oksanen et al. (1981) suggested that patterns of consumer control will change with increasing primary productivity. Others argued that differences in trophic structure are controlled by the types of organisms present, not the amount of energy at the base of the food web (Hairston and Hairston 1993). Increases in detritus quantity led to increases in food chain length (Jenkins et al. 1992); however, they measured food chain length and not overall organic matter flow. Large changes in food web structure may occur following a decrease in basal resources, in this case lower leaf litter inputs to stream. Such a decrease in resources may cause the trophic base of the food web to switch to another resource such as algae or wood. Average food chain length may decrease because of diet switching or loss of the highest trophic level.

We have two objectives in this paper. The first is to describe a stream food web that combines the detail of some binary webs with estimates of organic matter flow for each link. We document organic matter flow from detritus/microbes to detritivorous macroinvertebrates, and from individual prey to predator taxa in order to (1) determine the trophic base of the ecosystem and assess the degree to which metazoans are linked to microbial production, and (2) relate consumption by individual taxa with total detrital-invertebrate flows and predation. A major consideration of food web research is how many links need to be identified or measured, because the quality of information gained from food web analysis is influenced by the degree of resolution (Martinez 1991). On the other hand all links may not need to be quantified, because most of the energy flow is through a few links (Kenny and Loehle 1991). In this study we explicitly identify the degree to which we have assessed both flow of organic matter and total links in the food web, and we separate macroinvertebrate consumption of detritus from bacterial consumption of detritus to assess the role of bacterial production in the food web.

The second objective is to compare food webs based on organic matter flow from two streams: a reference stream and a stream that had all leaf litter excluded for the first year of a multiple-year study. How do patterns of organic matter flow differ between these two streams? Can differences in patterns of flows in food webs be detected other than through the reduced bio-

mass and production of invertebrate detritivores and predators previously observed (Wallace et al. 1997b, 1999)? Specifically, we examine differences in average trophic level of the invertebrate assemblage, changes in trophic base of the food web, changes in interaction between predators and prey, and the size distribution of flows in the food web between these two streams for two months during year 1 of a multiple-year study.

METHODS

Study site

We conducted this study in two perennial first-order streams at Coweeta Hydrologic Laboratory in Macon County, North Carolina, USA (Catchments 53 and 55). They drain steep, forested catchments dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), and yellow poplar (*Liriodendron tulipifera*). A dense understory of *Rhododendron maximum* shades the streams year round. Stream substratum is mostly mixed silt, sand, pebble, and cobble, with some areas of bedrock outcrop. These streams are strongly heterotrophic because heavy shading limits photosynthesis. Litter inputs are ~500 g ash-free dry mass (AFDM)·m⁻²·yr⁻¹ (Wallace et al. 1995), whereas primary production in a similar Coweeta stream is only 2.6 g AFDM·m⁻²·yr⁻¹ (Webster et al. 1983). The streams are fishless; the dominant vertebrate predators are salamanders, mostly *Desmognathus* spp.

All new leaf litter inputs were excluded from Catchment 55 using a 2.5-cm stretch mesh gill net canopy, which was placed over the first 180 m of the stream in August 1993 (Wallace et al. 1997b). Catchment 53 served as the reference stream. A 20 cm high plastic fence with 1-cm openings was placed along each bank along the treatment stream to prevent lateral inputs of litter. A large (>1 m) space between the fence and the net allowed aerial recolonization by insects. Leaf litter was removed from the net one time each week with a leaf blower during autumn and when necessary during other seasons. Leaves were blown so as to land beyond the lateral fence. The net canopy extended beyond the spring seep to prevent any downstream transport of leaf litter. This manipulation dramatically lowered leaf inputs and standing crop in the stream, as well as decreased fine benthic organic matter (FBOM; 0.45 μm < FBOM < 1 mm particle size) (Table 1; Wallace et al., 1999). The mesh caused a <1% decrease in light reaching the stream, and chlorophyll *a* concentrations on tiles were higher in the treatment stream relative to the reference stream during the first year of the manipulation (Table 1).

Food web construction

We constructed food webs for both the reference and the litter-excluded stream during two seasons: July 1994 (end of year 1 of the manipulation) and December 1994 (start of year 2). We chose these two contrasting

TABLE 1. Organic matter standing stocks in the study streams.

Measure	Reference stream		Litter-excluded stream	
	July	December	July	December
Leaf litter (g AFDM/m ²)	255	424	2.6	0.3
FBOM (g AFDM/m ²)	1250	1400	476	461
Chl <i>a</i> (mg/m ²)	1.6	0.5	4.1	4.3

Notes: Organic matter stocks were averaged through June, July, and August 1994 and November, December, and January 1994–1995 (*n* = 12). Leaf litter and fine benthic organic matter (FBOM) were collected with four benthic cores each month in mixed substratum habitat. Chlorophyll *a* was measured from five tiles incubated for 8 wk in each stream.

seasons to maximize intra-annual variation in leaf litter standing crop; leaf standing crop is high in December and low in July. We used the trophic basis of production method to estimate flows from resource to consumer (Benke and Wallace 1980). We multiplied animal production for an individual taxon by the percent of its production derived from a food type, and then divided by assumed net production efficiency and assimilation efficiency for the food source. Food types were assessed by analyzing gut contents. Production was estimated by multiplying animal biomass times growth rate. We estimated trophic significance of bacteria to invertebrate consumers by adding acetate enriched with carbon-13 (¹³C) to label bacteria and their consumers (Hall and Meyer 1998). The fraction of invertebrate carbon derived from bacteria was estimated using a mixing model (Peterson and Fry 1987). Here, we detail the methods used to construct the food webs.

Biomass and production estimates

We estimated invertebrate biomass in both streams monthly during June–August 1994 and November 1994–January 1995. We used three months of data that encompassed our one-month intensive study period, because of high variability in invertebrate biomass estimates. Four 400-cm² core samples were collected randomly, using a stovepipe corer in the mixed-substrate habitat. All material in the core was removed by hand using a cup to a depth of 10 cm. Moss-covered bedrock outcrops were sampled by scraping three randomly chosen 15 × 15 cm areas into a 250 μm mesh bag pressed to the rock surface.

In the laboratory, the samples were elutriated and poured through 1-mm and 250-μm sieves. Samples were fixed and preserved in 10% formalin and stained with Phloxine B dye to facilitate sorting. All animals were removed from the >1-mm fraction under 15× magnification. Invertebrates in the <1-mm fraction were subsampled using a sample splitter (Waters 1969). Insects were identified to species or genus, with the exception of Chironomidae, which were identified as

subfamily Tanypodinae (predators) or non-Tanypodinae (collectors), and Ceratopogonidae. Noninsect invertebrates were identified to family or higher. We determined biomass by measuring each animal to the nearest millimeter and converting to AFDM using length–mass regressions (Benke et al. 1999). Average invertebrate biomass from the mixed substrate and bedrock outcrop samples was habitat-weighted according to the proportion of bedrock outcrop and mixed substratum (Lugthart and Wallace 1992).

We estimated daily production (in units of milligrams AFDM per square meter per day) of most insects as biomass multiplied by a growth rate. Growth rates (measured on a per day basis) were determined by the following:

$$\text{growth rate} = [\ln(\text{mass}_t) - \ln(\text{mass}_1)]/\text{CPI} \quad (1)$$

where mass_1 and mass_t are individual invertebrate biomasses at 1 mm and terminal lengths, respectively. CPI is the cohort production interval, which is the mean length of time (in days) required for a taxon to complete the larval period of its life cycle. CPIs were taken from Lugthart and Wallace (1992). This method assumes a constant growth rate during larval growth, as does the commonly used size–frequency method to estimate secondary production (Benke 1984). Nontanypodine chironomid production was estimated using the assemblage-level method, whereby biomass of different chironomid size classes is multiplied by a temperature and size-corrected growth rate (Huryn and Wallace 1986, Huryn 1990). Copepod production was estimated using a production/biomass ratio (P/B) of 18/yr (O'Doherty 1988). Taxa for which we have limited knowledge of life histories (e.g., oligochaetes) were assigned a P/B of 5/yr, which probably underestimated their production.

Diet analyses

We collected invertebrates for diet analysis in various stream habitats during July and December 1994. Invertebrates were picked live and preserved in 10% formalin solution. Because other studies were carried out simultaneously to this project, we had to minimize disturbance and were not able to sample all rare taxa. Hence, some taxa were missing from this analysis. Common taxa, which constitute most of the secondary production, were adequately sampled (see *Results*).

Diets were assessed for detritivorous invertebrates by measuring the relative area of particles from various diet categories found in their guts (Cummins 1973). Guts were dissected, suspended in distilled water, filtered onto a membrane filter, placed onto a slide, and cleared with immersion oil (Cummins 1973). We used from one to three guts of individual invertebrates for each slide. Between two and six slides were made for each taxon. Gut contents were quantified from these slides by measuring the relative areas of diet categories on the filters at 400 \times using a phase-contrast compound

microscope equipped with a camera lucida and a computer sketchpad. Fifty particles were measured per slide. The six diet classes were amorphous (i.e., non-cellular) detritus, leaf detritus, wood detritus, diatoms, fungal hyphae, and animal material. Amorphous detritus particles comprise bacteria, microbes, polymeric fibrils, sediment particles, and tiny detrital fragments (Carlough 1994). Because amorphous detritus lacks defined cellular structure, we distinguished it from algal cells, fungal hyphae, leaf fragments, or animal material found in the guts. Using phase-contrast microscopy, an amorphous detritus particle appeared as a discrete aggregation of subcellular-sized particles.

Gut contents of predator taxa were teased out of guts and mounted onto a slide with lactophenol. Between 3–65 individuals were enumerated from each predator taxon, with a median of 10 individuals per taxon. Some predators were too rare for this analysis; for others (e.g., Ceratopogonidae, *Glutops*, *Rhyacophila*) it was difficult to determine gut contents because of excessively macerating their prey, or because they are piercing/sucking predators (see Martin and Mackay [1982] for a *Rhyacophila* example). We measured either the total length or head capsule width of each prey item found in the gut and used length–mass regressions (Benke et al. 1999; R. Hall, *unpublished data*) to estimate prey biomass. The fraction contributed by each prey taxon to predator ingestion was calculated as the sum of the mass of all prey items for each prey taxon, divided by the sum of all prey mass found in guts of the predator taxon.

One common problem with gut analyses is that soft-bodied organisms digest quickly and are not as visible in the gut relative to more sclerotized prey. We estimated this bias by assessing the fraction of chironomid head capsules associated with the soft thoracic and abdominal segments. Of 550 head capsules examined, 27% had no soft tissue, 45% had some recognizable tissue, and 18% were whole. Because <30% of chironomids' soft parts were completely digested, and therefore invisible using gut contents analyses, we should have been able to find a large proportion of ingested purely soft-bodied organisms, such as nematodes and oligochaetes. Most prey items available to predators had some sclerotized cuticle (i.e., insects). Oligochaetes were also visible, because their chaetae distinguished them as such.

Fraction of carbon derived from bacteria

We estimated the fraction of carbon derived from bacteria by adding ^{13}C -enriched sodium acetate to the stream for three weeks to label bacteria and their invertebrate consumers (Hall and Meyer 1998). Acetate is a substrate that bacteria can readily use, but its concentration was too low to label osmotrophic fungi and algae. Invertebrate and detrital samples were collected before and after the addition. Bacterial $\delta^{13}\text{C}$ was measured by collecting respired bacterial carbon. The con-

tribution of bacterial carbon was estimated using a mixing model for invertebrates and bacteria, which compares invertebrate ^{13}C enrichment relative to two end members: bacterial ^{13}C enrichment and nonbacterial carbon (e.g., pretreatment leaf $\delta^{13}\text{C}$) (Hall and Meyer 1998). This analysis was done directly for 76% of all detritivore secondary production. For the remaining invertebrates, we estimated the fraction of carbon derived from bacteria, because it was linearly related with percent amorphous detritus in the gut (Hall and Meyer 1998). Bacterial carbon refers to both cellular and extracellular carbon, as the labeling method cannot differentiate between the two (Hall and Meyer 1998). Extracellular organic material originating from bacteria may represent a larger carbon pool than bacterial cells (Couch and Meyer 1992) and can be assimilated by invertebrates with high efficiency (Couch et al. 1996).

Calculation of material flows

We used the trophic basis of production method to assess organic matter flow between consumers and resources (Benke and Wallace 1980, 1997). Units of flow are milligrams AFDM per square meter per day. We assumed assimilation efficiencies of 10% for leaves, wood, and amorphous detritus; 30% for diatoms; 50% for fungi and bacteria; and 80% for animal prey (Benke and Wallace 1980). These assimilation efficiencies are within the range of published values for each food type (Slansky and Scriber 1982, Wotton 1994). We have to use published values, because we used many taxa for which we could not do detailed growth and assimilation studies. The fraction of invertebrate production derived from a food type i (B_i) was calculated by dividing the fraction of area in the gut by the assimilation efficiency for that food type, and dividing again by the sum for all food types in the gut. B_{bacteria} was assessed directly as fraction of carbon derived from bacteria. Flow from each food type i to consumer j (F_{ij} , measured in milligrams AFDM per square meter per day) was calculated as follows:

$$F_{ij} = (B_i P_j) / (AE_i \times \text{NPE}) \quad (2)$$

where P_j is production of consumer j (same units as F_{ij}), AE_i is assimilation efficiency for food type i , and NPE is net production efficiency (assumed to be 0.4) (Benke and Wallace 1980). We calculated the trophic basis of production for the whole assemblage, which is the production-weighted average of B_i for each taxon in the assemblage.

We measured fraction of carbon derived from bacteria separately from the analyses of gut contents; thus, the sum of production derived for all food types exceeded unity for detritivores. Assimilated bacterial carbon was associated primarily with ingested amorphous detritus (Hall and Meyer 1998), so its flow was counted twice when we describe total flows in the food web. When calculating the trophic base of production for the entire food web, the fraction of production derived

from bacteria (B_{bacteria}) was subtracted from the fraction of production derived from amorphous detritus ($B_{\text{amorphous}}$). If $B_{\text{bacteria}} > B_{\text{amorphous}}$, we assigned $B_{\text{amorphous}}$ a value of zero and subtracted the remainder of B_{bacteria} from the fraction of production derived from leaves and wood, so that the sum of all $B_i = 1$.

Analysis of trophic structure

The mean trophic level for each taxon was calculated as one added to the average trophic level of food types in its diet, which were weighted by percent assimilation. This average estimates the trophic level on which an organism feeds, even though that taxon may be an omnivore (Wiegert and Owen 1971, Levine 1980, Ulanowicz 1986). The average trophic level of a consumer is the average trophic level of its food, plus one. Detritus and algae were assigned a value of one; microbes that fed on detritus would thus be trophic level two. An omnivorous detritivore (all detritivores are omnivores to some degree) that derived 50% of its organic matter from bacteria and 50% from leaf detritus would be trophic level 2.5. We calculated mean trophic level of each taxon for each site and season using methods described in Ulanowicz (1986). We assembled a matrix for each food web from each stream and season, with consumers as columns and resources as rows. Entries in this matrix are the fraction of a consumer's diet that is derived from a particular resource. This is the same as the \mathbf{G} matrix (Ulanowicz 1986). Using \mathbf{G} , we calculate the matrix \mathbf{A} :

$$\mathbf{A} = [\mathbf{I} - \mathbf{G}]^{-1} \quad (3)$$

where \mathbf{I} is the identity matrix (a matrix of zeros, with ones along the diagonal). Average trophic level for each consumer is the sum of all entries in each column of \mathbf{A} . Cannibalism is explicitly included in this analysis, as a consumer and a resource can be the same taxon.

Each entry of \mathbf{A} represents the extended diet of a consumer (Ulanowicz 1986). For instance, a predator that does not eat bacteria directly may derive 50% of its organic matter from bacteria, because that predator's prey are consuming bacteria. Hence, we can examine the dependencies of predators on a resource more than one trophic step away.

We identified some prey taxa in predator guts for which we did not analyze gut contents. Rather than treat these as external flows for which we could not assign a trophic level, we grouped these prey taxa as predators and detritivores, and assigned a trophic level of 3.5 and 2.5, respectively. These flows averaged 11% of total predator consumption.

To compare the average trophic level of invertebrates between streams or dates, we used paired t tests with individual taxa as replicates. Use of a paired t test accounted for between-taxa variability in average trophic level, so that we could assess whether, on average,

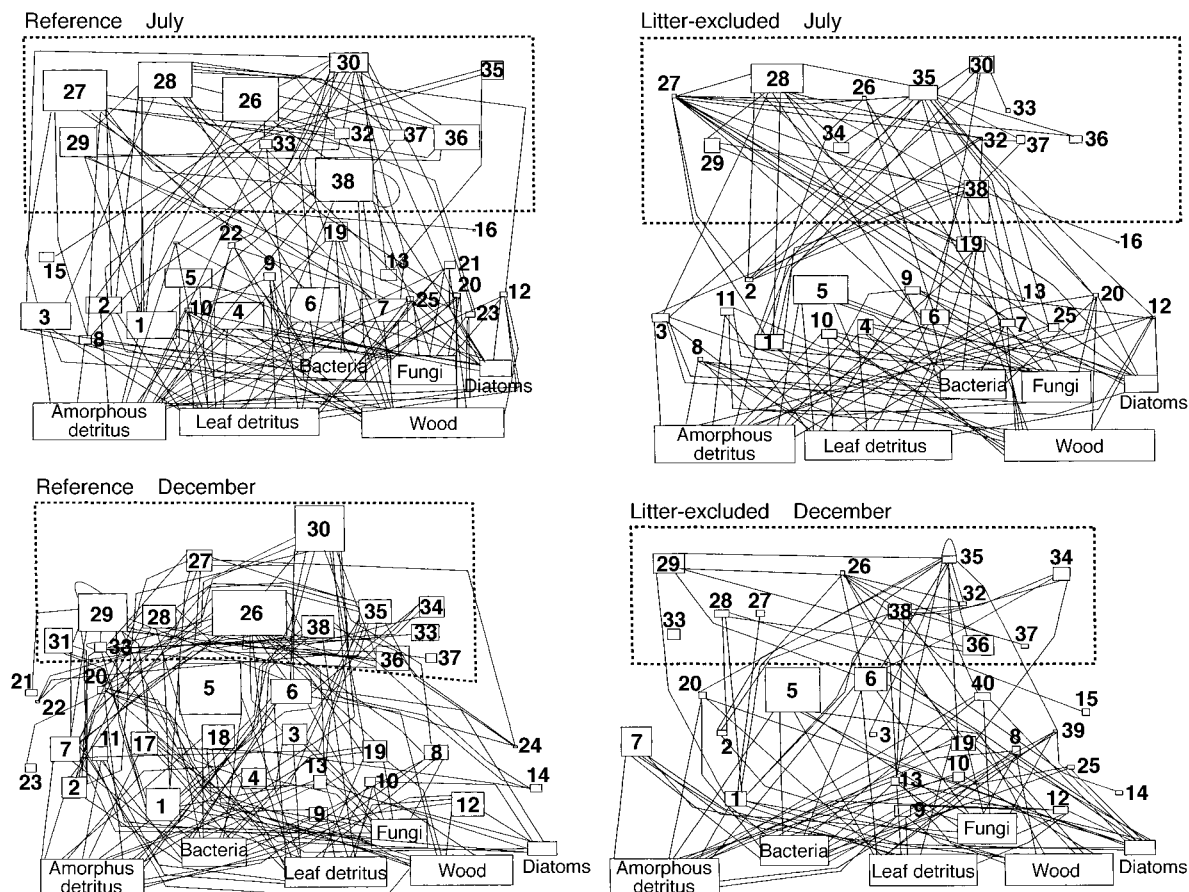


FIG. 1. Connectance food web for the reference and litter-excluded streams during July and December. The size of the boxes for animals corresponds to relative biomass. Detrital and microbial boxes would be much larger than what is pictured here if scaled to their mass. The dashed box encompasses predatory taxa. The taxa are as follows: (1) Chironomidae, (2) Harpacticoida, (3) *Leuctra* spp., (4) *Lepidostoma* spp., (5) *Tipula* spp., (6) *Tallaperla maria*, (7) Oligochaeta, (8) *Amphinemura wui*, (9) *Fattigia pele*, (10) *Lype diversa*, (11) *Sciara* spp., (12) *Stenonema* spp., (13) *Paraleptophlebia* sp., (14) Testate protozoa, (15) Nematoda, (16) *Alona* spp., (17) *Molophilus* spp., (18) *Pycnopsyche* spp., (19) *Diplectrona modesta*, (20) *Wormaldia moesta*, (21) *Dolophilodes distinctus*, (22) *Dixa* spp., (23) *Simulium* spp., (24) Ostracoda, (25) *Ectopria thoracica*, (26) *Beloneuria* sp., (27) *Cordulegaster* sp., (28) *Lanthus vernalis*, (29) *Hexatoma* spp., (30) salamander, (31) *Pedicia* spp., (32) Tanypodinae, (33) *Dicranota* spp., (34) *Rhyacophila* spp., (35) *Isoperla* spp., (36) Ceratopogonidae, (37) Acari, (38) *Parapsyche cardis*, (39) *Epeorus* sp., (40) *Serratella* sp.

individual taxa fed at a different trophic level between streams or seasons.

RESULTS

Scale of food web and adequacy of sampling

Before examining our constructed food webs, it is necessary to assess their completeness, because these food webs cannot encompass all links and all organic matter flow in the ecosystem. We probably only enumerated a small portion of the total links, because we did not sample all species and because we likely missed rare items in diets (Fig. 1). As an example, we estimated 200 flows in the July food web from the reference stream with 35 taxa (animal and detrital categories included) for which we can calculate a trophic connectance of 0.16 (trophic connectance = no. links/[no. species]²) (Warren 1989, Martinez 1991). However, there

were 62 taxa found in the stream in July, 27 more taxa than we were able to include in the food web. Assuming connectance is ~ 0.16 , with 62 taxa there should be 615 links, about three times as many as we were able to enumerate.

Another method to assess the completeness of our food webs is to divide the production of taxa included in the food web by total secondary production. Taxa not sampled tended to be rare and contributed little to total secondary production. Of the total invertebrate production (i.e., all taxa in the stream), we accounted for 90–97% of detritivore production and 65–81% of predator production in the food webs (Table 2). More detritivores than predators were included in these food webs, because we were unable to assess diets of all predatory taxa because they were too rare or had ambiguous gut contents. Nonetheless, 84–91% of total invertebrate secondary production was measured.

TABLE 2. Amount of production accounted for in food webs from the reference and litter-excluded streams.

Measure	Reference stream		Litter-excluded stream	
	July	December	July	December
Total detritivore production (mg AFDM·m ⁻² ·d ⁻¹)	17.8	12.4	5.7	6.1
Total predator production (mg AFDM·m ⁻² ·d ⁻¹)	9.3	6.9	2.5	1.6
Detritivore production accounted for in the food webs (%)	90	97	92	95
Predator production accounted for in the food webs (%)	80	81	65	71

The magnitude of each flow plotted against its rank shows a geometric decrease in flow magnitudes (measured in milligrams AFDM [ash-free dry mass] per square meter per day) (Fig. 2). Both seasons had nearly identical curves, but the curves from the litter-excluded stream were lower, because total flow through that food web was much less. Flow distribution was approximately lognormal; hence, most of the carbon flux in this food web flowed through just a few taxa, which is observed in the steep decline in flow magnitudes with the first few flows (Fig. 2). Numbers of flows drop off at ~ 0.01 mg AFDM·m⁻²·d⁻¹, when the slopes of the rank/flow curves became much steeper. We suggest that we are able to enumerate only a few of these small flows, because as flow magnitude decreased we had a lower probability of detecting them. Thus, the large fraction of total links that were not enumerated were probably ones that had flows < 0.01 mg AFDM·m⁻²·d⁻¹.

Trophic basis of production for the stream food webs

Stream food webs were dominated by secondary consumption (Table 3), such as bacterial and animal consumption, which accounted for more than half of macroinvertebrate secondary production. Little production was derived from diatoms, the main primary pro-

ducers in these streams. The fraction of production derived from fungi was apparently low in both streams during both seasons. However, we undoubtedly underestimated the contribution of fungi to the food webs, because we identified only visible hyphae in invertebrate guts. Much of cellular leaf detritus is invaded by fungal hyphae that are invisible unless the leaf is cleared and stained (see Newell and Hicks 1982). Most detritivores did derive a large fraction of their production from bacteria and their exopolymers as well as dead plant tissue; hence, bacteria were trophically important in the food webs.

There appeared to be little seasonal difference in the trophic base for the food web in the reference stream (Table 3), despite lower standing crops of leaf litter in July, relative to December (Table 1). Leaves and bacteria provided most of the organic matter (52–62%) for this food web during both seasons.

The trophic basis of production for the litter-excluded stream was different than that of the reference stream, although much of this difference was observed only during December (Table 3). By December, the litter-excluded stream had missed its second year of autumnal leaf litter input. As a fraction of invertebrate production, leaf consumption was lower in the litter-

FIG. 2. Flow magnitude (mg AFDM·m⁻²·d⁻¹) vs. rank. Flows are flow of organic matter from a resource to a consumer. Rank of flows appears along the *x*-axis; log₁₀(flow magnitudes) appears along the *y*-axis. The solid line is for July, and the dotted line is for December.

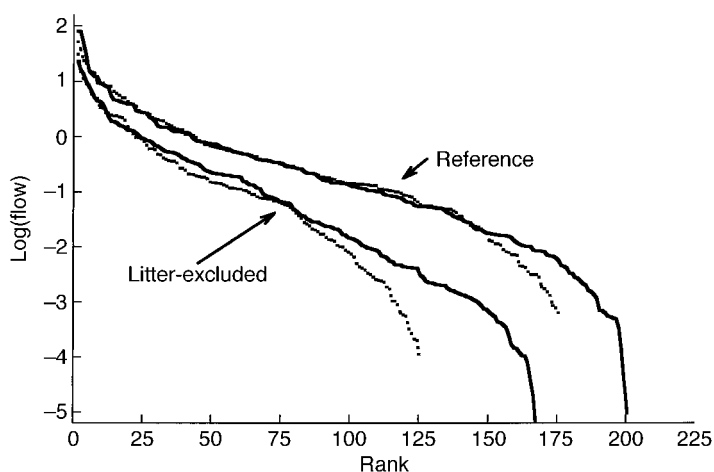


TABLE 3. Percentage of invertebrate secondary production derived from various food sources calculated from secondary production, gut analyses, and assimilation of bacteria.

Food source	Reference stream		Litter-excluded stream	
	July	December	July	December
Amorphous detritus	5	3	0	16
Bacteria	23	33	40	15
Leaf detritus	29	29	18	10
Wood detritus	3	1	10	27
Fungal hyphae	3	2	3	4
Diatoms	1	0	1	9
Animal	35	32	29	18

Note: The fraction of organic matter derived from amorphous detritus is low because most is attributed to bacteria.

excluded stream. The fraction of production derived from wood was higher in the litter-excluded stream. Production derived from diatoms was higher in the litter-excluded stream during December (Table 3). The litter-excluded stream showed a stronger seasonal difference in the trophic base of the food webs than did the reference stream, especially with bacteria. The fraction of production derived from bacteria was much lower in December than July in the litter-excluded stream.

Few taxa included both animal prey and detritus in their diets. Predatory Plecoptera and Odonata appeared to specialize upon invertebrate prey, as even small instars (~3 mm) consumed only invertebrates. Gut contents teased from predators indicated that detritus found in these predatory stoneflies and dragonflies represented the gut contents of their detritivore prey. Most detritivores consumed only detritus. *Parapsyche*, which ate both animal prey and detritus, was an exception to this observation. *Rhyacophila* may consume detritus as well as animal prey during early instars, however, we were unable to quantify the prey-to-detritus ratio because of ambiguous gut contents. Again, most detritivores were omnivorous, because they consumed both microbial biomass and dead plant tissue.

Patterns of detrital flows

Largest flows in the food webs were from leaf tissue and amorphous detritus to detritivores, because of low assimilation of these food items (Table 4). Flows from bacteria and amorphous detritus were counted twice so that it is possible to compare ingestion of bacteria and amorphous particles with other detrital/microbial sources. As observed for the trophic basis of production, there were few differences in total ingestion between July and December in the reference stream. In contrast, total ingestion was lower in the litter-excluded stream because of decreased insect production (Table 2, Appendix) (see also Wallace et al. 1997b, 1999). Ingestion of leaf detritus in the litter-excluded stream was ~20% that of the reference stream, and ingestion of amorphous detritus was ~30% that of the reference

stream. Despite lower invertebrate production in the litter-excluded stream, wood ingestion was higher (Table 4).

Although total flows were similar between seasons in the reference stream, taxa responsible for these flows differed between seasons (Fig. 3). These differences are attributable to seasonal changes in abundance, biomass, and production of taxa (see the Appendix). For example, *Tipula* was the dominant leaf consumer in December, while *Lepidostoma* dominated in July. Harpacticoid copepods and *Tallaperla* exhibited similar flows during July and December because of similar production between seasons. High detrital flows corresponded with foods having low assimilation efficiencies (e.g., leaves) being consumed by invertebrates with high production. Flows from bacterial carbon were smaller than detrital flows, in part because of higher assimilation efficiency for bacteria, so the only large bacterial flow was to chironomids in each season. Chironomids, because of their high productivity, had the largest flows, both as consumers (Fig. 3) and as prey (Fig. 4). They occupy an important position in the food web in terms of supplying energy to predators. Also, they are the most aggregated of insect taxa in this food web; individual species would not likely dominate the flows, as observed here. Because temperature strongly affects chironomid growth rate and production (Huryn and Wallace 1986, Huryn 1990), there were smaller flows during the colder month of December.

As observed for the food web in the reference stream, detritivore taxa responsible for the largest flows in the litter-excluded stream food web differed somewhat between July and December (Fig. 3). Wood consumption was more important in the litter-excluded stream than the reference stream. Patterns of change seemed to be similar between streams. Chironomids had smaller flows in December than during July. The largest flow was from wood to *Tipula* during December; *Tipula* was less abundant and productive during July. The filter-feeders, *Diplectrona* and *Parapsyche*, were important in both months in the litter-excluded stream. Harpacticoid copepods were nearly eliminated from the litter-excluded stream (see Appendix). Shredding caddisflies

TABLE 4. Total ingestion of various food sources (mg AFDM·m⁻²·d⁻¹).

Food source	Reference stream		Litter-excluded stream	
	July	December	July	December
Amorphous detritus	150	130	34	49
Bacteria	28	29	13	5.7
Leaf detritus	200	160	46	23
Wood detritus	23	6.1	34	48
Fungal hyphae	3.9	1.5	1.1	1.6
Diatoms	2.1	0.39	0.7	5.2
Animal	23	17	5.1	3.2

Note: Bacteria and amorphous detritus are considered separately here so that their flows are effectively measured twice.

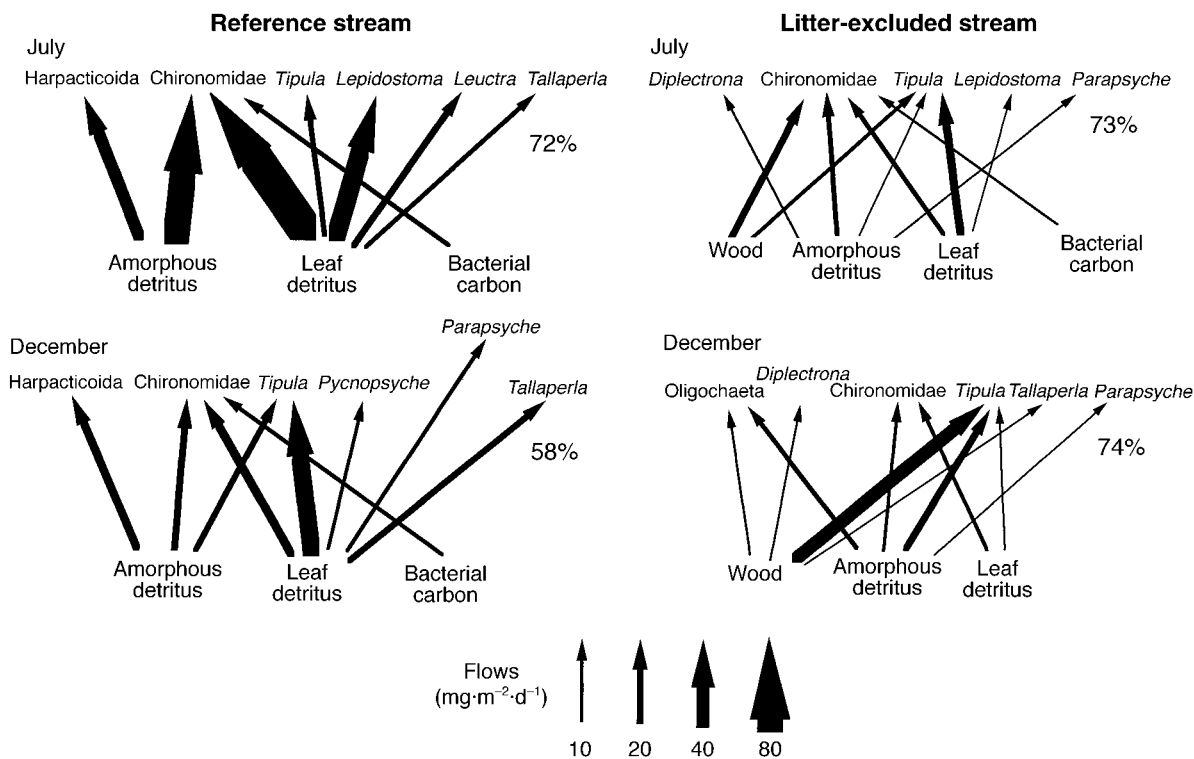


FIG. 3. Largest flows from detritus and bacteria to invertebrates in the reference and litter-excluded streams. The top panels are for July; the bottom panels are for December. The percentages on the right of each food web are the percentage of total organic matter flow represented by the diagrammed flows. The thickness of the arrows is proportional to flow magnitude ($\text{mg AFDM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$).

were strongly reduced by the manipulation (Wallace et al. 1997b); hence, leaf consumption by *Lepidostoma* was much lower in the litter-excluded stream in July. By December, there were no large flows to shredding caddisflies.

Despite large differences in taxonomic composition between seasons, there was little difference in the size distribution of the flows (Fig. 5). Indeed, between the reference and the treatment stream, the shapes of the curves are similar, but the curve for the litter-excluded stream is displaced downward because overall flows were lower.

Flows to predators

The proportion of production derived from predation was lower in the litter-excluded stream than in the reference stream. Total invertebrate production in July in the reference stream was $27.3 \text{ mg AFDM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, of which $23 \text{ mg AFDM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (84%) was consumed by predators. December invertebrate production was $19.3 \text{ mg AFDM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, of which $17 \text{ mg AFDM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (88%) was consumed. In the litter-excluded stream, total July production was $8.2 \text{ mg AFDM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, with $5.1 \text{ mg AFDM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (62%) of production consumed by predators; total December production was $7.7 \text{ mg AFDM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$, with $3.2 \text{ mg AFDM}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ (42%) consumed by predators. Much of the total invertebrate

production in the food webs was consumed by predators. Since we did not account for 100% of predator production in these food webs, the percentage of total secondary production consumed by predators may be higher than reported here.

Most predator taxa were omnivorous, because they ate both other predators and detritivores, thus feeding at two trophic levels. The percentage of predator production eaten by other predators was lower than the percent of predator production in the food webs. Predator taxa constituted 27% and 16% of total predator ingestion during July and December in the food web in the reference stream, with 9% and 5% of total secondary production of macroinvertebrates derived from consumption of predators. In the litter-excluded stream, ingestion of predators constituted 21% and 16% of total predator ingestion with 7% and 3% of total macroinvertebrate production derived from consumption of predators. There were several predators in each food web that all shared the same prey; thus, predation was diffuse (Menge et al. 1994). Diets were broad for each taxon; we did not find predators specializing on one or two prey taxa.

Patterns of flows to predators differed greatly between the reference and the litter-excluded streams. Total predator production was less in the litter-excluded stream; hence, flows to predators in the litter-excluded

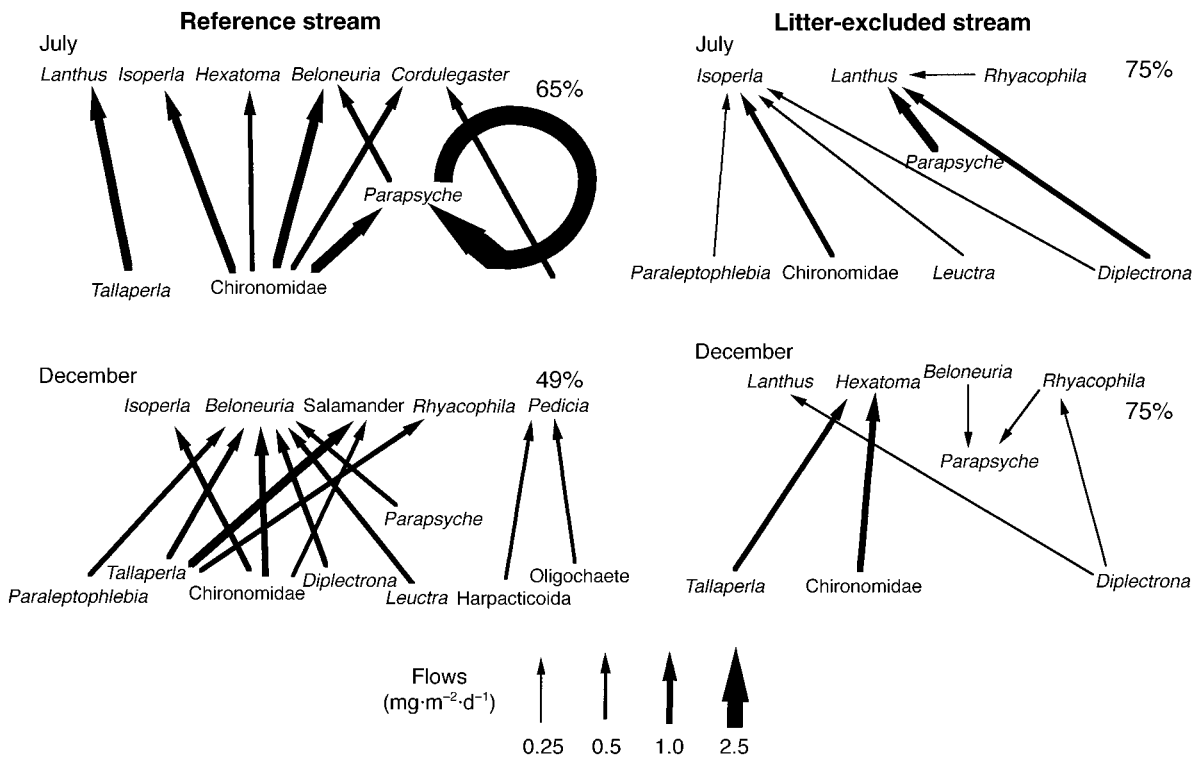


FIG. 4. Largest flows from invertebrate prey to predators in the reference and litter-excluded streams. The top panels are for July; the bottom panels are for December. The percentages on the right of each food web are the percentages of total organic matter flow represented by the diagrammed flows. The thickness of the arrows is proportional to flow magnitude (mg AFDM·m⁻²·d⁻¹).

stream were smaller than those of the reference stream. The flows in the litter-excluded stream were dominated to a greater extent by a few large flows, with 75% of the prey consumption concentrated in six or seven flows (Fig. 4). In contrast, nine flows constituted 65% of the total prey consumption in the reference stream during July, while 12 flows constituted only 50% of prey consumption during December. This pattern is more clearly evident by examining the distribution of flows to predators (Fig. 5). Unlike detrital flows, ranked flows to predators in the litter-excluded stream had a steeper slope than those of the reference stream; thus, the food web in the litter-excluded stream was dominated by only a few flows. Some of the largest flows in the winter in the litter-excluded stream were predators consuming other predators, which was not observed in the reference stream.

Large seasonal differences existed in taxa responsible for the largest flows to predators in the reference stream (Fig. 4), despite little seasonal variation in predation (Tables 3 and 4). In the reference stream, *Beloneuria* was much more abundant in December and was an important predator. In the litter-excluded stream, *Isoperla* was a dominant consumer in July, but not in December (Fig. 4). The largest predatory flow observed in July was *Parapsyche cardis* cannibalism; by December its biomass was lower and no cannibalism

was observed. Summer is a recruitment period for these filter-feeders (J. B. Wallace, *personal observation*), and they were likely space-limited on the bedrock habitats. Small instars were probably being consumed by larger instars already on the bedrock outcrop.

The difference in patterns of flows to predators between the reference and litter-excluded food webs suggests interaction strength changed between predators and prey. We calculated the per biomass consumption coefficient between prey and predators using a method described by Wootton (1997) and Moore et al. (1996) to predict interaction strength from prey consumption rates. Using diet observations of birds feeding upon rocky intertidal invertebrates, Wootton (1997) measured interaction strength based on the consumption coefficient from the Lotka–Volterra equation. Our analysis differs in that we normalize consumption to biomass and not to individuals, as did Moore et al. (1996). Consumption rate, F_{ij} (biomass of prey·[area]⁻¹·[time]⁻¹) is

$$F_{ij} = -cPN \quad (4)$$

where N is prey biomass per unit area, P is predator biomass per unit area, c is the per biomass effect of species P on N (Wootton 1997). The consumption coefficient cP has dimensions of (inverse time) and is equal to the ingestion rate divided by prey biomass per

TABLE 5. Consumption coefficients from total predator consumption of three common prey taxa.

Prey taxon	Per-biomass consumption coefficient ($d^{-1} \cdot [mg/m^2]^{-1}$) $\times 1000$				Consumption coefficient (d^{-1}) $\times 1000$			
	Reference		Litter-excluded		Reference		Litter-excluded	
	July	December	July	December	July	December	July	December
<i>Tallaperla</i>	0.03	0.08	0.21	0.24	17	41	35	18
Chironomidae	0.10	0.10	0.19	0.78	67	53	33	59
<i>Parapsyche</i>	0.06	0.04	0.44	0.06	39	19	75	5

unit area. Per biomass consumption coefficients (c) can be determined by dividing cP by predator biomass, giving dimensions of $time^{-1} \cdot (predator\ biomass/area)^{-1}$ (Wootton 1997).

Per biomass consumption coefficients were calculated for three common prey taxa for the sum of all predators that consumed them (Table 5). Per biomass consumption coefficients for each taxon were higher in the litter-excluded stream than in the reference stream (Table 5). These per biomass consumption coefficients are the flow from the prey to the predator divided by the product of predator biomass times prey biomass (F_{ij}/PN). Did the relative predation rate change or the biomass of the predator change? Prey consumption rates divided by prey biomass were not different between the two streams (Table 5), but rather the predator biomass was lower (see the Appendix). This means that, per unit predator biomass, predators in the litter-excluded stream were consuming more chironomids, *Tallaperla*, and *Parapsyche*.

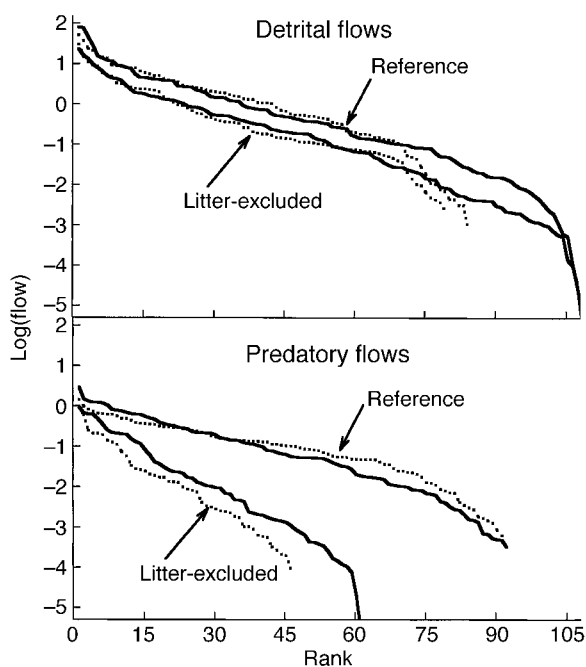


FIG. 5. Flow magnitude ($mg\ AFDM \cdot m^{-2} \cdot d^{-1}$) vs. rank for the detrital (top panel) and predatory (bottom panel) flows. $\log_{10}(\text{flow magnitude})$ appears along the y-axis. The solid line is for July, and the dotted line is for December.

Trophic structure

The production-weighted trophic level for invertebrates and salamanders in each of the stream food webs was slightly less than three (Table 6). The December food web in the litter-excluded stream appeared to have a lower production-weighted trophic level than the other three food webs, because the relative production of predators was lower at that time (Table 2). The average trophic level of detritivores was also lower in December, compared to July, in the litter-excluded stream (paired t test, $P = 0.016$), because assimilation of bacteria was lower during December than July (Tables 4 and 6). When the two sampling dates from each stream were combined, there was no between-stream difference in production-weighted trophic level of the invertebrate taxa in the two streams (paired t test, $P = 0.62$) (Table 6).

On excess of 92% of the extended diet of predators was derived from detritus (Table 7), because most organic matter inputs to the stream were allochthonous detritus. The significance of different sources of detritus to predators was not examined because we did not estimate which fraction of bacterial and fungal production was derived from leaves, wood, dissolved organic matter, or amorphous detritus; we assume that nearly 100% of microbial production was derived from allochthonous detrital inputs. Predators derived more of their carbon from diatoms in the litter-excluded stream than the reference stream, although this fraction was small.

Considerable biomass of predators was derived from bacteria, because most detritivorous prey consumed bacteria directly. Predator dependence on bacteria ranged within 8–73%. Predators derived less organic matter from bacteria in the litter-excluded stream during December, compared to July or to the reference stream. The calculated fraction of predator production derived from bacteria was compared with ^{13}C enrichment of the same predators from the same streams (Hall and Meyer 1998). Predator ^{13}C enrichment was calculated the same way as for detritivores, i.e., using a mixing model of predator enrichment relative to bacteria and unlabeled detrital carbon (Hall and Meyer 1998). There is significant correlation ($r = 0.65$, $P < 0.02$) between fraction of predator organic matter derived from bacteria based on gut contents analysis and with relative ^{13}C enrichment (Fig. 6). This shows that

TABLE 6. Effective trophic level of each taxon for both the treatment and reference stream during July and December.

Functional group	Order	Taxon	Reference		Litter-excluded	
			July	December	July	December
Shredders	Plecoptera	<i>Leuctra</i> spp.	2.80	2.47	2.41	...
	Plecoptera	<i>Tallaperla maria</i>	2.16	2.35	2.58	2.25
	Trichoptera	<i>Fattigia pele</i>	2.21	2.12	2.34	2.03
	Trichoptera	<i>Lepidostoma</i> spp.	2.12	2.25	2.34	...
	Trichoptera	<i>Pycnopsyche</i> spp.	...	2.51
	Diptera	<i>Molophilus</i> spp.	...	2.92
	Diptera	<i>Tipula</i> spp.	2.68	2.10	2.33	2.02
Scrapers	Ephemeroptera	<i>Epeorus</i> spp.	2.63
	Ephemeroptera	<i>Stenonema</i> spp.	2.46	2.45	2.80	2.76
	Coleoptera	<i>Ectopria thoracica</i>	2.54	...	2.50	2.04
Gatherers	Ephemeroptera	<i>Paraleptophlebia</i> spp.	...	2.91	2.86	2.94
	Ephemeroptera	<i>Serratella</i> sp.	2.72
	Plecoptera	<i>Amphinemura wui</i>	2.14	2.69	2.71	2.65
	Trichoptera	<i>Lype diversa</i>	2.79	2.17	2.33	2.20
	Diptera	Chironomidae	2.40	2.77	2.84	2.67
	Diptera	<i>Sciara</i> spp.	2.40	2.99	2.43	...
		Harpacticoida	2.60	3.00
Filterers	Trichoptera	<i>Diplectrona modesta</i>	2.87	2.58	3.08	2.29
	Trichoptera	<i>Dolophilodes</i> sp.	2.47
	Trichoptera	<i>Parapsyche cardis</i>	3.48	2.90	3.02	2.99
	Trichoptera	<i>Wormaldia moesta</i>	2.45	2.95	2.98	2.90
		Odonata	<i>Cordulegaster</i> sp.	3.88	3.82	3.86
Predators	Odonata	<i>Lanthus vernalis</i>	3.74	4.12	4.01	3.34
	Plecoptera	<i>Beloneuria</i> sp.	3.76	3.88	3.60	3.61
	Plecoptera	<i>Isoperla</i> spp.	3.41	3.80	3.83	3.71
	Trichoptera	<i>Rhyacophila</i> spp.	...	3.58	...	3.25
	Diptera	<i>Hexatoma</i> spp.	3.83	3.89	...	3.51
	Diptera	<i>Pedicia</i> spp.	...	3.69
	Diptera	Tanypodinae	3.62	3.93	3.75	...
		Salamander larvae	3.90	3.62	4.21	3.74
		Production-weighted average	2.87	2.92	2.97	2.45

Note: Ellipses (...) indicate taxa for which no data were obtained.

diet determinations for predators do relate to larger patterns of organic matter flow in stream food webs as determined using a ¹³C isotope addition.

DISCUSSION

Food web resolution

It is easier to construct a food web that quantifies most of the organic matter flow than it is to quantify most of the links. We quantified most of the organic matter flow in this food web, but we could not deter-

mine the majority of links. Unlike other food web studies (Martinez 1991, Polis 1991), literature data were not used to indicate links, because our main interest was in quantifying flow between links and not simply determining presence/absence. Using literature data may overestimate the number of links in a food web (Hall and Raffaelli 1997). The question remains: what proportion of links or flow in a food web must be quantified to determine a representative food web? Because we were able to assess diets of invertebrates that comprised 84–91% of total production, we believe our model of the food web is reasonably complete. This degree of resolution is enough to estimate the trophic base of the food web and important detrital and flows to predators. It is impossible to identify most of the links in these food webs, because there were many taxa that were rarely found. It is also difficult to assign some insects to species in the larval stages, so that generic levels were employed (subfamily for chironomids). One of the assumptions in analysis of binary food webs is that all of the links have been determined, because aggregating species can distort observed web patterns (Martinez 1991) unless the aggregated species share the same set of predators and prey (Martinez et al. 1999). It is impossible to define an evenly and highly resolved taxonomically based food web for this stream

TABLE 7. Extended diet of all predators as a percentage of total assimilation in the reference and litter-excluded stream during July and December.

Food source	Reference stream		Litter-excluded stream	
	July	December	July	December
Detritus	98	100	97	92
Bacterial carbon	41	59	67	32
Fungal hyphae	3.7	2.9	4.9	8.9
Diatoms	1.9	0.2	2.3	8.1

Note: We pooled all detritus types (leaf, wood, amorphous detritus, DOM) for this analysis, because we could not apportion fungal and bacterial production among the different detrital sources. The columns sum to >1 because microbes consume detritus; hence, both are in the extended diet.

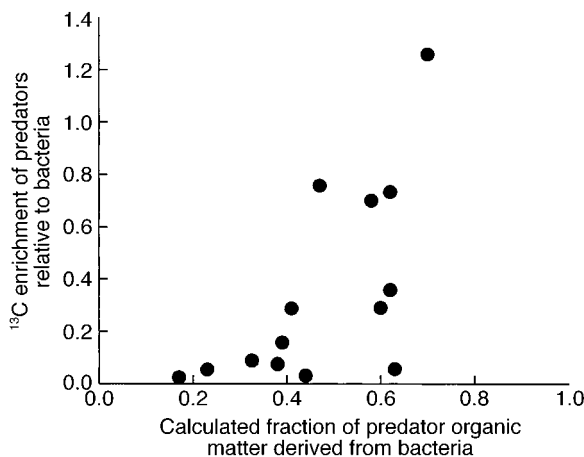


FIG. 6. Relationship between fraction of predator production derived from bacteria estimated from gut contents analysis of detritivore prey vs. that estimated from relative ^{13}C enrichment from a ^{13}C addition experiment, which was designed to determine the fraction of invertebrate carbon derived from bacteria (Hall and Meyer 1998). The correlation is significant ($r = 0.65$, $P < 0.02$).

because of our inability to assess many of the trophic interactions. For example, complete diets for certain predators cannot be determined, and relative consumption of individual hyphomycete fungal species by invertebrates is also unknown.

An omission from our food web is meiofauna (invertebrates $< 0.5\text{mm}$). Although we determined diets of harpacticoid copepods which were $\sim 0.5\text{mm}$ long, many other small taxa were not included in this analysis, such as bdelloid rotifers, nematodes, testate protozoans, tardigrades, and nauid and enchytraeid oligochaetes (Vila 1996). Some of these organisms (nematodes, testate protozoans, and oligochaetes) were found in predator guts; however, none was energetically significant to macroinvertebrate predators, because few were found.

We did not include diet information for the large, adult salamanders living in the stream (mostly *Desmognathus* spp.). Adults tend to feed upon terrestrial or aerial adults of aquatic insects (Krzysik 1979; R. Hall, *personal observation*), whereas larvae eat aquatic insects and were included in our food webs. The biggest predator in the streams, *Desmognathus quadramaculatus*, can consume salamanders (R. Hall, *personal observation*); it was not analyzed here because it was too rare.

Trophic base of the food web

The food webs were almost completely based upon allochthonous inputs, with little primary production. Streams at Coweeta are light limited, even during winter, because of the evergreen rhododendron understory and deeply incised valleys. Primary production is only 0.3% of litter input (Webster et al. 1983), similar to the percentage of macroinvertebrate secondary pro-

duction derived from diatoms that we found in the reference stream ($< 1\%$). Some invertebrate production may be based on algal exudates; however, these would have to be many times more prevalent for diatoms to be energetically significant to consumers in these food webs. Other studies of heterotrophic forest streams have found primary production to be more important. In Bear Brook, New Hampshire, diatoms supported 75% of the production of *Neophylax*, an abundant scraping caddisfly (Mayer and Likens 1987). Walker Branch, Tennessee, is a wooded stream that supports up to 1000 grazing snails/ m^2 , and can have primary production rates of $40\text{g C}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Rosemond 1994). Unlike Coweeta streams, neither Bear Brook nor Walker Branch has an evergreen rhododendron understory. Although primary production can be important in some forest streams, it does not play a large role in the food web in the reference stream. Only a few taxa in the reference stream derived a large fraction of their production from diatoms. We found 40% of the production of a relatively rare beetle larva, *Ectopria* supported by diatom production. *Tallaperla*, a common stonefly, derived 18% of its production from diatoms.

The fraction of invertebrate production derived from diatoms was higher in the litter-excluded stream during December than in the other three food webs. We hypothesize that, with the deciduous overstory gone and no leaves falling onto the streambed during this first year of the study, more light was available for algae. During December, we observed small patches of cyanobacteria in the litter-excluded stream, normally rare in forest streams at Coweeta (R. Hall, *personal observation*).

Bacterial carbon accounts for much of the secondary production in this food web, which is not surprising in a food web dominated by allochthonous inputs. Most published food webs do not deal quantitatively with bacteria, and they often refer to the combination of bacteria and their organic substrate as detritus. This omission ignores bacteria, the dominant consumer of carbon in many ecosystems. An exception is a detailed food web of Chesapeake Bay that considered the roles of pelagic and benthic bacteria using results from the literature (Baird and Ulanowicz 1989). In the Chesapeake food web, bacteria were a sink for carbon because of high respiration.

Bacteria may be a carbon sink in Coweeta streams, even though bacterial production is important to the food web. Respiration in the treatment stream, measured prior to installation of the litter-exclusion canopy, was $214\text{g AFDM}\cdot\text{m}^{-2}\cdot\text{y}^{-1}$ (Wallace et al. 1997a), $20\times$ higher than invertebrate production. Microbes therefore must assimilate more organic matter than other organisms in order to maintain this high respiration rate. Much of the trophic role of bacteria may be based upon bacterial extracellular compounds (Hall and Meyer 1998); this may explain why we find high use of bacterial carbon by invertebrates, compared to other

studies in which extracellular compounds were not considered (e.g., Findlay et al. 1986). The trophic role for bacteria is unusual: they provide carbon that can be consumed by higher trophic levels (Couch 1992, Couch et al. 1996), yet that carbon is largely abiotic/extracellular material. Additionally, animals may assimilate organic matter that has adsorbed to these extracellular compounds.

There was little seasonal difference in the detrital/microbial base of the food web in the reference stream. Although large amounts of leaves entered the stream during autumn, invertebrates ingested similar quantities in winter and summer. More leaf material may have remained in the reference stream in July 1994 because of decreased export by storms (Wallace et al. 1995), thus making it available to invertebrates. Food webs in an intermittent Australian stream exhibited large seasonal changes driven by seasonal drying (Closs and Lake 1994). In contrast, Coweeta streams have relatively constant baseflow discharge throughout the year, so there are no large seasonal hydrologic fluctuations, such as stream drying, to influence invertebrate populations. However, size of individual organic matter flows varied greatly between seasons (Figs. 4 and 5) as abundance, biomass, production, and diets shifted. These changes were driven by varied life cycles of insects, such that different taxa were dominant at different times. For instance, *Lepidostoma* production was high in July (Fig. 4; also see the Appendix), because late-instar individuals with high production were present. *Lepidostoma* were abundant during December, but as early instars, with low biomass and production and low rates of leaf consumption. *Tipula* leaf consumption was high in December, and it dominated leaf consumption at that time. Some changes in population sizes may also be driven by predation, such as *Parapsyche* cannibalism during July sampling. This hydropsychid caddisfly is a space-holding filter-feeder, which exhibits strong defensive behavior when another individual enters its retreat (Jansson and Vuoristo 1979). Total organic matter flow in the entire assemblage was similar between seasons, but individual flows were different because of changing taxonomic composition, developmental stage, diet, and production.

The trophic base of the food web in the litter-excluded stream was based as much upon wood as leaves. Wood was the dominant form of organic matter remaining in the litter-excluded stream. We suggest that wood was trophically important in the litter-excluded stream for two reasons: first, without leaves, a number of invertebrates switched diets to this lower quality food; second, wood in the litter-excluded stream had a more developed microbial biofilm, which enhanced its quality with higher microbial biomass per unit surface area, compared with wood from the reference stream (Tank and Webster 1998). Fungal biomass and respiration on woody substrates were much higher in the litter-excluded stream (Tank and Webster 1998). This

more active microbial assemblage may have allowed invertebrates to use this relatively refractory carbon resource. Leaf tissue contributed much less to invertebrate production in the litter-excluded stream. Leaf tissue was found in invertebrate guts, although leaves contributed little to benthic organic matter standing crop. Leaf particles ingested by invertebrates may have been smaller than the 1-mm cutoff for coarse benthic organic matter (CBOM). The fraction of leaf tissue in guts should decline in future seasons as these remaining small leaf particles are degraded.

The proportion of production derived from animal predation was high in these food webs, as previously noted by Lugthart and Wallace (1992) and Wallace et al. (1997b, 1999). They suggested that high invertebrate predation might be due to low vertebrate predation rates because fishes were absent. In a coastal plain stream, predatory invertebrates consumed 94% of detritivore production (Smith and Smock 1992). In our study, 42–88% of all invertebrate secondary production was consumed, including other predators. Fully 16–27% of predator consumption was intraguild predation, resulting in interesting dynamics, because potential competitors eat each other (Polis and Holt 1992). This intraguild predation may eliminate the possibility of a four-link invertebrate food chain with discrete trophic levels as observed by Power (1990) (detritus and microbes, detritivore, predator, predator) in our stream, because an animal at trophic level 4 (e.g., *Lanthus*, Table 6) can consume predators as well as detritivores. Additionally, intraguild predation may have unpredictable beneficial impacts on shared prey taxa, if the dominant predator is being consumed by another predator within the same guild (Polis and Holt 1992). Even though the fraction of predator consumption of other predators was similar in the reference and litter-excluded streams, some of the largest flows in the litter-excluded stream were predator–predator, suggesting that those interactions were important.

Omnivory was common in this food web, because most detritivores assimilated both detritus and accompanying microbes that also consumed detritus. Predators consumed both other predators and detritivores and thus were omnivores. Few taxa consumed both animal prey and detritus (e.g., *Parapsyche*), in contrast with Tavares-Cromar and Williams (1996), who found detritus in guts of most predatory taxa. Most predator production was from stoneflies and dragonflies, which contained only animal prey in their guts. *Parapsyche* was an important exception; it is an omnivore that can have high biomass and production. A small increase in the fraction of animal prey in its diet may increase its impact on prey taxa. These hydropsychids can select animal prey over detritus in their nets (Georgian and Thorp 1992), even though most ingestion was actually detritus.

Patterns of flows

A few pathways in this food web accounted for most organic matter flow; this pattern is apparent by examining the rank/flow curves (Figs. 2 and 5). A geometric decrease in ranked flows (Fig. 2) is a pattern that has been previously noted (Ulanowicz and Wolff 1991, Kenny and Loehle 1991). Kenny and Loehle (1991) found a decrease in flow magnitude with each successive rank increment that was ranged 11–24%. We found that the percentage decrease for flow magnitudes ≥ 0.01 mg AFDM·m⁻²·d⁻¹ in the reference stream was 4% for each of the combined flows, and 6–8% for detrital and flows to predators alone, suggesting that a more inclusive data set will be closer to zero percent decrease. The initial steep decline in flow magnitudes for the first few taxa shows that only a few taxa are responsible for most of the organic matter flow in these streams. The distribution of flows in the reference stream was similar in the two seasons, despite large differences in taxa present, and the taxa responsible for these flows were different between seasons in each stream.

Although certain taxa disappeared (e.g., harpacticoid copepods, *Pycnopsyche* [see Wallace et al. 1997b]) and total flows decreased, size distribution of detrital flows was not different between the litter-excluded and reference stream. The ranked distribution was displaced downward because flows were lower in the litter-excluded stream; however, the distribution was not more skewed, as it was with predatory taxa. Flows from wood became large relative to other flows; however, there were still some large flows from leaf detritus, probably because all leaf particles had not broken down during the first and second year of the experiment.

Per-biomass consumption coefficients among all predators and three common prey taxa were higher in the litter-excluded stream relative to the reference stream. This result is attributed to lower predator biomass, rather than higher specific consumption rates (d⁻¹). We suggest that fewer predators were having the same total impact on remaining common prey taxa, because the common prey taxa represent a larger fraction of the predators' diets in the litter-excluded stream. As common prey taxa (e.g., harpacticoid copepods, *Leuctra*, and *Lepidostoma*) disappeared, predators were consuming (per unit biomass) more of the remaining taxa. This result may explain why the size distribution of flows to predators was steeper in the litter-excluded stream, relative to the reference stream. With fewer prey taxa available, the dominant flows were from the remaining common prey taxa to predators.

An interesting implication of higher per biomass consumption coefficients in the litter-excluded stream is that interaction strength between predators and prey may also be higher. Energy flow or diet composition by themselves do not correlate with experimentally determined interaction strength (Paine 1980, Hall et al.

1990, Polis 1994, Raffaelli and Hall 1996). Indeed small flows can be important to the dynamics of a particular species (Paine 1980). However, when ingestion rates are divided by prey biomass, they can relate to actual interaction strength. Wootton (1997) showed that per capita consumption coefficients correlated with experimentally measured species impact; this is the degree to which populations differed in experimental treatments with and without predators. We have no experimental evidence to support this relationship in our streams. However, if this relationship were true, then it suggests that per biomass interactions were stronger in the food web of the litter-excluded stream. Our finding is opposite of Ruesink (1998) who found higher per capita interaction strengths between hermit crabs and their diatom resource when the diatom resource was high, probably because diatoms at low densities can compensate for grazing with high production and because crabs do not respond numerically to differences in diatom density. Because predator production in our streams was coupled to prey production (Wallace et al. 1997b), per biomass effects can be high with decreasing predator biomass. Overall specific consumption rates were similar, suggesting that the degree to which prey were limited by predators was not different in the two streams. Because predation in the reference stream was more diffuse, interaction strengths are probably not strong. Even if there were strong interactions (perhaps *Beloneuria* in December in the reference stream), these would likely change seasonally, due to large changes in invertebrate abundance.

The method used to calculate average trophic level of the entire food webs is analogous to the mean chain length given by Pimm (1982). The method used here (Levine 1980, Ulanowicz 1986) is advantageous, because it weights each trophic transfer according to its production, so that an energetically small seven-link food chain is weighted less than an energetically dominant three-link food chain. We also were able to consider the average trophic level of each taxon, even if these animals were omnivores. Given that food chain length is considered an important attribute of food web structure (Hairston and Hairston 1993, Persson et al. 1996, Sterner et al. 1997), this method provides a robust means to determine average chain length in an ecosystem. Some authors suggest that trophic levels are not useful constructs because many taxa are omnivorous (Cousins 1987). While true, the method used here allows us to partition a taxon's feeding into more than one trophic level as suggested by Wiegert and Owen (1971). Furthermore, the method allows calculation of average chain length in the absence of discrete trophic levels and provides a trophic continuum with consumers variously placed along it. A potential problem with this analysis, identified by Cousins (1987), is that we assign all detritus to trophic level 1. This means that dead animals from a higher trophic level are im-

mediately relegated to level 1. They should, in fact, remain at their higher trophic level. However, most (>99%) organic matter in this stream is dead plant material, so the correction for dead animals would be small, assuming feeding is not selective for animal detritus. Another consideration is that, while we were able to include bacteria in these calculations, we could not include other members of the microbial loop (e.g., flagellates, small ciliates, etc.); hence, mean trophic level could be higher for detritivores if they consume a large amount of bacterivorous protozoa.

The production-weighted trophic level of the food webs was lower in the litter-excluded stream, relative to the reference stream, only during December. Considering this measure of average trophic level as the relative placement of consumers along a trophic continuum, we see that litter exclusion caused a large decrease in the amount of energy at the bottom of the food web, but there was no decrease in average trophic level in July, and only a small change in December. While the amount of biomass and production was clearly lower in the litter-excluded stream, the distribution of production along the trophic continuum was little affected. Several different hypotheses have been presented examining potential determinants of food chain length (Oksanen et al. 1981, Pimm 1988, Hairston and Hairston 1993). Energy flow may determine food chain length, because thermodynamic energy losses at each trophic transfer make available energy for a top trophic level vanishingly small (Oksanen et al. 1981). Alternatively, exogenous disturbance can keep food chains short, since top predators have less stable populations than basal species (Pimm 1988), although this idea is disputed on theoretical grounds (Sternner et al. 1997). Hairston and Hairston (1993) suggested that trophic structure is not controlled by the amount of energy at the base of the food web, but rather by the attributes of species within trophic levels.

The decrease in mean trophic level in December corresponded to lower use of bacterial carbon and lower predator production. The average trophic level should positively relate to the fraction of food web production derived from animal predation and bacterial consumption. If the fraction of predator production were low relative to total production, then we would expect shorter food chains. Only during December were animal predation and bacterial consumption lower in the litter-excluded stream, relative to the other three measurements. The lower fraction of predator production observed here, using short-term measurements, does not hold up when compared with long-term annual production estimates. Long-term data collected before and during the litter exclusion show that predator production in these streams was linearly related to nonpredator production (Wallace et al. 1997b, 1999). Predator production was a constant fraction of prey production, and the average trophic level may not be different with lower inputs of basal resources. These long-term pred-

ator production data suggest that the low ratio of predator production in December in the litter-excluded stream may be caused by the short time period through which we measured production. We do not know if lower assimilation of bacterial carbon in the litter-excluded stream continued beyond the second year of the experiment, because these are the only measurements. Because of the variable nature of the isotope labeling (Hall and Meyer 1998), we hesitate to suggest that this trend is robust.

The extended diet of predators (cf. Baird and Ulanowicz 1989) was derived from microbes and detritus, similar to their detritivore prey. However, variation in the fraction of predator production derived from bacteria, using the food web based on gut contents analysis, positively correlated with results derived from stable isotope analyses. This correlation represents the first independent test of the algebraic method of calculating the extended diet of a predator (Ulanowicz 1986), and shows how a tracer can follow patterns of element flow more than one trophic transfer beyond its initial uptake by bacteria and consumption by detritivores. This analysis underscores the importance of bacteria to higher trophic levels in these stream food webs.

Conclusions

Detailed food webs based on organic matter flow can be used to accurately describe ecosystems by considering both the population dynamics of invertebrates (Benke 1993) and their trophic interactions, then integrating these with organic matter flow. Our food webs provide more information than binary food webs (Winemiller 1990, Martinez 1991). Furthermore, by assessing organic matter flow for each link, these food webs are more resolved than those concentrating on energy flow (e.g., Teal 1962; but see Baird and Ulanowicz [1989]) and they allow us to address the inherent complexity in food webs as suggested by Polis and Strong (1996). Our approach, based on organic matter flow, showed several effects of detritus reduction to this stream ecosystem that could not have been found by only examining overall energy flow (e.g., decomposition, secondary production) or just the presence/absence of feeding links. For example, per biomass consumption coefficients were higher in the litter-excluded stream, the distribution of flows to predators was highly skewed to just a few large flows, and wood was a more important trophic resource in the litter-excluded stream.

Population ecology has often been considered separately from ecosystem ecology (see Jones and Lawton 1993). Population ecology focuses on controls on abundances of populations of organisms and their change in numbers with time, while ecosystem approaches deal with stocks and fluxes of elements. (e.g., Teal 1957, Baird and Ulanowicz 1989). More simplistically, each discipline uses different units: numbers of organisms compared with biomass. By estimating production and

energy flow for individual taxa as described by Benke and Wallace (1980, 1997), we can consider the trophic role of individual taxa, such as *Tipula* in leaf litter processing and *Beloneuria* in total predation. Indeed, leaf consumption and predation were similar between seasons, yet the individual flows changed greatly. Ecosystem functions such as leaf litter processing can be similar even if the taxa involved are different. Combining these two approaches provides a more detailed understanding of material flow through ecosystems, and its relationship with population dynamics and interactions.

ACKNOWLEDGMENTS

Chris Peredney, Brian Keeley, and Kate Dowell helped immensely with much of the field and laboratory work for this study. Thelma Richardson provided a computer and program to digitize gut contents. Judy Meyer, Cathy Pringle, Karen Porter, Dave Coleman, Amy Rosemond, John Hutchens, Dave Strayer, Cliff Dahm, and two anonymous reviewers read and provided improvements to earlier versions of the manuscript. Financial support was provided by NSF Dissertation Improvement Grant DEB 93-21566 to R. O. Hall and J. L. Meyer; NSF grant DEB-9207498 to J. B. Wallace, J. L. Meyer, and J. R. Webster; and Coweeta LTER site support (BSR 91-11661). A portion of J. B. Wallace's time was supported by CSRS project GEO 00784. Additional support for R. O. Hall while writing this paper was provided by the Andrew W. Mellon Foundation to G. E. Likens.

LITERATURE CITED

- Baird, D., and R. E. Ulanowicz. 1989. The seasonal dynamics of the Chesapeake Bay ecosystem. *Ecological Monographs* **59**:329-364.
- Bengtsson, J., and N. Martinez. 1996. Causes and effects in food webs: do generalities exist? Pages 179-184 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York, New York, USA.
- Benke, A. C. 1984. Secondary production of aquatic insects. Pages 289-322 in V. H. Resh and D. M. Rosenberg, editors. *Ecology of aquatic insects*. Praeger, New York, New York, USA.
- Benke, A. C. 1993. Concepts and patterns of invertebrate production in running waters. *Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen* **25**:15-38.
- Benke, A. C., A. D. Huryn, L. A. Smock, and J. B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* **18**:308-343.
- Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology* **61**:108-118.
- Benke, A. C., and J. B. Wallace. 1997. Trophic basis of production among riverine caddisflies: implications for food web analysis. *Ecology* **78**:1132-1145.
- Borchardt, M. A., and T. L. Bott. 1995. Meiofaunal grazing of bacteria and algae in a Piedmont stream. *Journal of the North American Benthological Society* **14**:278-298.
- Briand, F., and J. E. Cohen. 1987. Environmental correlates of food chain length. *Science* **238**:956-960.
- Carlough, L. A. 1994. Origins, structure, and trophic significance of amorphous seston in a blackwater river. *Freshwater Biology* **31**:227-237.
- Carpenter, S. R., J. F. Kitchell, and J. R. Hodgson. 1985. Cascading trophic interactions and lake productivity. *BioScience* **35**:634-649.
- Closs, G. P. and P. S. Lake. 1994. Spatial and temporal variation in the structure of an intermittent-stream food web. *Ecological Monographs* **64**:1-21.
- Cohen, J. E. 1978. *Food webs and niche space*. Princeton University Press, Princeton, New Jersey, USA.
- Cohen, J. E., and C. M. Newman. 1985. A stochastic theory of community food webs I. Models and aggregated data. *Proceedings of the Royal Society of London Series B* **224**:421-448.
- Couch, C. A., and J. L. Meyer. 1992. Development and composition of the epixylic biofilm in a blackwater river. *Freshwater Biology* **27**:43-51.
- Couch, C. A., J. L. Meyer, and R. O. Hall. 1996. Incorporation of bacterial extracellular polysaccharide by black fly larvae (Simuliidae). *Journal of the North American Benthological Society* **15**:289-299.
- Cousins, S. 1987. The decline of the trophic level concept. *Trends in Ecology and Evolution* **2**:312-316.
- Cuffney, T. F., J. B. Wallace, and G. J. Lugthart. 1990. Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. *Freshwater Biology* **23**:281-299.
- Cummins, K. W. 1973. Trophic relations of aquatic insects. *Annual Review of Entomology* **18**:183-206.
- deRuiter, P. C., A.-M. Neutel, and J. C. Moore. 1995. Energetics, patterns of interaction strengths and stability in real ecosystems. *Science* **269**:1257-1260.
- Elton, C. 1927. *Animal ecology*. Sidgwick and Jackson, London, UK.
- Findlay, S., J. L. Meyer, and P. J. Smith. 1986. Incorporation of microbial biomass by *Peltoptera* sp. (Plecoptera) and *Tipula* sp. (Diptera). *Journal of the North American Benthological Society* **5**:306-310.
- Georgian, T., and J. H. Thorp. 1992. Effects of microhabitat selection on feeding rates of net-spinning caddisfly larvae. *Ecology* **73**:229-240.
- Hairston, N. G., Jr., and N. G. Hairston Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *American Naturalist* **142**:379-411.
- Hairston, N. G., F. E. Smith, and L. B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist* **94**:421-425.
- Hall, R. O., and J. L. Meyer. 1998. The trophic significance of bacteria in a detritus-based stream food web. *Ecology* **79**:1995-2012.
- Hall, S. J., and D. G. Raffaelli. 1997. Food web patterns: what do we really know? Pages 395-417 in A. C. Gange and V. K. Brown, editors. *Multitrophic interactions in terrestrial systems*. Blackwell, Oxford, UK.
- Hall, S. J., D. Raffaelli, and W. R. Turlee. 1990. Predator-caging experiments in marine systems: a reexamination of their value. *American Naturalist* **136**:657-672.
- Huryn, A. D. 1990. Growth and voltinism of lotic midge larvae: patterns across an Appalachian Mountain basin. *Limnology and Oceanography* **35**:339-351.
- Huryn, A. D., and J. B. Wallace. 1986. A method for obtaining in situ growth rates of larval Chironomidae (Diptera) and its application to studies of secondary production. *Limnology and Oceanography* **31**:216-222.
- Jansson, A., and T. Vuoristo. 1979. Significance of stridulation in larval Hydropsychidae (Trichoptera). *Behaviour* **71**:167-186.
- Jenkins, B., R. L. Kitching, and S. L. Pimm. 1992. Productivity, disturbance and food web structure at a local spatial scale in experimental container habitats. *Oikos* **65**:249-255.
- Jones, C. G., and J. H. Lawton, editors. 1993. *Linking species*

- and ecosystems. Chapman & Hall, New York, New York, USA.
- Kenny, D., and C. Loehle. 1991. Are food webs randomly connected? *Ecology* **72**:1794–1799.
- Krzysik, A. J. 1979. Resource allocation, coexistence, and the niche structure of a streambank salamander community. *Ecological Monographs* **49**:173–194.
- Levine, S. 1980. Several measures of trophic structure applicable to complex food webs. *Journal of Theoretical Biology* **83**:195–207.
- Lindeman, R. L. 1942. The trophic-dynamic aspect of ecology. *Ecology* **23**:399–418.
- Lugthart, G. J., and J. B. Wallace. 1992. Effects of disturbance on benthic functional structure and production in mountain streams. *Journal of the North American Benthological Society* **11**:138–164.
- Martin, I. D., and R. J. Mackay. 1982. Interpreting the diet of *Rhyacophila* larvae from gut analyses: an evaluation of techniques. *Canadian Journal of Zoology* **60**:783–789.
- Martinez, N. D. 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. *Ecological Monographs* **61**:367–392.
- Martinez, N. D., B. A. Hawkins, H. A. Dawah, and B. P. Feifarek. 1999. Effects of sampling effort on characterization of food web structure. *Ecology* **80**:1044–1055.
- Mayer, M. S., and G. E. Likens. 1987. The importance of algae in a shaded headwater stream as food for an abundant caddisfly. *Journal of the North American Benthological Society* **6**:262–269.
- Menge, B. A., E. L. Berlow, C. A. Blanchette, S. A. Navarrete, and S. B. Yamuda. 1994. The keystone species concept: variation in interaction strength in a rocky intertidal habitat. *Ecological Monographs* **64**:249–286.
- Meyer, J. L. 1994. The microbial loop in flowing waters. *Microbial Ecology* **28**:195–199.
- Moore, J. C., P. C. deRuiter, H. W. Hunt, D. C. Coleman, and D. W. Freckman. 1996. Microcosms and soil ecology: critical linkages between field studies and modeling food webs. *Ecology* **77**:694–705.
- Newell, S. Y., and R. E. Hicks. 1982. Direct-count estimates of fungal and bacterial biovolume in dead leaves of smooth cordgrass (*Spartina alterniflora* Loisel.) *Estuaries* **5**:246–260.
- O'Doherty, E. C. 1988. The ecology of meiofauna in an Appalachian headwater stream. Dissertation, University of Georgia, Athens, Georgia, USA.
- Odum, H. T., and E. P. Odum. 1955. Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. *Ecological Monographs* **25**:291–320.
- Oksanen, L., S. D. Fretwell, J. Arruda, and P. Niemela. 1981. Exploitation ecosystems in gradients of primary production. *American Naturalist* **118**:240–261.
- Pace, M. L., G. B. McManus, and S. E. G. Findlay. 1990. Planktonic community structure determines the fate of bacterial production in a temperate lake. *Limnology and Oceanography* **35**:795–808.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* **100**:65–75.
- Paine, R. T. 1980. Food webs: linkage, interaction strength, and community infrastructure. *Journal of Animal Ecology* **49**:667–685.
- Paine, R. T. 1988. Food webs: road maps of interactions or grist for theoretical development? *Ecology* **69**:1648–1654.
- Paine, R. T. 1992. Food-web analysis through field measurement of per capita interaction strength. *Nature* **355**:73–75.
- Persson, L., J. Bengtsson, B. A. Menge, and M. E. Power. 1996. Productivity and consumer regulation—concepts, patterns, and mechanisms. Pages 396–434 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York, New York, USA.
- Peterson, B. J., and B. Fry. 1987. Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* **18**:293–320.
- Pimm, S. L. 1982. *Food webs*. Chapman & Hall, London, UK.
- Pimm, S. L. 1988. Energy flow and trophic structure. Pages 263–278 in J. J. Alberts and L. R. Pomeroy, editors. *Concepts in ecosystem ecology*. Springer-Verlag, New York, New York, USA.
- Polis, G. A. 1991. Complex trophic interactions in deserts: an empirical critique of food web theory. *American Naturalist* **138**:123–155.
- Polis, G. A. 1994. Food webs, trophic cascades and community structure. *Australian Journal of Ecology* **19**:121–136.
- Polis, G. A., and R. D. Holt. 1992. Intraguild predation: the dynamics of complex trophic interactions. *Trends in Ecology and Evolution* **7**:151–154.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* **147**:813–846.
- Porter, K. G. 1996. Integrating the microbial loop and the classic food chain into a realistic planktonic food web. Pages 51–59 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York, New York, USA.
- Power, M. E. 1990. Effects of fish on river food webs. *Science* **250**:411–415.
- Raffaelli, D. G., and S. J. Hall. 1996. Assessing the relative importance of trophic links in food webs. Pages 185–191 in G. A. Polis and K. O. Winemiller, editors. *Food webs: integration of patterns and dynamics*. Chapman & Hall, New York, New York, USA.
- Rosemond, A. D. 1994. Multiple factors limit seasonal variation in periphyton in a forest stream. *Journal of the North American Benthological Society* **13**:333–344.
- Rosemond, A. D., P. J. Mulholland, and J. W. Elwood. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* **74**:1264–1280.
- Ruesink, J. L. 1998. Variation in per capita interaction strength: thresholds due to nonlinear dynamics and non-equilibrium conditions. *Proceedings of the National Academy of Sciences* **95**:6843–6847.
- Sherr, E. B., and B. F. Sherr. 1994. Bacterivory and herbivory: key roles of phagotrophic protists in pelagic food webs. *Microbial Ecology* **28**:223–235.
- Slansky F., and J. M. Scriber. 1982. Selected bibliography and summary of quantitative food utilization by immature insects. *Bulletin of the Entomological Society of America* **28**:43–55.
- Smith, L. C., and L. A. Smock. 1982. Ecology of invertebrate predators in a coastal plain stream. *Freshwater Biology* **28**:319–329.
- Sturner, R. W., A. Bajpai, and T. Adams. 1997. The enigma of food chain length: absence of theoretical evidence for dynamic constraints. *Ecology* **78**:2258–2262.
- Tank, J. L., and J. R. Webster. 1998. Interaction of substrate and nutrient availability on wood biofilm processes in streams. *Ecology* **79**:2168–2179.
- Tavares-Cromar, A. F., and D. D. Williams. 1996. The importance of temporal resolution in food web analysis: evidence from a detritus-based stream. *Ecological Monographs* **66**:91–113.
- Teal, J. M. 1957. Community metabolism in a temperate cold spring. *Ecological Monographs* **27**:283–302.
- Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology* **43**:614–624.
- Ulanowicz, R. E. 1986. Growth and development: ecosys-

- tems phenomenology. Springer-Verlag, New York, New York, USA.
- Ulanowicz, R. E. 1997. Ecology, the ascendent perspective. Columbia University Press, New York, New York, USA.
- Ulanowicz, R. E., and W. F. Wolff. 1991. Ecosystem flow networks: loaded dice? *Mathematical Biosciences* **103**:45–68.
- Vila, P. B. 1996. Size structure of the zoobenthos in headwater streams: meiofaunal–macroinvertebrate interactions. Dissertation. University of Georgia, Athens, Georgia, USA.
- Wallace, J. B., T. F. Cuffney, S. L. Eggert, and M. R. Whiles. 1997a. Stream organic matter inputs, storage, and export for Satellite Branch at Coweeta Hydrologic Laboratory, North Carolina, USA. Pages 67–74 in J. R. Webster and J. L. Meyer, editors. Stream organic matter budgets. *Journal of the North American Benthological Society* **16**:3–161.
- Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1997b. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* **277**:102–104.
- Wallace, J. B., S. L. Eggert, J. L. Meyer, and J. R. Webster. 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* **69**:409–442.
- Wallace, J. B., M. R. Whiles, S. Eggert, T. F. Cuffney, G. J. Lugthart, and K. Chung. 1995. Long-term dynamics of coarse particulate organic matter in three Appalachian Mountain streams. *Journal of the North American Benthological Society* **14**:217–232.
- Warren, P. H. 1989. Spatial and temporal variation in the structure of a freshwater food web. *Oikos* **55**:299–311.
- Waters, T. F. 1969. Sub-sampler for dividing large samples of stream invertebrate drift. *Limnology and Oceanography* **14**:813–815.
- Webster, J. R., M. E. Gurtz, J. J. Hains, J. L. Meyer, W. T. Swank, J. B. Waide, and J. B. Wallace. 1983. Stability of stream ecosystems. Pages 355–395 in J. R. Barnes and G. W. Minshall, editors. Stream ecology. Plenum Press, New York, New York, USA.
- Wiegert, R. G., and D. F. Owen. 1971. Trophic structure, available resources and population density in terrestrial vs. aquatic ecosystems. *Journal of Theoretical Biology* **30**:69–81.
- Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* **60**:331–367.
- Wootton, J. T. 1997. Estimates and tests of per capita interaction strength: diet abundance and impact of intertidally foraging birds. *Ecological Monographs* **67**:45–64.
- Wootton, J. T., and M. E. Power. 1993. Productivity, consumers, and the structure of a river food chain. *Proceedings of the National Academy of Science* **90**:1384–1387.
- Wotton, R. S. 1994. Particulate and dissolved organic matter as food. Pages 235–288 in R. S. Wotton, editor. *Biology of particles in aquatic systems*. CRC Press, Boca Raton, Florida, USA.

APPENDIX

The abundance, biomass, and production of all taxa studied during the two seasons are detailed in ESA's Electronic Data Archive: *Ecological Archives* E081-031.