The Role of Benthic Macroinvertebrates in Detritus Dynamics of Streams: A Computer Simulation

Jackson R. Webster

THE ROLE OF BENTHIC MACROINVERTEBRATES IN DETRITUS DYNAMICS OF STREAMS: A COMPUTER SIMULATION[1]

JACKSON R. WEBSTER[2]
*Environmental Sciences Division, Oak Ridge National Laboratory,
Oak Ridge, Tennessee 37830 USA*

Abstract. Detritus dynamics in Big Hurricane Branch, a second-order stream at Coweeta Hydrologic Laboratory in the southern Appalachian Mountains, were simulated with a computer model, using data from a variety of Coweeta stream studies. The model was used to evaluate the role of macroinvertebrates in the stream. Macroinvertebrates accounted for only a small portion of the respiration of detritus; their major role was conversion of benthic detritus into transported detritus. Macroinvertebrates were responsible for 27% of annual particulate organic matter (POM) transport, though when they were removed there was only a 10% reduction in POM transport because of a compensatory increase in storm transport. The contribution of macroinvertebrates to POM transport during nonstorm periods was much more significant, as high as 83% in late summer.

Based on an annual budget, macroinvertebrates decrease the efficiency of detritus processing in low-order streams, because they increase transport loss. On a longer time scale, however, macroinvertebrates prevent accumulation of large amounts of detritus in the stream and major losses during infrequent large storms. By stabilizing long-term detritus export dynamics, they provide an important link between low-order and higher-order streams.

Key words: aquatic insects; detritus; macroinvertebrates; model; simulation; stream.

INTRODUCTION

The role of macroinvertebrates in stream detritus dynamics has been difficult to define and quantify (Anderson and Sedell 1979). Evidence from leaf breakdown studies points to a very important role for these organisms. Hart and Howmiller (1975), Iverson (1975), Sedell et al. (1975), and Kirby et al. (1983) compared leaf breakdown rates in various streams and in each case suggested differences in breakdown rates were due to differences in macroinvertebrate fauna. Also, Petersen and Cummins (1974) found slower leaf breakdown rates in artificial stream channels where shredders were excluded than in channels with shredders present, and Wallace et al. (1982*b*) demonstrated significant changes in detritus dynamics when macroinvertebrates were eliminated from a small stream by application of a pesticide. Budget studies have been less clear in establishing the importance of macroinvertebrates. Cummins (1971) estimated that macroinvertebrates ingested 32% of the leaves put into a large experimental stream, and Webster and Patten (1979) calculated that macroinvertebrates annually ingested 80% of the leaf input to a small forest stream. On the other hand, Fisher and Likens (1973) estimated that macroinvertebrates in Bear Brook utilized only a small percent of leaf detritus. Other studies (e.g., Cummins

et al. 1973, Short and Maslin 1977, Grafius and Anderson 1979, Short et al. 1980) also suggested that shredders have an important influence on energy flow in detritus-dominated streams.

In order to evaluate the role of macroinvertebrates, I used a computer model to integrate data collected in a variety of stream studies at Coweeta Hydrologic Laboratory, Macon County, North Carolina, USA. An organic matter budget was calculated with this model, and the model was subsequently modified in various ways to evaluate the effects of some of the assumptions made in constructing the model and to demonstrate the effect of eliminating macroinvertebrates.

Modeling stream ecosystems

Stream ecosystem models have been used for a variety of purposes. Budget models emphasizing annual flows of energy or nutrients have been widely used as a means of summarizing stream studies (Cummins 1971, Hall 1972, Fisher and Likens 1973, Fisher 1977, Meyer and Likens 1979, Mulholland 1981), making comparisons among streams (Fisher 1977, Webster and Patten 1979), and comparing streams with other types of ecosystems (O'Neill et al. 1975, Webster et al. 1975, O'Neill 1976). Other stream models have been used to address specific questions. Hall (1972) used a model to determine the role of upstream fish migration in phosphorus dynamics of New Hope Creek. Webster et al. (1979) evaluated the effect of impoundment on seston transport with a model. The more extensive stream ecosystem models of Boling et al. (1975) and McIntire and Colby (1978) were designed to meet sev-

eral objectives including synthesis of results, evalua-
tion of data base weaknesses, and evaluation of the
strengths and weaknesses of various theories. Mc-
Intire and Colby (1978) pointed out that one of their
main objectives was to provide an integrated view of
lotic ecosystems. O'Neill et al. (1979b) described how
modeling was a central part of a stream research proj-
ect. Throughout their project they used several models
to screen hypotheses, to design experiments, to ana-
lyze results, and to provide a framework for synthesis
of results (see also O'Neill et al. 1979a, Newbold et
al. 1981, Newbold et al. 1982a, b, Elwood et al., in
press, Newbold et al. 1983).

In many ways stream ecosystems are quite similar
to other ecosystems, such as the adjacent forest floor.
Flowing water ecosystems present a challenge for
modeling, however, because of the unidirectional flow
of water. Leopold (1941) pointed out that in all terres-
trial ecosystems there is a net downhill movement of
nutrients and that living organisms must perform work
against gravity. This downhill motion is exaggerated
in streams. Cycles of nutrient and food utilization are
drawn out spatially in patterns described as spiraling
(Webster and Patten 1979). Vannote et al. (1980) point-
ed to the continuously changing character of stream
ecosystems as headwaters grade into large rivers. These
spatial aspects of streams have been ignored in for-
mulating most conceptual and computer models of
streams. Streams were treated in much the same way
as lakes or forests, i.e., as spatially homogeneous sys-
tems. The models of Boling et al. (1975) and McIntire
and Colby (1978) are point models; transport was
treated only as an input or output to a point. Hall
(1972) recognized this problem, and his model of New
Hope Creek is divided into upstream and downstream
components with upstream and downstream ex-
changes. O'Neill et al. (1979a) dealt with the spatial
problem by treating a stream as 10 linearly connected
point models. Their study showed how spatial heter-
ogeneity can affect conclusions about the dynamic be-
havior of ecosystems.

The approach used in this model of stream dynamics
over distance is based on techniques developed for
modeling transport in rivers (e.g., Streeter and Phelps
1925, O'Connor 1962, Dobbins 1964, Thomann 1972).
This approach has only recently been used in stream
ecosystem models (Webster et al. 1979, Newbold et
al. 1983), but it is the sort of approach that is es-
sential for understanding the longitudinal dynamics
of stream ecosystems.

The results presented in this paper are entirely de-
pendent on the model structure and parameter values
discussed below. I attempted to use a logical model
structure (Fig. 1), and I chose parameter values either
from an extensive data base on streams at Coweeta
Hydrologic Laboratory or from published values when
site data were missing. However, I perceive it as es-
sential to warn readers that results of this study are
site and model specific. Appropriate discretion should
be used in more extended application of these results.

DESCRIPTION OF STUDY SITE

Big Hurricane Branch drains a 58.7-ha watershed
(WS 7) at Coweeta Hydrologic Laboratory. Other than
the chestnut blight which occurred in the Coweeta area
in the early 1930s, the only disturbance to the wa-
tershed since the area came under forest service man-
agement in 1924 was a woodland grazing experiment.
Six cattle grazed the watershed from 1941 to 1952. The
watershed was not further disturbed between 1952 and
1976. At the time data were collected for this study
(1974–1976), the watershed supported a hardwood for-
est dominated by oaks and hickories. There was a dense
understory canopy of rhododendron in many areas,
especially along the stream.

There are 2445 m of stream on WS 7 with an average
bankfull channel width of 1.65 m. Mean midstream
depth averages 5.4 cm. The second-order mainstream
is 1225 m in length, beginning at an elevation of 1160
m and ending at 926 m. The mean gradient of the stream
is 0.191 m/m but varies from sections of steep exposed
bedrock to short low gradient reaches with infrequent
small pools.

Big Hurricane Branch is equipped with a V-notch
weir for measurement of streamflow, which for wa-
teryear 1975 (November 1974–October 1975) averaged
22.2 L/s, ranging from 5.5 to 304.3 L/s. Highest flows
occurred during late winter and spring, and lowest flows
were recorded in summer and fall. The peak flow dur-
ing the study period (September 1974–September 1975)
had a recurrence interval of ≈2.5 yr. Average flow for
the year was 23% above the 30-yr average, with most
of the difference due to higher flows in February,
March, and April. Stream water temperature was re-
corded continuously at a point in Big Hurricane Branch
just above the weir pond. During the study period water
temperature varied from 4.4° to 19.4°C and averaged
12.9° (L. Swift, personal communication). Further
characteristics of Big Hurricane Branch and its wa-
tershed have been described elsewhere (e.g., Swank
and Douglass 1975, Gurtz et al. 1980). In addition to
using data from Big Hurricane Branch, I used data
from another stream, Hugh White Creek, for compar-
ison with some simulations. This second-order stream
is very similar in size to Big Hurricane Branch and
drains a similar-sized (61.1-ha) watershed.

MATHEMATICAL REPRESENTATION
OF STREAM PROCESSES

Physical variables

Geomorphic variables were based on three empiri-
cal equations relating gradient, stream channel width,
and mean annual streamflow to stream distance. Ele-
vation of the mainstream channel was measured every
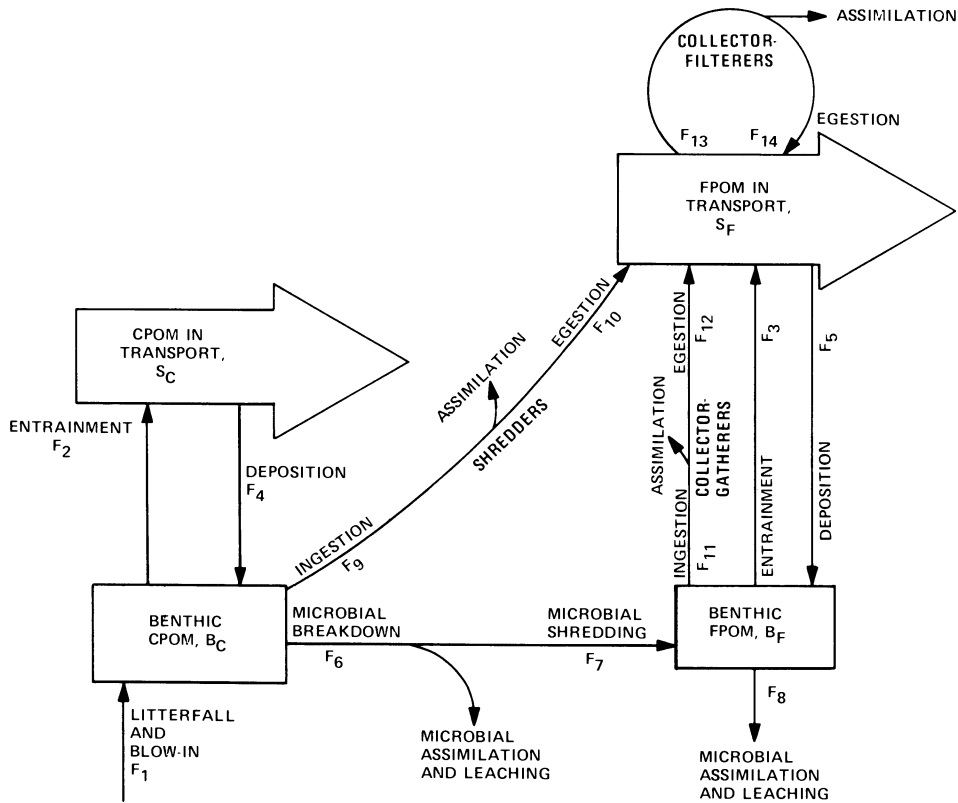100 m. Logarithms of elevation were regressed on

FIG. 1. Compartments used in the model. Arrows indicate flows of particulate organic matter into and out of the compartments.

stream distance ($r = 0.99$, $N = 14$), and the resulting equation was differentiated to obtain an equation for gradient:

$$G = 0.215\, e^{-0.000188x}, \tag{1}$$

where G is stream gradient, and x is stream distance measured from the headwaters.

Measurements of bankfull channel width were made every 5 m along the stream. Mean width of each 100 m reach was regressed against distance ($r = 0.86$, $N = 12$), resulting in the following linear equation:

$$W = 1.11 + 0.00143x, \tag{2}$$

where W is bankfull channel width. Stream channel width was treated as a constant through time. That is, I assumed that changes in steamflow were expressed as changes in depth and velocity and that any organic matter within the banks was an active part of the ecosystem. Actually, this is seldom the case. At any streamflow with a recurrence interval $< \approx 1.5$ yr, stream width is less than bankfull (Dunne and Leopold 1978). Contraction of the stream creates areas which might not be considered part of the stream ecosystem because, at least temporarily, there is no interaction with the rest of the stream. I have not dealt with this form of spatial variability here.

An equation relating streamflow to stream distance was obtained by first regressing the logarithm of drainage area (estimated from a 1:7200 scale topographic map) on distance ($r = 0.93$, $N = 11$). Then I used the ratio of total watershed area and mean annual streamflow at the weir (0.359 L·s^{-1}·ha^{-1}) to convert drainage area to mean annual streamflow at points upstream of the weir:

$$Q = (0.359)(1.0 + 0.000887x^{1.56}), \tag{3}$$

where Q is mean annual streamflow (in litres per second) at a particular distance x along the stream. Streamflow for a particular day was then calculated by dividing this value of Q by mean annual streamflow at the weir and multiplying by streamflow at the weir for that day.

Other hydrodynamic parameters (velocity, mean depth) were calculated from Eqs. 1 through 3, using the Manning equation. Hydraulic radius was approximated with mean depth (Leopold and Maddock 1953), and I used a roughness coefficient (Manning's n) of 0.04, a typical value for mountain streams (Chow 1959).

An equation for stream water temperature was developed by regressing mean monthly temperatures for the study period on the sine of the time of year ($r = 0.96$, $N = 12$):
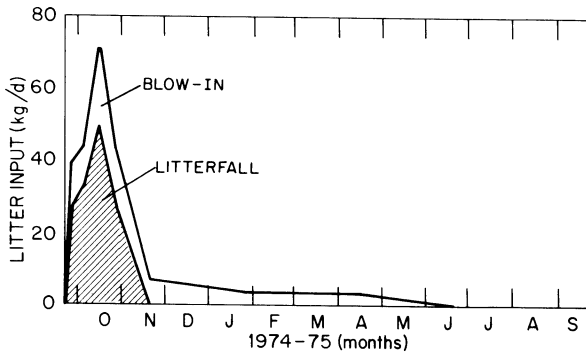
Fig. 2. Litter inputs to Big Hurricane Branch. The shaded area indicates direct litter fall. The upper line is total litter input, including direct litter fall and blow-in. Data from Webster (1977) and Webster and Waide (1982).

$$T = 4.64 \sin(t) + 12.9, \qquad (4)$$

where T is temperature in degrees Celsius, and t is time of year in radians with a phase shift such that average annual temperatures occurred on 15 April and 15 October.

Equations for material flows

Detritus dynamics in Big Hurricane Branch were conceptualized in terms of four compartments: course particulate organic matter (CPOM, ≥ 1 mm) and fine particulate organic matter (FPOM, < 1 mm) on the bottom and in transport (Fig. 1). The living components of the system, macroinvertebrates and microbes, were not treated as model compartments but rather as processes mediating the exchange of POM among compartments. The following section describes equations used to model biological and physical transfers in and out of compartments. For convenience, each transfer or flow is identified with a subscripted F as indicated in Fig. 1.

Litter fall and blow-in (F_1).—Webster and Waide (1982) measured leaf fall and blow-in to Big Hurricane Branch in 1974–1975 as 259.2 g·m⁻²·yr⁻¹ and 174.8 g·m⁻¹·yr⁻¹, respectively. Total litter inputs, including twigs and other debris, during the same period were 286.8 g·m⁻²·yr⁻¹ and 232.0 g·m⁻¹·yr⁻¹. Based on an average channel width of 1.65 m, this gives a total input of 568.0 g·m⁻²·yr⁻¹. Data collected in that study were entered into the model as a table, and daily input values were calculated by linear interpolation between sampling dates. Total litter input (F_1) at a particular time and point in the stream was calculated as:

$$F_1 = LF + \frac{2BI}{W}, \qquad (5)$$

where LF is litter fall (in grams per square metre per day), and BI is blow-in (in grams per metre per day). Total litter input to the stream (Fig. 2) peaked in October but decreased rapidly after leaf fall ended. There

was a continued low input into early summer due to blow-in. Spring and summer litter fall were not measured. Based on model results, input ranged from 705 g·m⁻²·yr⁻¹ in the first 100 m of stream, where the channel is narrow and blow-in on an areal basis is very large, to 470 g·m⁻²·yr⁻¹ in the most downstream reach.

Litter fall and blow-in were assumed to go directly onto the stream bottom (Fig. 1). In reality, many leaves fall in the water and are transported some distance before stopping. In experiments in a small mountain stream in Virginia, J. R. Webster and E. F. Benfield (*personal observation*) have shown that this distance is very short. Dry oak leaves placed in the channel moved an average distance of < 5 m during a storm. Malmqvist et al. (1978) and Bilby and Likens (1980) also observed that CPOM moved very short distances. Young et al. (1978) found much longer travel distances, but their study was done in a much larger stream (10.4 m wide).

Autochthonous production was not included in the model. Periphyton primary production (as carbon) in Hugh White Creek averages ≈ 0.3 mg·m⁻²·h⁻¹, which is $< 1\%$ of allochthonous inputs on an annual basis (Hains 1981, Webster et al., *in press*).

Entrainment of FPOM (F_3).—There has been almost no research on the physical entrainment of FPOM in streams. The main problem with directly using models developed for inorganic sediment transport (e.g., Yalin 1977) is that they generally assume an inexhaustible supply of material to be transported (T. Dunne, *personal communication*). Therefore, I used inorganic sediment principles only to set maximum potential FPOM concentrations. Bagnold (1966) developed formulas based on physical principles relating sediment transport (both suspended and bedload) to stream power. On the basis of that work, I assumed that the potential FPOM concentration of a stream is directly proportional to stream power.

It has also been shown that concentrations are usually much higher during the rising limb of a storm hydrograph than during the descending limb (e.g., Fisher and Likens 1973, Bilby and Likens 1979, Meyer and Likens 1979, Gurtz et al. 1980). Some recent experiments have shown that the concentration of FPOM during increasing flows is directly proportional to the rate of increase in flow (J. R. Webster and E. F. Benfield, *personal observation*). For example, for the storm data shown in Fig. 3, the correlation coefficient relating FPOM concentration to the rate of change of streamflow was 0.96 $(N = 5)$. The drop in concentration during the rising flow (Fig. 3) corresponds to a period when the rate of increase in flow was lower than during sampling periods on either side. This suggests that as flow increases and the stream expands in the channel, it encounters areas that have not been exposed to flowing water but were protected pools or backwaters, moist areas, or, if the stream rises high enough, areas that have been completely dry (Fisher

and Likens 1973, Bilby and Likens 1979, Meyer and Likens 1979). As the stream expands into these areas, it picks up easily transported material that has collected there since the last storm. The faster the stream rises, the faster the channel expands, and the higher the FPOM concentration becomes.

From this information concerning FPOM entrainment, the following equations were selected as the simplest possible which described these phenomena:

$$S_{Fmax} = 30 \, QG, \tag{6}$$

where S_{Fmax} is the maximum FPOM concentration (in milligrams per litre), and flow times gradient (QG) is proportional to stream power (e.g., Leopold et al. 1964);

$$E_F = 1 + 5\frac{dQ}{dt}, \tag{7}$$

where E_F is the entrainment rate of FPOM (in days), $\frac{dQ}{dt}$ is the positive rate of change of flow (in litres per second per day; i.e., if flow was decreasing, $\frac{dQ}{dt}$ was set to zero), and

$$F_3 = E_F \, (S_{Fmax} - S_F), \tag{8}$$

where F_3 is FPOM entrainment (milligrams per litre per day), and S_F is the existing FPOM concentration. The FPOM entrainment (F_3) was limited so as not to exceed benthic FPOM during an integration interval. The parameter values in Eqs. 6 through 8 were determined by fitting model output to data. The model was set up to run on a 15-min time interval using streamflow values from Hugh White Creek for a storm which occurred on 30 June–1 July 1981. The equation parameters were then adjusted to achieve the simulation shown in Fig. 3.

When there is sufficient benthic FPOM available, Eq. 8 shows that FPOM entrainment is proportional to the difference between potential concentration (S_{Fmax}) and actual concentration (S_F). Under most conditions S_F is much less than S_{Fmax}, so that entrainment is directly proportional to stream power. Under rapidly rising flow conditions, if the FPOM concentration approaches the maximum, entrainment decreases. The suspended load reduces internal turbulence of the stream (e.g., Leopold et al. 1964, Morisawa 1968) and acts as a negative feedback to reduce further entrainment. Actually it may be more proper to say that the reduction in turbulence increases deposition, thus shifting the balance between the continuous processes of entrainment and deposition. Fisher and Likens (1973) suggested that just the opposite occurs with CPOM. As the stream picks up CPOM, its erosive power increases and the process assumes positive-feedback characteristics because as debris accumulations are dislodged, the velocity of the stream increases.
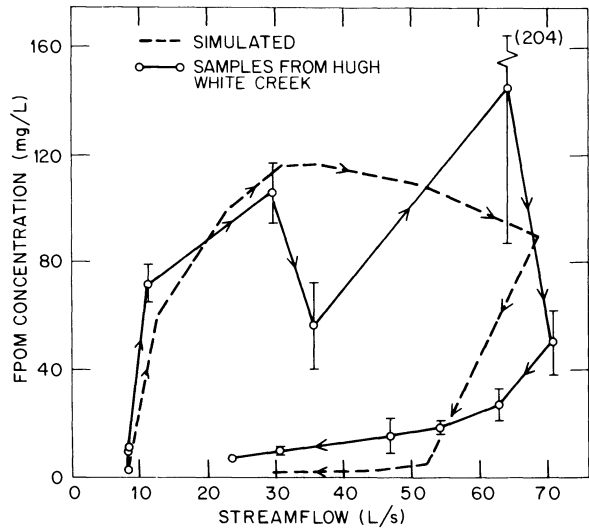
Entrainment of CPOM (F₂).—There is little infor-

FIG. 3. Comparison of simulated FPOM concentrations during a storm with samples taken from Hugh White Creek during a storm on 30 June–1 July 1981. Samples from Hugh White Creek were taken every 15 min. The error bars are 95% confidence intervals. Data from Webster et al. (*in press*).

mation available on mechanisms of CPOM transport. Some of the processes involved are quite different from those involved with FPOM or inorganic sediment transport. However, a number of studies have shown a correlation between CPOM concentration and streamflow (e.g., Fisher and Likens 1973, Meyer and Likens 1979, Webster and Patten 1979). In the attempt to construct a similar rating curve for samples collected from Big Hurricane Branch in 1974–1976, I was unable initially to find any significant relationships between CPOM concentration and streamflow. However, after dividing the data into four seasons, I obtained statistically significant regressions (Fig. 4). Nelson and Scott (1962) and Fisher (1977) found a similar seasonal separation of POM rating curves, and Meyer and Likens (1979) found it necessary to use a different regression equation for transport of phosphorus on CPOM in autumn than in other seasons. The different curves in Fig. 4 are probably related to the availability of CPOM on the streambed. CPOM concentrations were always low at low flows. During leaf fall, recently fallen and still partially dry leaves were scattered over the streambed, and even small increases in flow caused large increases in CPOM concentration. The first large storm after leaf fall, 20 November in 1974, removed leaves from most areas of the streambed and clumped them together into rather stable packs behind rocks, sticks, and logs. Increases in streamflow for the rest of the winter caused little increase in CPOM concentration. By early spring, the leaves had decayed and fragmented to the point where the packs were less stable, and storms may again have
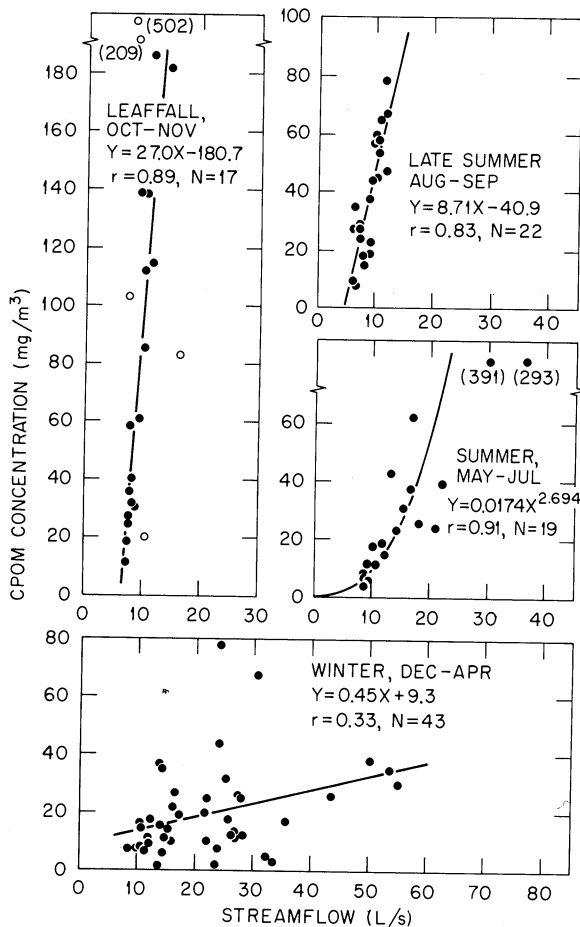
Fig. 4. CPOM concentration as a function of streamflow in Big Hurricane Branch. Open circle points for the leaf fall period were not used in calculating the regression line. Data from Webster (1977). Samples collected over 4- or 24-h periods were regressed against mean flow over the collection period.

caused large increases in CPOM concentration. Later in the summer this became even more pronounced.

The regression equations in Fig. 4 were used in the model to establish maximum CPOM concentrations as a function of mean daily flow:

$$S_{Cmax} = 1000 f(Q), \qquad (9)$$

where S_{Cmax} is the maximum CPOM concentration, and $f(Q)$ is the appropriate regression equation relating CPOM concentration (in milligrams per cubic metre) to streamflow. CPOM entrainment (F_2) was assumed to be directly proportional to the difference between the existing CPOM concentration (S_C) and the maximum:

$$F_2 = E_C (S_{Cmax} - S_C), \qquad (10)$$

with the entrainment rate (E_C) set to a very large value (1000 d^{-1}) to ensure that entrainment would be very rapid and the CPOM concentration near the maximum

at all times. F_2 was limited so as not to exceed available benthic CPOM during an integration interval.

Functions for deposition of CPOM and FPOM were included in the model. These functions were formulated such that deposition would occur only if there were a decrease in streamflow. Since streamflow was treated as a continuously increasing function of distance and was constant within any day, deposition never occurred in the simulations presented here. Therefore, once POM was entrained, it was transported out of the system. Much of the POM transported in Big Hurricane Branch is probably carried as bedload, with any individual particle frequently shifting from transported POM to benthic POM and back. Entrainment and deposition are both occurring continuously, and what I have modeled is the net effect. Under the simulated conditions, there was never a net deposition.

Microbial transformations (F_6–F_8).—In order to estimate microbially mediated decomposition of CPOM independent of invertebrate activity, I used leaf breakdown data from a small stream at Coweeta, which had been treated with methoxychlor to eliminate insects (Wallace et al. 1982b). Rhododendron (*Rhododendron maximum*), white oak (*Quercus alba*), red maple (*Acer rubrum*), and dogwood (*Cornus florida*) leaves were exposed in the stream in large mesh bags (5 × 5 mm opening). Leaf breakdown rates (e.g., Olson 1963) were calculated by regressing the logarithms of leaf mass remaining on cumulative degree-days (Table 1). Suberkropp et al. (1975), Petersen and Cummins (1974), Paul et al. (1978), and others have demonstrated the significant effect of temperature on decomposition. Minshall et al. (1983) used the degree-day rate as a means of expressing this effect.

Table 1. Degree-day breakdown rates measured in a stream treated with methoxychlor to eliminate insects (Wallace et al. 1982b), and weighting factors for the leaf breakdown rate categories, based on proportional leaf input to Big Hurricane Branch (Webster and Waide 1982), that were used in calculation of a mean breakdown rate for all benthic CPOM.

Species	Breakdown rate (degree-day^{-1})	Coefficient of determination, r^2	Breakdown rate category	Weighting factor
Rhododendron maximum (rhododendron)	0.0001	0.85	very slow	0.11
Quercus alba (white oak)	0.0003	0.83	slow	0.39
Acer rubrum (red maple)	0.0004	0.76	medium	0.48
Cornus florida (dogwood)	0.0007	0.84	fast	0.02

TABLE 2. Most abundant tree leaf species found in leaf fall and blow-in to Big Hurricane Branch (Webster and Waide 1982). Assignment to breakdown rate categories was based on published rates (e.g., Petersen and Cummins 1974, Webster and Waide 1982) and taxonomic similarities.

Very slow	Slow	Medium	Fast
Rhododendron maximum	*Quercus alba*	*Acer rubrum*	*Cornus florida*
Kalmia latifolia	*Quercus prinus*	*Carya ovata*	*Oxydendron arboreum*
	Quercus rubra	*Carya tomentosa*	*Tilia americana*
	Quercus velutina	*Carya glabra*	*Fraxinus* sp.
	Quercus coccinea	*Liriodendron tulipifera*	
	Fagus grandifolia	*Betula lenta*	
		Betula lutea	
		Hamamelis virginiana	

Species of leaves in litter fall and blow-in to Big Hurricane Branch were placed into four categories according to published breakdown rates (e.g., Petersen and Cummins 1974, Webster and Waide 1982) and taxonomic similarities (Table 2). The proportion of the input in each category was used as a weighting factor on exponentially transformed rates to calculate a mean breakdown rate of 0.0003 degree-day^{-1} which was applied to all benthic CPOM. This was expressed in the model as:

$$F_6 = 0.0003\ TB_C, \qquad (11)$$

where B_C is the benthic CPOM standing crop (in milligrams per square metre).

The flow, which I have labeled microbial breakdown (F_6), includes at least four components: microbial assimilation, leaching, mechanical fragmentation, and microbial shredding, i.e., fragmentation due to microbial decomposition (Fig. 1). In experiments with aquatic hyphomycetes, Suberkropp and Klug (1980) showed that 56–74% of the mass loss from leaves resulted in the formation of FPOM. In the model I assumed that 50% of the breakdown of CPOM resulted in FPOM (F_7) either by mechanical or shredder fragmentation and that the rest went to microbial assimilation and leaching.

I am not aware of any measurements of the rate of breakdown of FPOM in streams. I assumed that the rate of microbial breakdown of FPOM was equal to the rate of leaching and microbial assimilation of CPOM (i.e., half the total CPOM breakdown rate):

$$F_8 = 0.00015\ TB_F, \qquad (12)$$

where B_F is the benthic FPOM standing crop.

Macroinvertebrate equations (F_9–F_{14}).—Macroinvertebrates were not actually modeled; that is, they were not treated as model compartments, but rather as processes mediating the exchange of POM among compartments. Estimates of macroinvertebrate standing crops (Table 3) were calculated from data collected from Grady Branch, a small stream draining an undisturbed Coweeta watershed (WS 18, Woodall 1971, Woodall and Wallace 1972). Insects were placed into functional feeding groups (Table 4) based on the classification given by Merritt and Cummins (1978). Among the taxa listed in Table 4, tipulids, *Peltoperla, Stenonema,* and hydropsychids accounted for 93% of the detritivore biomass (Webster and Patten 1979). Crayfish were classified as shredders. Daily standing crops of macroinvertebrates were calculated from seasonal values (Table 3) by linear interpolation. For insects in all three functional groups, I used a feeding rate of 0.17 mg·mg^{-1}·d^{-1}. This was calculated by assuming a turnover ratio (annual production/mean annual biomass) of 5, a net production efficiency (NPE = production/assimilation) of 40%, and an assimilation efficiency (AE = assimilation/ingestion) of 20%.

A turnover ratio of five is typical for univoltine stream insects (Waters 1977), though it is probably low for benthic-insect community production because of

TABLE 3. Standing crops (mg/m²) of macroinvertebrate functional feeding groups. Seasonal means were calculated from data collected by Woodall (1971).

	Shredders		Collector-gatherers	Collector-filterers
	Insects	Crayfish		
Summer	724	2700	249	131
Fall	528	100	184	195
Winter	1459	3100	275	152
Spring	1180	600	198	100

TABLE 4. Most abundant insect taxa comprising the detritivorous feeding groups. Data from Woodall (1971); functional group assignment from Merritt and Cummins (1978).

Shredders	Collector-gatherers	Collector-filterers
Chironomidae	Elmidae	Simuliidae
Ceratopogonidae	*Stenonema*	*Parapsyche*
Tipulidae	*Baetis*	*Diplectrona*
Nemoura	*Paraleptophlebia*	Psychomyiidae
Leuctra	*Ephemerella*	Philopotamidae
Peltoperla		
Pycnopsyche		
Sericostomatidae		
Lepidostomatidae		

the abundance of many insects, such as chironomids, with much higher turnover ratios. The NPE of 40% is somewhat less than the 50% used by Benke and Wallace (1980) for net-spinning caddisflies but seems to be a more appropriate average for all aquatic insects. The NPEs (and net growth efficiencies, which are approximately equivalent) measured for stream insects range from 4 to 82% (Trama 1957, Cummins 1969, Vannote 1969, McDiffett 1970, Edington and Hildrew 1973, Otto 1974, Wooton 1978, Grafius and Anderson 1979, Iverson 1979, McCullough et al. 1979a, b, Sweeney and Vannote 1981). Heal and MacLean (1975) suggested that 40% is a typical NPE for noncarnivorous invertebrates. Benke and Wallace (1980) used a conservative AE of 10% for detritus-feeding caddisflies; however, 20% is closer to the average of reported values for stream detritivores (Cummins 1969, Vannote 1969, McDiffett 1970, Otto 1974, Winterbourn and Davis 1976, Grafius and Anderson 1979, Iverson 1979, Short and Ward 1981a, Golladay et al. 1983). These parameter values were chosen to give a conservative estimate of feeding rate, i.e., I used a low estimate of turnover ratio and relatively high estimates of AE and NPE. In this way, any bias introduced by my selection of values is toward an underestimate of the role of macroinvertebrates.

Feeding rates reported for detritus-feeding stream insects range over more than two orders of magnitude (Vannote 1969, McDiffett 1970, Wallace et al. 1970, Cummins 1973, Cummins et al. 1973, Mackay and Kalff 1973, Grafius and Anderson 1979, Iverson 1979, Short and Ward 1981a, Golladay et al. 1983). The estimated feeding rate of 0.17 mg·mg^{-1}·d^{-1} is slightly lower than the average of published values (0.27 mg·mg^{-1}·d^{-1}), reflecting an intentional bias away from overestimating the role of macroinvertebrates.

A number of studies have shown that ingestion rate is temperature dependent (e.g., Lawton 1971, Otto 1974, Grafius and Anderson 1979, Iverson 1979, Short and Ward 1981a). Assuming that this relationship is linear within the range of normally encountered temperatures, I estimated a slope of 0.03 mg·mg^{-1}·d^{-1}·°C^{-1} based on studies by Otto (1974), Grafius and Anderson (1979), and Short and Ward (1981a). With the assumption that the average ingestion rate (0.17 mg·mg^{-1}·d^{-1}) occurs at the mean annual stream temperature (12.9°C), the equation relating ingestion rate (I) to temperature becomes:

$$I = 0.03T - 0.22. \qquad (13)$$

For crayfish I used the same NPE and AE as for insects and a turnover ratio of 0.9 based on the studies summarized by Momot et al. (1978) to estimate a feeding rate of 0.031 mg·mg^{-1}·d^{-1}. I did not vary this rate with temperature.

The equations for macroinvertebrate mediated flows were:

$$F_9 = IM_1 + 0.031 M_2, \qquad (14)$$

$$F_{10} = (1 - A) F_9, \qquad (15)$$

$$F_{11} = IM_3, \qquad (16)$$

$$F_{12} = (1 - A) F_{11}, \qquad (17)$$

$$F_{13} = IM_4, \qquad (18)$$

$$F_{14} = (1 - A) F_{13}, \qquad (19)$$

where M_1 through M_4 are the standing crop biomasses of shredder insects, crayfish, collector-gatherers, and collector-filterers, respectively. A constant value of 0.2 was used for the assimilation efficiency (A), as several studies have shown that assimilation efficiency does not vary with temperature (Otto 1974, Grafius and Anderson 1979, Iverson 1979, Short and Ward 1981a). Feeding rates (F_9, F_{11}, F_{13}) were limited so as not to exceed available material during an integration interval. However, in the nominal simulation discussed below, shredder and collector-gatherer feeding limitation never occurred. Collector-filterer limitation occurred in the headwaters of the stream, but 1 or 2 m downstream from the headwaters, there was sufficient FPOM to support collector-filterer ingestion.

Simulation equations

Simulation of the standing crops of the four compartments in Fig. 1 was accomplished by numerical solution of differential equations derived from mass balance (i.e., rate of change equals input minus output). Since these standing crops are functions of both time and distance, it was necessary to use partial differential equations. Solution of partial differential equations for transport of material in rivers (e.g., Thomann 1972) is normally accomplished by transforming the partial differential equations with two independent variables into ordinary differential equations with a single independent variable, using the method of characteristics (e.g., Chester 1971). This is made possible by assuming that transport occurs at the velocity of water, so that $x = Vt$, where x is distance, and t is time. Essentially this solution technique involves a downstream sweep at the water velocity, so that the same parcel of water is followed from the stream source to the end of the study reach.

It was impossible to use this technique for the simultaneous solution of partial differential equations for all four compartments in my stream model, because two different velocities were involved; material in the benthic compartment was not moving, whereas material in the suspended compartments was. Therefore, it was necessary to approximate the downstream change of benthic standing crops by modeling these components as series of compartments within which there was no change with distance. For both CPOM and FPOM, I used a series of 12 compartments, each representing a 100-m reach of stream (125 m for the

most downstream reach). The equation for each of these compartments was an ordinary differential equation. The complete equations were:

$$\frac{dB_C}{dt} = F_1 + DF_4 - DF_2 - F_6 - F_9, \qquad (20)$$

$$\frac{dB_F}{dt} = F_7 + DF_5 - DF_3 - F_8 - F_{11}, \qquad (21)$$

$$\frac{\partial S_C}{\partial t} = \frac{-1}{A}\frac{\partial QS_C}{\partial x} + \frac{S_{CT}}{A}\frac{\partial Q}{\partial x} + F_2 - F_4, \qquad (22)$$

$$\frac{\partial S_F}{\partial t} = \frac{-1}{A}\frac{\partial QS_F}{\partial x} + \frac{S_{FT}}{A}\frac{\partial Q}{\partial x} + F_3 - F_5$$
$$+ \frac{F_{10} + F_{12} + F_{14} - F_{13}}{D}. \qquad (23)$$

The units of the terms in Eqs. 20 and 21 are $g \cdot m^{-2} \cdot d^{-1}$, and in Eqs. 22 and 23, they are $mg \cdot L^{-1} \cdot d^{-1}$. Division or multiplication by depth (D) is necessary to convert between the two units. The first terms in Eqs. 22 and 23 express the effect of dilution as flow increases downstream. The second terms represent the inputs of FPOM (S_{FT}) and CPOM (S_{CT}) entering the main stream from tributaries or groundwater. I could not treat these inputs explicitly because I did not have measurements of either tributary flows or POM concentrations. Instead, I treated the increase in mainstream flow as a continuous function of distance (Eq. 3). If all the increase in flow came from groundwater, I could have assumed S_{FT} and S_{CT} were essentially zero. Alternatively, if the stream network were a perfectly dendritic system with no groundwater inputs, I could have assumed that tributary concentrations equaled mainstream concentrations at the point where they entered the main stream. I assumed something between these extremes. Based on measurements of drainage basin areas from a 1:7200 scale topographic map, 52.6% of the water entering the mainstream of Big Hurricane Branch comes from the tributaries; the rest presumably enters as subsurface seeps. Therefore, I used the following equations to estimate the average POM concentrations of incoming water:

$$S_{CT} = 0.526 S_C, \qquad (24)$$

and

$$S_{FT} = 0.526 S_F. \qquad (25)$$

The partial differential equations for transported POM were converted to ordinary differential equations by the method of characteristics. Eqs. 22 and 23 were solved using the Runge-Kutta technique for numerical integration with a time step of 0.0001 d. Within each sweep, B_F and B_C were kept constant. Eqs. 20 and 21 were solved by Euler integration between sweeps. The time between the starts of successive sweeps was 1 d.

For suspended CPOM and FPOM concentrations (S_C and S_F), I set initial conditions of zero at the headwaters of the stream. It is difficult to measure POM

concentrations at headwater seeps because it is almost impossible to avoid stirring up benthic material; however, seep concentrations are often lower than downstream concentrations (Webster and Golladay, *in press*). Initial conditions for benthic CPOM and FPOM (B_C and B_F) were determined by running the model for six years with zero initial conditions and then using the values at the end of that time as initial conditions in subsequent simulations. Six years was sufficient time for the model to approach equilibrium (i.e., the values of B_F and B_C at the end of six years were <1% different than the values at the end of five years).

RESULTS AND DISCUSSION

Comparison of simulations and field data

Benthic CPOM.—The simulated benthic CPOM standing crop (B_C) of Big Hurricane Branch was substantially higher than measured values (Fig. 5). The model indicated a peak standing crop of 510 g/m², while the highest measured value was only 198 g/m². This discrepancy could be the result of inaccurate model parameters: overestimation of litter inputs, underestimation of microbial breakdown, underestimation of shredder ingestion, or underestimation of entrainment. While each of these errors is possible, the measured and simulated variables being compared are not actually the same. The simulation is for the average CPOM standing crop throughout the width of the bankfull channel, whereas the CPOM samples were collected in midstream. During late-fall and early-winter storms, material in midstream is either washed out of the system or accumulated in packs, often in marginal areas of the stream channel. Also, blow-in is deposited primarily in parts of the channel nearest the banks. Thus it is not surprising that the simulated average CPOM standing crop for the entire channel is larger than the CPOM standing crop measured in midstream.

The simulation and field data show similar trends. The field data show an earlier decrease in standing crop, but this may be due to redistribution within the channel. Studying a stream of similar size (1335 m long) in Kentucky, Minshall (1967) found the same trend in allochthonous leaf detritus; peak standing crop occurred in fall and minimum in summer. Short and Ward (1981b) found a rapid winter decline in CPOM standing crop in a third-order mountain stream, which they attributed to biological activity. In his study of Walker Branch, Tennessee, Comiskey (1978) found that the standing crop of leaves in riffles decreased from 180 to ≈20 g/m² in November and December, a period which included the largest storm of the year.

The simulated rate at which benthic CPOM disappeared following its peak standing crop in November can be compared with rates of leaf disappearance observed in a leaf breakdown study conducted in Big
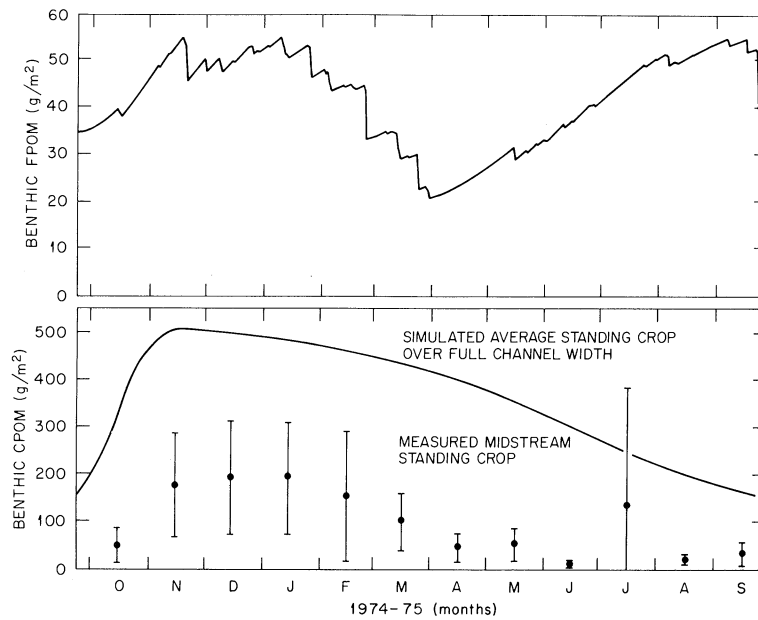
FIG. 5. Benthic CPOM and FPOM in Big Hurricane Branch. Upper panel: simulated benthic FPOM averaged over the entire stream length. Lower panel: the solid line is the simulated average CPOM standing crop over the full channel width. The data points are means (with 95% confidence intervals) of 10 samples taken in midstream. Data from Webster (1977).

Hurricane Branch in 1974–1975 (Webster and Waide 1982). The simulated disappearance of benthic CPOM shown in Fig. 6 was produced by modifying the model so that there was no input after the peak standing crop had been reached, to make the simulation comparable with the breakdown study. The simulated rate of disappearance of benthic CPOM was very similar to the observed rate of white oak breakdown. This is reasonable since nearly one-half of the leaf input to Big Hurricane Branch was slow and very slow material (Table 1). This comparison lends support to the parameter values used in the model.

There was good agreement between the simulated and measured longitudinal trend in CPOM standing crop (Fig. 7), though the magnitudes of the curves differed as discussed above. Regression of the mean measured standing crops showed a significant decrease with distance ($r = -0.76$, $N = 10$). Minshall (1967) did not find this sort of decrease in Morgan's Creek; however, in their study of streams in four different biomes, Minshall et al. (1983) found a general decrease in benthic CPOM with distance at all sites. Wallace et al. (1982a) also showed a decrease in CPOM standing crop with distance in Dryman Fork, a fourth-order stream at Coweeta, Meyer and Likens (1979) and Bilby and Likens (1980) reported decreases in CPOM standing crop with increasing stream order in Hubbard Brook streams, and Naiman and Sedell (1979b) reported a similar situation in the McKenzie River drainage.

Benthic FPOM.—The main peak in FPOM standing

crop occurred in late fall–early winter (Fig. 5). A subsequent depletion in FPOM occurred when, because of low temperature, biological production of FPOM did not keep up with removal during storms. Beginning in spring and throughout the summer, production exceeded transport, and FPOM accumulated. Effects of individual storms are evident in the figure.

The simulated longitudinal distribution of benthic FPOM (Fig. 7) shows a large upstream to downstream decrease. In the most upstream reach of the stream, there was seldom sufficient power to move FPOM, but in the lower reaches, there was nearly always sufficient power, and little FPOM accumulated. The greatest seasonal changes in FPOM standing crop occurred in the middle reaches of the stream.

The FPOM standing crop has never been measured at Coweeta, but comparison of simulated FPOM standing crop with standing crops measured in other studies suggests that the model results are low. Minshall et al. (1983) found average FPOM (their FPOM plus UPOM) standing crops in low-order streams ranging from ≈200 to 700 g/m². The ratio of benthic FPOM to CPOM in their first- and second-order streams ranged from ≈0.5 to 7. My model produced a mean FPOM to CPOM ratio of 0.12, although it ranged from 0.59 in the headwaters to 0.004 downstream. Newbold et al. (1983) reported a FPOM standing crop of 150 g/m² in Walker Branch in summer and a FPOM/CPOM ratio of 1.8. The discrepancy between model results and available data is because all of the model FPOM is available for transport. Actually, some FPOM is bur-

ied in the streambed and, under most conditions (i.e., except major storms), is not available for transport. Future models might be improved by including FPOM pools that are protected from entrainment during all but exceptionally large storms. However, in the present model, I have attempted only to simulate what might be termed the hydrologically active pool of FPOM.

CPOM in transport.—Simulated CPOM concentrations in transport at the downstream end of the study reach correspond to measured concentrations (Fig. 8). However, this is not a useful test of the adequacy of the model, since it is an empirical result. The model-predicted concentrations are a direct reflection of the regression equations (Fig. 4), which are based on the data in Fig. 8. However, the comparison does support my use of these values in calculating annual transport of CPOM.

FPOM in transport.—The FPOM concentration data used for comparison against simulations (Fig. 8) were collected from Hugh White Creek over a period of several years. The reported data points are for samples taken during nonstorm periods only. The most important observation is that the data and model show the same trend: lowest concentrations during winter when flows are highest and highest FPOM concentrations in summer when flows are low. In general, the model shows slightly higher-than-measured nonstorm FPOM concentrations in fall and winter and slightly lower-than-measured concentrations in early summer.

The seasonal pattern is strongly influenced by dilution. Total FPOM transport is higher in winter than in summer (Fig. 9), but because of higher streamflow, concentrations are lower. Several things might be done to produce simulated FPOM concentrations that more
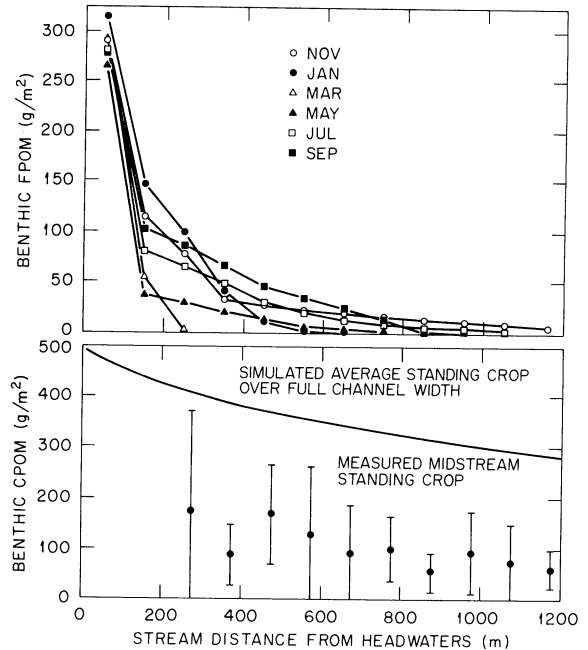
FIG. 7. Benthic CPOM and FPOM in Big Hurricane Branch vs. stream distance from headwaters. Upper panel: simulated bimonthly distribution of benthic FPOM. Lower panel: the solid line is the simulated average annual standing crop of CPOM over the full channel width. The data points are means (with 95% confidence intervals) of monthly samples taken in midstream. Data from Webster (1977).

nearly match measured values: decrease nonstorm FPOM entrainment, increase the temperature dependence of macroinvertebrate ingestion rate, adjust macroinvertebrate standing crops, or increase the temperature effect on microbial processing. In the simulation experiments described below, I have tried some of these modifications where it seemed most justified.

In addition to obvious increases in FPOM concentration during days of high flows (Fig. 8), there was an apparent "washout" effect. FPOM concentrations following storms were often less than concentrations prior to the storm (Fig. 8). Bilby and Likens (1979) speculated that this phenomenon was due to depletion of available FPOM in the streambed. They observed increasing FPOC concentration over a period of 5 d following a storm, such as can be seen for a number of storms in Fig. 8. However, the results in Fig. 8 can be attributed entirely to dilution. There was never a period of increasing transport (concentration times streamflow) in the first few days following a storm.

Model predictions of transported FPOM concentrations over distance are compared with data from Hugh White Creek in Fig. 10. The magnitudes of the curves reflect the differences described above. In general, the data support the model's prediction of a downstream increase in FPOM concentration. However, we have not
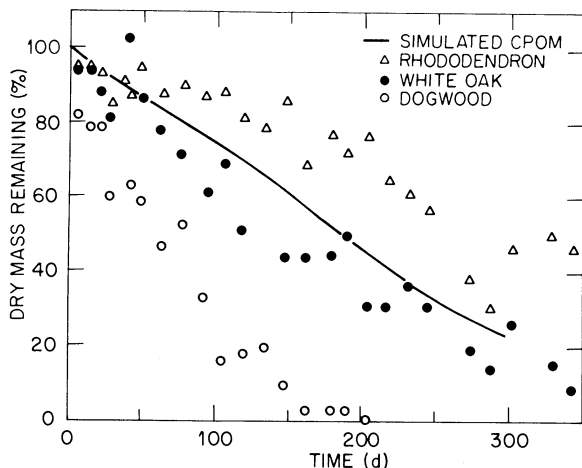
FIG. 6. Simulated CPOM disappearance compared to breakdown of three different leaf species. Data points are means of four to six samples. Data from Webster and Waide (1982).
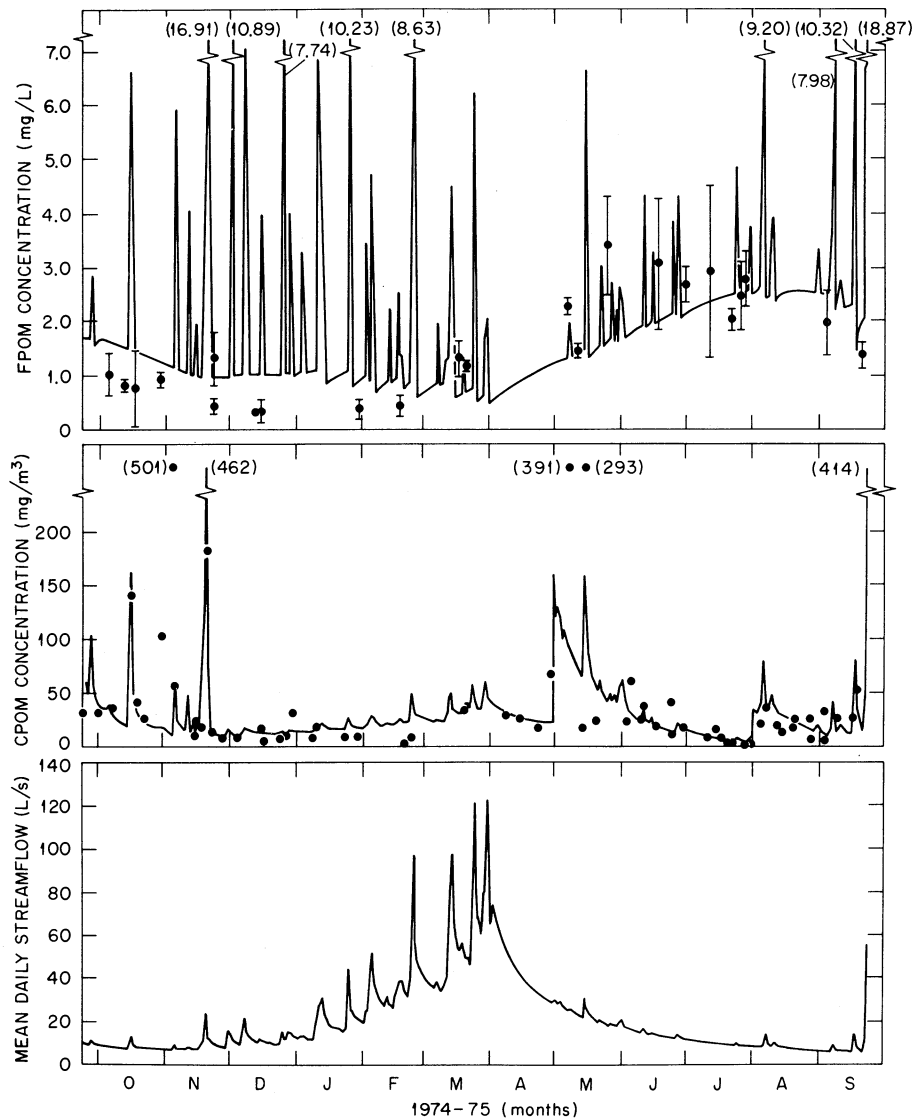
FIG. 8. Mean daily streamflow, CPOM concentration, and FPOM concentration in Big Hurricane Branch. The solid lines for CPOM and FPOM are simulations. Streamflow data from Coweeta Hydrologic Laboratory. CPOM data (from Webster 1977 and Webster et al., *in press*) are from samples taken from Big Hurricane Branch in 1974–1975. FPOM samples (means and 95% confidence intervals) were collected from Hugh White Creek from 1977 through 1982 during nonstorm periods. FPOM data from Gurtz et al. (1980) and Webster et al. (*in press*).

often found the sharp change in FPOM that the model predicts to occur in the first 100 m (Webster and Golladay, *in press*). It is difficult to collect good transport samples in the headwaters of the stream because the water is shallow. This is especially true during low flows, which typically occur in fall when the first 100–150 m is essentially a seep. The assumption that groundwater FPOM concentrations are zero may be invalid, yet this had little effect on the model's predictions. Changing the FPOM initial conditions from 0 to 1.0 mg/L changed the total annual transport of FPOM in Big Hurricane Branch from 1327 to 1410 kg. Other studies have shown no general trend in FPOM

concentration with stream distance (Minshall 1967, Fisher and Likens 1973, Naiman and Sedell 1979a, Cummins et al. 1981, Minshall et al. 1983, Wallace et al. 1982a). However, in these studies, there was no high-intensity sampling in the uppermost reaches of the stream. Below the first few hundred metres, the FPOM concentration appeared to remain constant (Fig. 10).

Most of the POM in transport was FPOM. CPOM averaged 1.8% of the total transport, with monthly averages ranging from 0.6 to 4.3%. These values are consistent with other studies at Coweeta. During nonstorm periods CPOM averaged 4% in Hugh White

Creek (Gurtz et al. 1980), and Wallace et al. (1982a) found that CPOM averaged 4.1–7.8% in Dryman Fork. However, other studies indicate wide variability. Fisher and Likens (1973) reported ≈20% CPOM in Bear Brook based on netted CPOM samples but 81% using data on weir pond sediments. McDowell and Fisher (1976) estimated that CPOM accounted for 60% of the transport from a small New England stream in autumn. CPOM in a swamp-stream system ranged from 9 to 67% at different sites (Mulholland 1981). Sedell et al. (1978) found that CPOM in streams in four different biomes was ≈5% or less at all sites except one site in Pennsylvania, where CPOM was ≈20% of total POM. At the smaller (first- and third-order) Oregon sites, CPOM was always <3% and usually much less (Naiman and Sedell 1979a). Studies of larger streams and rivers have generally reported very low (≤1%) CPOM (Fisher 1977, Naiman and Siebert 1978, Cudney and Wallace 1980, Newbern et al. 1981), though Naiman and Sedell (1979a) reported higher percent CPOM in the McKenzie River than in their smaller stream sites. Cummins et al. (1981) found higher CPOM concentration in the Kalamazoo River in fall than in its tributary, Augusta Creek, but this was due to dieback of aquatic macrophytes.

Budgetary analysis

In order to evaluate the importance of macroinvertebrate and other pathways within the model, the annual flow along each pathway was determined at steady state (Fig. 11). Small differences between inputs and outputs are due to errors inherent in the numerical solution technique and the fact that the model was not quite at steady state. Separation of transport into fractions carried at baseflow and stormflow was accomplished by using a modified table of mean daily flows from which stormflow has been eliminated. Flow separation was approximated by extending the tail of the recession curve of each storm back to the day of peak flow and by assuming a linear increase in baseflow between the day the storm started and the day of peak flow. This technique is a simplified application of the flow separation technique described by Barnes (1939).

Less than 1% (0.8%) of CPOM input was transported out of the system as CPOM. About one-fourth of this transport occurred with stormflows. Other studies have shown similarly high CPOM retention and within-system processing. Hall (1972) estimated ≈2% of CPOM input was transported downstream, and Mulholland (1981) found that ≈0.3% of the CPOM input to a swamp-stream ecosystem was transported out. Based on study of a small Coweeta stream, Webster and Patten (1979) calculated a fluvial output of 4.2% of the CPOM input. Also, McDowell and Fisher (1976) found that 3.6% of input was transported out in autumn. In contrast, Fisher and Likens (1973) reported ≈30% transport loss of CPOM.

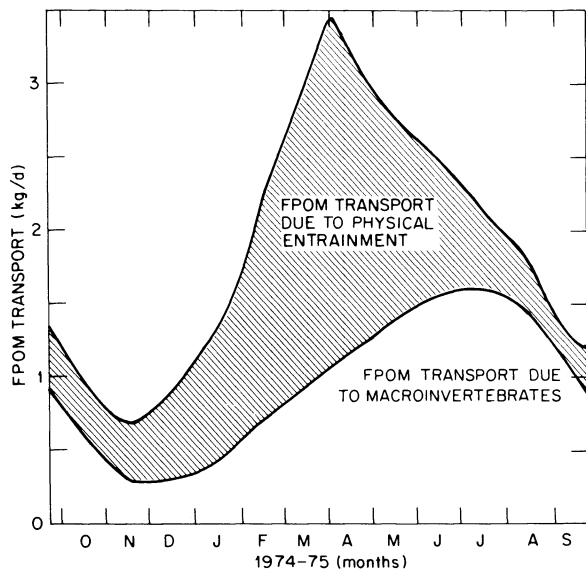The major losses of benthic CPOM were shredder

FIG. 9. Simulated baseflow FPOM transport in Big Hurricane Branch. The upper line is total transport, the lower line is that part of the normal transport due to macroinvertebrate input, and the shaded area between represents transport due to physical entrainment. The simulations were run with normal daily streamflows (i.e., with storms, as in Fig. 8), but only baseflow transport is illustrated.

ingestion and microbial breakdown. Shredders accounted for ≈13% of the transformation of CPOM. By comparison, study of an experimental stream by Cummins (1971) showed that shredders ingested 32% of the CPOM input. From results of an extensive laboratory study, Cummins et al. (1973) estimated that shredders accounted for 20% of the mass loss from leaves. Webster and Patten (1979) estimated that detritivore ingestion was as much as 80% of litter fall inputs. In another study at Coweeta, Wallace et al. (1982b) treated a stream with insecticide and found a significant reduction of leaf breakdown rates. Calculations from their study show 14% less mass loss during a 1-yr exposure from leaves in the treated stream relative to a reference stream. In contrast, Fisher and Likens (1973) estimated a very small role for macroinvertebrates in Bear Brook. However, recalculation using their standing crop (1.51 g/m²) and values used in this study ($P/B = 5$, NPE = 40%, AE = 20%) suggest that ingestion may have been as high as 18% of the CPOM input.

In contrast to CPOM, biological losses of benthic FPOM were fairly small. Macroinvertebrates and microbes accounted for only 5.4 and 18.3% of the losses, respectively, with the major loss being transport. Transport attributable to stormflows (41.9%) was only slightly more than transport at baseflow (34.3%).

On an annual basis, shredders and collector-gatherers were responsible for 27% of the FPOM put into transport. However, detritivores were responsible for
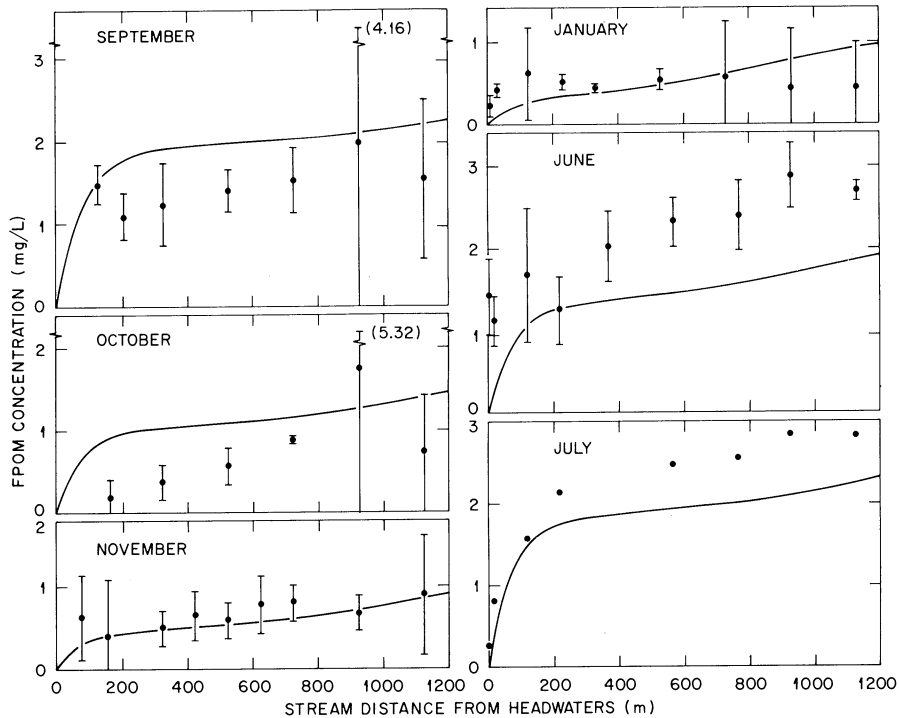
FIG. 10. FPOM concentrations vs. stream distance from headwaters. Solid lines are simulations. Data points (with 95% confidence intervals) are from High White Creek, samples taken during nonstorm periods only (data from Webster and Golladay [in press]).

a much larger fraction of the FPOM transported at baseflow (Fig. 9). The proportion of FPOM transport due to egestion by macroinvertebrates reached a peak of ≈83% in late summer. In contrast, in late winter they produced only 32% of baseflow transport.

Collector-filterers had very little impact on the simulations. They ingested only 4% of transported FPOM and much of that was returned to the water column as feces. Actually, this estimate for collector-filterers is probably an overestimate because some of the organisms probably feed on drifting invertebrates rather than detritus (Benke and Wallace 1980, Georgian and Wallace 1981). Several studies have shown that collector-filterers remove little of the POM from streams (McCullough et al. 1979b, Benke and Wallace 1980, Cudney and Wallace 1980, Haefner and Wallace 1981a, Newbold et al. 1983). Though it has been shown that collector-filterers may remove a large amount of the algae from transport (Maciolek and Tunzi 1968), they probably have little impact on the total quantity of POM transport (Oswood 1979).

Total POM (CPOM + FPOM) transport was 45% of the input. This number is very much a function of stream size (c.f. Fisher 1977, Newbold et al. 1982a), so comparison with other studies is tentative at best. However, a similarly calculated number for Bear Brook is 37% (Table 5).

Another possible method for comparing stream bud-

gets is ecosystem efficiency, the ratio of total respiration to total input (Fisher and Likens 1973). Assuming that leaching is 10% of the mass loss from CPOM and FPOM (e.g., Cummins 1971), that all microbial assimilation is respired, and that macroinvertebrate respiration is 60% of assimilation, I calculated microbial respiration of CPOM as 1033 kg/yr, microbial respiration of FPOM as 188 kg/yr, and macroinvertebrate respiration as 59 kg/yr. Total respiration was 43% of inputs, quite a bit smaller than the 64% efficiency calculated by difference for Bear Brook (Table 5).

Fisher (1977) pointed out that there is little utility in these comparisons for open systems such as streams and suggested as an alternative a stream metabolism index (SMI), which is the ratio of observed respiration to the respiration required for zero loading. For a headwater stream, SMI is equal to ecosystem efficiency with the assumption that groundwater inputs are zero. Fisher and Likens (1973) found no difference in carbon concentrations along the reach of Bear Brook they studied, and therefore Fisher (1977) calculated an SMI of 1.0 for Bear Brook.

Another method of comparing carbon processing efficiency in streams is by calculating carbon turnover length, i.e., the average distance traveled by an atom of organic carbon before it is oxidized (Newbold et al. 1982a). This parameter is a measure of the rate at which the stream utilizes carbon relative to the rate at which
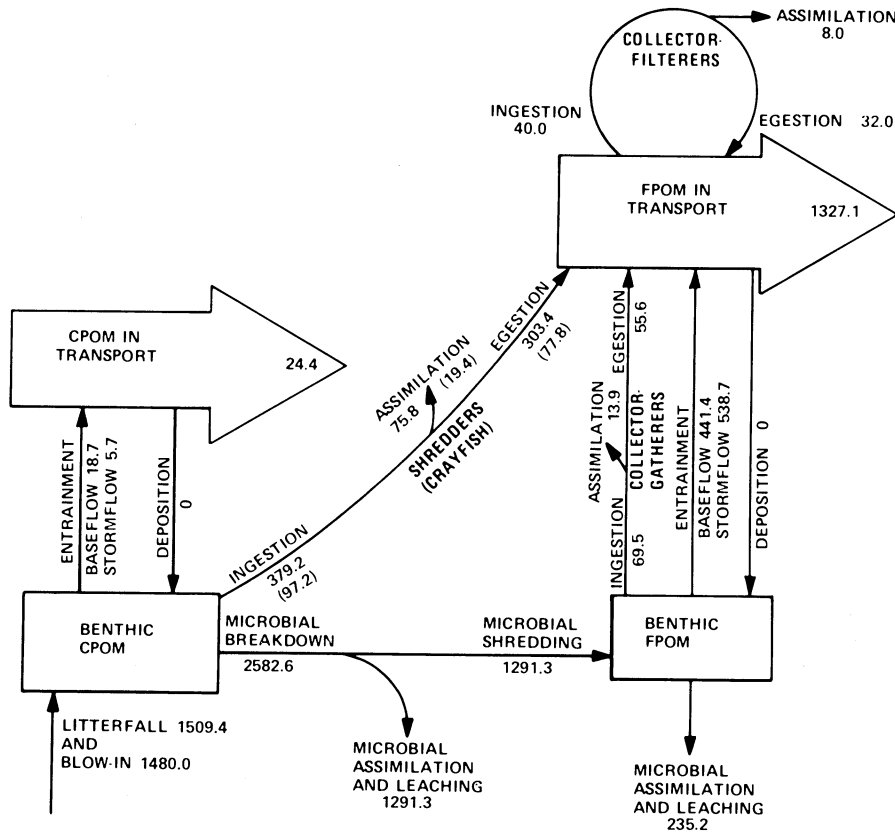
FIG. 11. Annual budget for particulate organic matter in Big Hurricane Branch. Values are kg/yr. Parenthetical numbers associated with the diagonal arrow for shredders are the ingestion, assimilation, and egestion of crayfish alone.

it is transported downstream. A longer carbon turnover length indicates lower relative carbon utilization. The carbon turnover length for Big Hurricane Branch was 2.0 km, compared to 0.8 km for Bear Brook (Table 5).

All the indices in Table 5 indicate that Bear Brook is a more retentive, more efficient ecosystem than Big Hurricane Branch. The major difference appears to be the low FPOM transport in Bear Brook. FPOM concentrations in Bear Brook were generally <1 mg/L and often <0.1 mg/L (Fisher and Likens 1973, Hobbie and Likens 1973). In contrast, model estimated and measured FPOM concentrations in Big Hurricane Branch were usually >1 mg/L at baseflow and much greater during storms. Invertebrate consumption and subsequent egestion of POM may be a large part of the difference between the two streams. There may be other factors that are responsible for the difference, such as differences in the physical retentiveness of the streams. Bilby and Likens (1980) and Bilby (1981) demonstrated that log-created debris dams are important in the retention of FPOM. However, comparison of Hubbard Brook and Coweeta streams suggests little difference in the frequency of debris dams (c.f. Bilby and Likens 1980, Wallace et al. 1982a). Also, Bilby

and Likens (1980) found that removal of debris dams affected FPOM concentrations only at high flows.

Comparison of Big Hurricane Branch with low gradient streams (Table 5) illustrates the many factors that affect turnover length. Because of low particulate transport and higher respiration (Minshall et al. 1983), turnover lengths in Pennsylvania are short. In contrast, in the headwaters of Augusta Creek, Michigan, where particulate transport is high and respiration (per unit mass) is low (Minshall et al. 1983), the turnover length of particulate carbon is relatively long. Camp Creek, Idaho, in which streamflow is dominated by snowmelt, is clearly different from Big Hurricane Branch or any of the other streams listed in Table 5. Even though its turnover length is very similar to Augusta Creek, it is the result of a combination of very different factors (Minshall et al. 1983).

Modifications of the basic model

After completing the model as described above, which I will call the normal model, I tested several modifications designed to evaluate the importance of macroinvertebrates and the sensitivity of the simulation results to some of the assumptions concerning macroinvertebrates made during model construction.

TABLE 5. Efficiencies and turnover lengths for streams similar to Big Hurricane Branch. Dots indicate no data.

Stream	Order	Gradient (%)	Mean annual streamflow (L/s)	POM transport/ input (%)	Ecosystem efficiency (%)	Stream metabolism index*	POM turnover length (km)
Big Hurricane Branch, North Carolina	2	19	18	45	43	0.43	2.0
Bear Brook, New Hampshire†	2	14	28	37	64‡	1.00‡	0.8‡
Devil's Club Creek, Oregon§	1	40	2	⋯	⋯	⋯	1.0
Camp Creek, Idaho§	2	11	38	⋯	⋯	⋯	10.8
Augusta Creek, Michigan§	1	0.8	14	⋯	⋯	⋯	10.4
White Clay Creek, Pennsylvania§	1	1.0	6	⋯	⋯	⋯	0.9
White Clay Creek, Pennsylvania§	2	0.6	29	⋯	⋯	⋯	1.0

* Fisher (1977).
† Fisher and Likens (1973).
‡ These figures differ from Newbold et al. (1982a) because they are based on particulate material only.
§ Minshall et al. (1983).

Elimination of macroinvertebrates from the model.—When all macroinvertebrates were eliminated from the model, FPOM transport at steady state decreased from 1330 (Fig. 11) to 1190 kg/yr. Mean annual standing crops of benthic CPOM and FPOM increased from 366 and 43 g/m², respectively, to 418 and 55 g/m². Ecosystem efficiency increased from 43 to 48%, and turnover length was shortened from 2.0 to 1.6 km. The decrease in transport was entirely due to decrease in baseflow FPOM concentrations (Fig. 12: bottom panel). The FPOM concentrations during storms increased because of the increased availability of benthic FPOM, which was not being consumed by collector-gatherers. Despite the fact that in the normal model macroinvertebrates only produced 27% of the annual FPOM transport, their removal greatly reduced baseflow FPOM concentrations during most of the year.

Results from this modified model can be compared with results of an actual field experiment in which the macroinvertebrates were removed from a Coweeta stream by application of a pesticide (Wallace et al. 1982b). In that study, FPOM concentrations in the treated stream were reduced to as low as 0.03 mg/L, and annual baseflow transport was estimated to be ≈25% of transport in a reference stream. This effect is greater than that predicted by the model, but there is a large difference in stream size, since the treated stream was only 135 m long. When I modified the model to simulate a 135-m stream (Fig. 13), macroinvertebrates accounted for 35% of total annual FPOM transport and nearly all the transport at baseflow (Fig. 13). When macroinvertebrates were removed from the model, annual FPOM transport was reduced by 35% since entrainment was never limited by availability.

Macroinvertebrate removal from the 135-m stream model reduced baseflow concentrations to very low levels similar to those observed in Wallace et al.'s (1982b) experimental study.

Increased macroinvertebrate ingestion.—Because the macroinvertebrate standing crops used in the model were based on measurements made with a fairly large mesh sampler (≈0.45-mm opening) and not picked under a binocular microscope, it is likely that they are underestimates (Haefner and Wallace 1981b). Also there is certainly latitude in published ingestion rates to warrant use of a rate much higher than the rate used in the normal model. Doubling either the ingestion rate or the macroinvertebrate standing crops produced an 8% increase in FPOM transport, a 19% decrease in benthic CPOM, and a 20% decrease in benthic FPOM. Ecosystem efficiency decreased from 43 to 40%, and turnover length increased from 2000 to 2350 m. Baseflow FPOM concentrations were increased primarily in summer (Fig. 12: bottom panel).

Modification of temperature control of macroinvertebrate ingestion.—I tried two modifications of the parameters through which temperature affected macroinvertebrate ingestion rate: (1) increasing the slope of the curve relating ingestion rate to temperature (Eq. 13) from 0.03 to 0.04, closer to the range of slopes found by Short and Ward (1981a), and (2) using a Q_{10} function with a Q_{10} of 2 and a mean ingestion rate of 0.17 mg·mg⁻¹·d⁻¹ at 12.9°C. Neither modification changed the simulations significantly. Annual FPOM transport was changed <1%. Increasing the temperature effect slightly decreased winter baseflow FPOM concentrations and increased summer concentrations (Fig. 12: middle panel). The Q_{10} function, which re-

duced the temperature effect, produced just the opposite result. The results of the first modification fit the field data slightly better than the normal model.

Modification of model structure.—One of the more critical assumptions made in model construction was the direction of arrows in Fig. 1. I assumed that microbial processing of CPOM resulted in benthic FPOM but that macroinvertebrate production of FPOM was injected directly into the water column. To evaluate the effect of this assumption, I modified the model so that macroinvertebrate egestion (including collector-filterer egestion) was directed into the benthic FPOM compartment. As a result of these changes, annual averages and totals were not greatly affected. CPOM dynamics were unaffected. Benthic FPOM was increased from 42.6 to 62.8 g/m², and annual FPOM transport was somewhat decreased, from 1330 to 1220 kg/yr. Ecosystem efficiency increased from 43 to 46%, and turnover length decreased from 2.0 to 1.7 km. However, baseflow FPOM concentrations were much less than the normal model, particularly during summer and fall (Fig. 12: upper panel). Concentrations were also usually less than for the modification with no macroinvertebrates (Fig. 12: bottom panel) because of the removal from transport by collector-filterers.

FIG. 13. Simulated FPOM concentrations and transport 135 m from the stream source. Upper lines represent total transport or concentration, shaded areas represent FPOM due to physical entrainment, and unshaded areas represent macroinvertebrate-produced FPOM. Only baseflow concentration and transport are shown.

Results of this modification were not as compatible with field data as were results of the normal model.

CONCLUSIONS

Based on the calculation of an annual budget, the role of macroinvertebrates in Big Hurricane Branch was not large. They were responsible for 27% of the annual FPOM transport, but if they were eliminated, there was only a 10% reduction in annual FPOM transport because of a compensatory increase in storm transport. Shredders were responsible for only 12% of the breakdown of benthic CPOM, and collector-gatherers had an even smaller role in FPOM processing. However, these figures may conceal the real importance of macroinvertebrates because of the large fraction of FPOM transport that occurred during storms. The significance of transported FPOM is in its potential use as an energy source by organisms in downstream ecosystems. FPOM transported during storms has little chance of being filtered out or deposited immediately downstream (Wallace et al. 1982b), and baseflow transport is much more important to organisms in the mid-order reaches of the stream system. With this in mind, macroinvertebrates in low-order streams have a significant role because they stabilize the temporal pattern of FPOM transport (Wallace et al. 1982b). If macroinvertebrates are removed, a much larger fraction of the annual transport occurs during
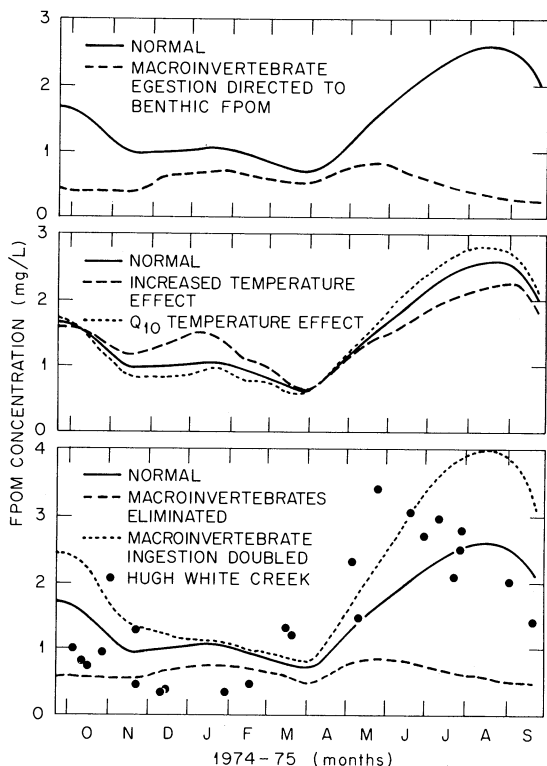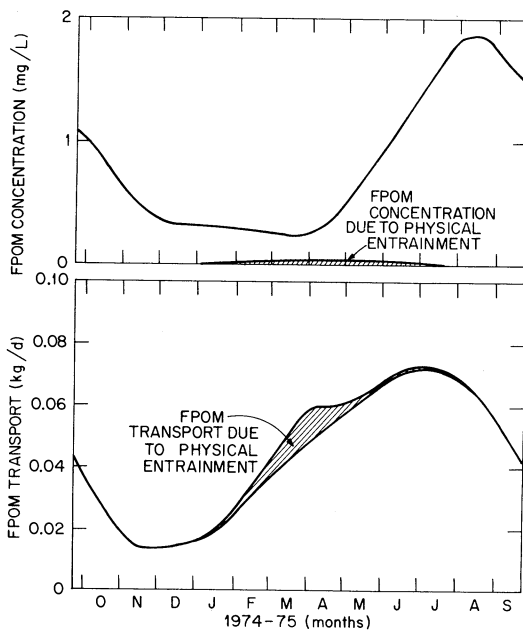

FIG. 12. FPOM concentrations resulting from model modifications. Only baseflow concentrations are shown. Data points in the bottom panel are the same as those in Fig. 8.

storms. As shown in Fig. 12 (bottom panel), elimination of macroinvertebrates greatly decreased baseflow transport, but annual transport was reduced only 10% because of a concomitant increase in stormflow transport.

The importance of macroinvertebrates increases upstream. In the first several hundred metres of stream, nearly all baseflow transport can be attributed to detritivorous macroinvertebrates (Fig. 13). However, as flow increases downstream, physical entrainment becomes more important. Also, because depth increases downstream, the ratio of benthic surface area to stream volume decreases, and macroinvertebrate FPOM production, which occurs on a surface area basis, decreases in importance.

Based on the simulations presented here, macroinvertebrates appear to decrease the efficiency of stream ecosystems. They increase the downstream loss of FPOM so that less is used (i.e., respired) within the system. However, Wallace et al. (1982b) pointed out that this may not be the case when viewed on a longer time scale. Without macroinvertebrates there may be a long-term accumulation of POM within a stream. During infrequent large storms (perhaps those with recurrence interval >10 yr), large amounts of this material may be flushed out so that on a long-term basis streams without macroinvertebrates have a lower efficiency. Bormann et al. (1969) observed the effects of a large storm on a small stream at Hubbard Brook, where macroinvertebrates do not appear to have a significant role (Fisher and Likens 1973). The 12-h storm accounted for 54% of that year's transport. POM transport in the year when the storm occurred was almost five times that of the previous year.

This sort of annual variation in POM transport could not occur in Big Hurricane Branch. A storm with a recurrence interval of 100 yr occurred in May 1976. If that storm had occurred in May 1975 and had removed all benthic POM from the bankful channel, annual transport, based on the model, would have been only ≈2.2 times the normal value. Benthic samples taken in 1976 suggest some decrease in CPOM standing crops but certainly not complete removal. A major storm would have its maximum effect if it occurred during leaf fall (as was the case at Hubbard Brook in 1966) when the CPOM standing crop is greatest. In this case, there would be only a 2.7-fold increase in annual transport from Big Hurricane Branch, again assuming complete removal of benthic POM.

The difference in the effect of major storms on Coweeta and Hubbard Brook streams is largely due to the difference in standing crops of benthic POM. Meyer and Likens (1979) estimated the average CPOM standing crop in Bear Brook as 700 g/m² (not including branches) in midsummer, much greater than simulated or measured standing crops in Big Hurricane Branch at that time of year (Fig. 5). I suggest that detritivorous macroinvertebrates are a major factor contributing to this difference. In Big Hurricane Branch and other low-order streams in the southern Appalachian region, macroinvertebrates accelerate the turnover of POM so that by the end of summer there is almost none left in the stream. In contrast, studies from Hubbard Brook (Fisher and Likens 1973, Meyer and Likens 1979) suggest a large accumulation of detritus, largely in debris dams, so that the stream is quite susceptible to major storms.

Vannote et al. (1980) discussed the linkages between upstream and downstream areas. They suggested that downstream communities are structured to capitalize on upstream inefficiencies. Results of this study show that because of their influence on the quantity and timing of FPOM transport, macroinvertebrates are an important component of the longitudinal linkage.

The results of this study are based on one particular conceptualization of the role of benthic macroinvertebrates in streams. In this conceptualization, their major role is conversion of benthic POM into transported POM. Evolution of this model and development of other stream models will certainly involve modification of this role. A particularly valuable approach might be to expand the particle size distribution from two to possibly the six sizes treated by Boling et al. (1975) and to consider more fully the role of macroinvertebrates in the transformation of particle sizes. This treatment would probably require a trade-off in the precision with which temporal and spatial changes are treated. I chose to emphasize changes occurring on a daily basis and over fairly short stream reaches, but this was at the expense of a very limited compartmentalization of POM. It also necessitated a limited treatment of macroinvertebrate functional groups.

Another aspect of the role of invertebrates involves the non-insect fauna of which I considered only crayfish. Fenchel and Harrison (1975), Fenchel (1977), and Lopez et al. (1977) reviewed the evidence, which is primarily from marine studies, that bacterial grazers significantly affect decomposition rates. There is growing evidence that small, non-insect invertebrates such as copepods and oligochaetes are abundant in Coweeta streams and that they may have a significant role in the energy dynamics of these ecosystems (Gurtz 1981, Haefner and Wallace 1981b, O'Hop and Wallace, *in press*; T. F. Cuffney, J. B. Wallace, and J. R. Webster, *personal observation*). When the functions of these organisms become better known, the role of invertebrates in streams will probably be more significant than I have estimated in this study.

Hall, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53:585–604.

Hart, S. D., and R. P. Howmiller. 1975. Studies on the decomposition of allochthonous detritus in two southern California streams. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 19:1665–1674.

Heal, O. W., and S. F. MacLean, Jr. 1975. Comparative productivity in ecosystems—secondary productivity. Pages 89–108 in W. H. van Dobben and R. H. Lowe-McConnell, editors. Unifying concepts in ecology. W. Junk, The Hague, The Netherlands.

Hobbie, J. E., and G. E. Likens. 1973. Output of phosphorus, dissolved organic matter and fine particulate carbon from Hubbard Brook watersheds. Limnology and Oceanography 18:734–742.

Iverson, T. M. 1975. Disappearance of autumn shed beech leaves placed in bags in small streams. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 19:1687–1692.

———. 1979. Laboratory energetics and growth of Sericostoma personatum (Trichoptera). Holarctic Ecology 1:1–5.

Kirby, J. M., J. R. Webster, and E. F. Benfield. 1983. The role of shredders in detrital dynamics of permanent and temporary streams. Pages 425–435 in T. D. Fontaine III and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Press, Ann Arbor, Michigan, USA.

Lawton, J. H. 1971. Maximum and actual field feeding rates in larvae of the damselfly Pyrrhosoma nymphyla (Sulzer). Freshwater Biology 1:99–111.

Leopold, A. 1941. Lakes in relation to terrestrial life patterns. Pages 17–22 in A Symposium on hydrobiology. University of Wisconsin Press, Madison, Wisconsin, USA.

Leopold, L. B., and T. Maddock, Jr. 1953. The hydraulic geometry of stream channels and some physiographic implications. Professional Paper No. 252, United States Geologic Survey, Washington, D.C., USA.

Leopold, L. B., M. G. Wolman, and J. P. Miller. 1964. Fluvial processes in geomorphology. W. H. Freeman, San Francisco, California, USA.

Lopez, G. R., J. S. Levinton, and L. B. Slobodkin. 1977. The effect of grazing by the detritivore Orchestia grillus on Spartina litter and its associated microbial community. Oecologia (Berlin) 30:111–127.

Maciolek, J. A., and M. G. Tunzi. 1968. Microseston dynamics in a simple Sierra Nevada lake-stream system. Ecology 49:60–75.

Mackay, R. J., and J. Kalff. 1973. Ecology of two related species of caddisfly larvae in the organic substrate of a woodland stream. Ecology 54:499–511.

Malmqvist, B., L. M. Nilsson, and B. S. Svensson. 1978. Dynamics of detritus in a small stream in southern Sweden and its influence on the distribution of the bottom animal community. Oikos 31:3–16.

McCullough, D. A., G. W. Minshall, and C. E. Cushing. 1979a. Bioenergetics of a stream "collector" organism, Tricorythodes minutus (Insecta, Ephemeroptera). Limnology and Oceanography 24:45–48.

McCullough, D. A., G. W. Minshall, and C. E. Cushing. 1979b. Bioenergetics of lotic filter-feeding insects Simulium spp. (Diptera) and Hydropsyche occidentalis (Trichoptera) and their function in controlling organic transport in streams. Ecology 60:585–596.

McDiffett, W. F. 1970. The transformation of energy by a stream detritivore Pteronarcys scotti (Plecoptera). Ecology 51:975–988.

McDowell, W. H., and S. G. Fisher. 1976. Autumnal processing of dissolved organic matter in a small woodland stream ecosystem. Ecology 57:561–569.

McIntire, C. D., and J. A. Colby. 1978. A hierarchical model of lotic ecosystems. Ecological Monographs 48:167–190.

Merritt, R. W., and K. W. Cummins, editors. 1978. An introduction to the aquatic insects of North America. Kendell-Hunt, Dubuque, Iowa, USA.

Meyer, J. L., and G. E. Likens. 1979. Transport and transformation of phosphorus in a forest stream ecosystem. Ecology 60:1255–1269.

Minshall, G. W. 1967. Role of allochthonous detritus in a trophic structure of a woodland springbrook community. Ecology 48:139–149.

Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing, and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. Ecological Monographs 53:1–25.

Momot, W. T., H. Gowing, and P. D. Jones. 1978. The dynamics of crayfish and their role in ecosystems. American Midland Naturalist 99:10–35.

Morisawa, M. 1968. Streams, their dynamics and morphology. McGraw-Hill, New York, New York, USA.

Mulholland, P. J. 1981. Organic carbon flow in a swamp-stream ecosystem. Ecological Monographs 51:307–322.

Naiman, R. J., and J. R. Sedell. 1979a. Characterization of particulate organic matter transported by some Cascade mountain streams. Journal of the Fisheries Research Board of Canada 36:17–31.

Naiman, R. J., and J. R. Sedell. 1979b. Benthic organic matter as a function of stream order in Oregon. Archiv für Hydrobiologie 87:404–422.

Naiman, R. J., and J. R. Sibert. 1978. Transport of nutrients and carbon from the Nanaimo River to its estuary. Limnology and Oceanography 23:1183–1193.

Nelson, D. J., and D. C. Scott. 1962. Role of detritus in the productivity of a rock outcrop community in a piedmont stream. Limnology and Oceanography 7:396–413.

Newbern, L. A., J. R. Webster, E. F. Benfield, and J. A. Kennedy. 1981. Organic matter transport in an Appalachian Mountain river in Virginia, USA. Hydrobiologia 83:73–83.

Newbold, J. D., J. W. Elwood, R. V. O'Neill, and A. L. Sheldon. 1983. Phosphorus dynamics in a woodland stream ecosystem: a study of nutrient spiralling. Ecology 64:1249–1265.

Newbold, J. D., J. W. Elwood, R. V. O'Neill, and W. Van Winkle. 1981. Measuring nutrient spiralling in streams. Canadian Journal of Fisheries and Aquatic Sciences 38:860–863.

Newbold, J. D., P. J. Mulholland, J. W. Elwood, and R. V. O'Neill. 1982a. Organic carbon spiralling in stream ecosystems. Oikos 38:266–272.

Newbold, J. D., R. V. O'Neill, J. W. Elwood, and W. Van Winkle. 1982b. Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity. American Naturalist 120:628–652.

O'Connor, D. J. 1962. The effect of stream flow on waste assimilation capacity. Proceedings of the 17th Purdue Industrial Waste Conference. Purdue University, Lafayette, Indiana, USA.

O'Hop, J., and J. B. Wallace. In press. Invertebrate drift, discharge, and sediment relations in a southern Appalachian headwater stream. Hydrobiologia.

Olson, J. S. 1963. Energy storage and the balance of producers and decomposers in ecological systems. Ecology 44:322–332.

O'Neill, R. V. 1976. Ecosystem persistence and heterotrophic regulation. Ecology 57:1244–1253.

O'Neill, R. V., J. W. Elwood, and S. G. Hildebrand. 1979a. Theoretical implications of spatial heterogeneity in stream ecosystems. Pages 79–101 in G. S. Innis and R. V. O'Neill, editors. Systems analysis of ecosystems. International Cooperative Publishing House, Fairland, Maryland, USA.

LITERATURE CITED

Anderson, N. H., and J. R. Sedell. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Annual Review of Entomology 24:351–377.

Bagnold, R. A. 1966. An approach to the sediment transport problem of general physics. Professional Paper No. 422-1, United States Geologic Survey, Washington, D.C., USA.

Barnes, B. S. 1939. The structure of discharge-recession curves. Transactions of the American Geophysical Union 20:721–725.

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.

Bilby, R. E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. Ecology 62:1234–1243.

Bilby, R. E., and G. E. Likens. 1979. Effect of hydrologic fluctuations on the transport of fine particulate organic carbon in a small stream. Limnology and Oceanography 24:69–75.

Bilby, R. E., and G. E. Likens. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61:1107–1113.

Boling, R. H., Jr., E. D. Goodman, J. A. Van Sickle, J. O. Zimmer, K. W. Cummins, S. R. Reice, and R. C. Peterson. 1975. Toward a model of detritus processing in a woodland stream. Ecology 56:141–151.

Bormann, F. H., G. E. Likens, and J. S. Eaton. 1969. Biotic regulation of particulate and solution losses from a forest ecosystem. BioScience 19:600–611.

Chester, C. R. 1971. Techniques in partial differential equations. McGraw-Hill, New York, New York, USA.

Chow, V. T. 1959. Open channel hydraulics. McGraw-Hill, New York, New York, USA.

Comiskey, C. E. 1978. Aspects of the organic carbon cycle on Walker Branch Watershed: a study of land/water interaction. Dissertation. University of Tennessee, Knoxville, Tennessee, USA.

Cudney, M. D., and J. B. Wallace. 1980. Life cycles, microdistribution and production dynamics of six species of net-spinning caddisflies in a large southeastern (USA) river. Holarctic Ecology 3:165–182.

Cummins, K. W. 1969. Energy budgets. Pages 30–37 in The stream ecosystem. Technical Report No. 7, Institute of Water Research, Michigan State University, East Lansing, Michigan, USA.

———. 1971. Predicting variations in energy flow through a semi-controlled lotic ecosystem. Technical Report No. 19, Institute of Water Research, Michigan State University, East Lansing, Michigan, USA.

———. 1973. Trophic relations of aquatic insects. Annual Review of Entomology 18:183–206.

Cummins, K. W., M. J. Klug, G. M. Ward, G. L. Spengler, R. W. Speaker, R. W. Ovink, D. C. Mahan, and R. C. Petersen. 1981. Trends in particulate organic matter fluxes, community processes and macroinvertebrate functional groups along a Great Lakes drainage basin river continuum. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 21:841–849.

Cummins, K. W., R. C. Petersen, F. O. Howard, J. C. Wuycheck, and V. I. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54:336–345.

Dobbins, W. E. 1964. BOD and oxygen relationships in streams. American Society of Civil Engineering Journal Sanitary Engineering Division 70:53–78.

Dunne, T., and L. B. Leopold. 1978. Water in environmental planning. W. H. Freeman, San Francisco, California, USA.

Edington, J. M., and A. H. Hildrew. 1973. Experimental observations relating to the distribution of net-spinning Trichoptera in streams. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 18:1549–1558.

Elwood, J. W., J. D. Newbold, R. V. O'Neill, and W. Van Winkle. 1983. Resource spiralling: an operational paradigm for analyzing lotic ecosystems. Pages 3–27 in T. D. Fontaine III and S. M. Bartell, editors. Dynamics of lotic ecosystems. Ann Arbor Press, Ann Arbor, Michigan, USA.

Fenchell, T. 1977. The significance of bactivorous protozoa in the microbial community of detrital particles. Pages 529–544 in J. Cairns, Jr., editor. Aquatic microbial communities. Garland, New York, New York, USA.

Fenchell, T., and P. Harrison. 1975. The significance of bacterial grazing and mineral cycling for the decomposition of particulate detritus. Pages 285–299 in J. M. Anderson and A. Macfadyen, editors. The role of terrestrial and aquatic organisms in decomposition processes. Blackwell, Oxford, England.

Fisher, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, USA. Internationale Revue der Gesamten Hydrobiologie 62:701–727.

Fisher, S. G., and G. E. Likens. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.

Georgian, T. J., Jr., and J. B. Wallace. 1981. A model of seston capture by net-spinning caddisflies. Oikos 36:147–157.

Golladay, S. W., J. R. Webster, and E. F. Benfield. 1983. Factors affecting food utilization by a leaf shredding aquatic insect: leaf species and conditioning time. Holarctic Ecology 6:157–162.

Grafius, E., and N. H. Anderson. 1979. Population dynamics, bioenergetics, and the role of Lepidostoma quercina Ross (Trichoptera: Lepidostomatidae) in an Oregon woodland stream. Ecology 60:433–441.

Gurtz, M. E. 1981. Ecology of stream invertebrates in a forested and a commercially clearcut watershed. Dissertation. University of Georgia, Athens, Georgia, USA.

Gurtz, M. E., J. R. Webster, and J. B. Wallace. 1980. Seston dynamics in southern Appalachian streams: effects of clear-cutting. Canadian Journal of Fisheries and Aquatic Sciences 37:624–631.

Haefner, J. D., and J. B. Wallace. 1981a. Production and potential seston utilization by Parapsyche cardis and Diplectrona modesta (Trichoptera: Hydropsychidae) in the two streams draining contrasting southern Appalachian watersheds. Environmental Entomology 10:433–441.

Haefner, J. D., and J. B. Wallace. 1981b. Shifts in aquatic insect populations in a first-order southern Appalachian stream following a decade of old field succession. Canadian Journal of Fisheries and Aquatic Sciences 38:353–359.

Hains, J. J. 1981. The response of stream flora to watershed perturbations. Thesis. Clemson University, Clemson, South Carolina, USA.

O'Neill, R. V., W. R. Emanuel, J. D. Newbold, and J. W. Elwood. 1979b. Simulation in the service of environmental research: experience with a stream ecosystem project. Pages 401–405 *in* Proceedings of the 1979 Summer Computer Simulation Conference. Society for Computer Simulation, La Jolla, California, USA.

O'Neill, R. V., W. F. Harris, B. S. Ausmus, and D. E. Reichle. 1975. A theoretical basis for ecosystem analysis with particular reference to elemental cycling. Pages 28–40 *in* F. G. Howell, J. B. Gentry, and M. H. Smith, editors. Mineral cycling in southeastern ecosystems. Energy Research and Development Administration Symposium Series (CONF-740513), Washington, D.C., USA.

Oswood, M. W. 1979. Abundance patterns of filter-feeding caddisflies (Trichoptera: Hydropsychidae) and seston in a Montana (USA) lake outlet. Hydrobiologia 63:177–183.

Otto, C. 1974. Growth and energetics in a larval population of *Potamophylas cingulatus* (Steph.) (Trichoptera) in a south Swedish stream. Journal of Animal Ecology 43:339–361.

Paul, R. W., Jr., E. F. Benfield, and J. Cairns, Jr. 1978. Effects of thermal discharge on leaf decomposition in a river ecosystem. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 20:1759–1766.

Petersen, R. C., and K. W. Cummins. 1974. Leaf processing in a woodland stream. Freshwater Biology 4:343–368.

Sedell, J. R., R. J. Naiman, K. W. Cummins, G. W. Minshall, and R. L. Vannote. 1978. Transport of particulate organic material in streams as a function of physical processes. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 20:1366–1375.

Sedell, J. R., F. J. Triska, and N. S. Triska. 1975. The processing of conifer and hardwood leaves in two conifer forest streams: I. Weight loss and associated invertebrates. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 19:1617–1627.

Short, R. A., S. P. Canton, and J. V. Ward. 1980. Detrital processing and associated macroinvertebrates in a Colorado mountain stream. Ecology 61:727–732.

Short, R. A., and P. E. Maslin. 1977. Processing of leaf litter by a stream detritivore: effect on nutrient availability to collectors. Ecology 58:935–938.

Short, R. A., and J. V. Ward. 1981a. Trophic ecology of three winter stoneflies (Plecoptera). American Midland Naturalist 105:341–347.

Short, R. A., and J. V. Ward. 1981b. Benthic detrius dynamics in a mountain stream. Holarctic Ecology 4:32–35.

Streeter, H. W., and E. B. Phelps. 1925. A study of the pollution and natural purification of the Ohio River. Bulletin No. 146, United States Public Health Service, Washington, D.C., USA.

Suberkropp, K., and M. J. Klug. 1980. The maceration of deciduous leaf litter by aquatic hyphomycetes. Canadian Journal of Botany 58:1025–1031.

Suberkropp, K., M. J. Klug, and K. W. Cummins. 1975. Community processing of leaf litter in a woodland stream. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 19:1653–1658.

Swank, W. T., and J. E. Douglass. 1977. Nutrient budgets for undisturbed and manipulated hardwood forest ecosystems in the mountains of North Carolina. Pages 343–362 *in* D. L. Correll, editor. Watershed research in eastern North America. Smithsonian Institution Press, Washington, D.C., USA.

Sweeney, B. W., and R. L. Vannote. 1981. *Ephemerella* mayflies of White Clay Creek: bioenergetic and ecological relationships among six coexisting species. Ecology 62:1353–1369.

Thomann, R. V. 1972. Systems analysis and water quality management. McGraw-Hill, New York, New York, USA.

Trama, F. B. 1957. The transformation of energy by an aquatic herbivore *Stenonema pulchellum* (Ephemeroptera). Dissertation. University of Michigan, Ann Arbor, Michigan, USA.

Vannote, R. C. 1969. Detrital consumers in natural systems. Pages 20–23 *in* The stream ecosystem. Technical Report No. 7, Institute of Water Research, Michigan State University, East Lansing, Michigan, USA.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

Wallace, J. B., D. H. Ross, and J. L. Meyer. 1982a. Seston and dissolved organic carbon dynamics in a southern Appalachian stream. Ecology 63:824–838.

Wallace, J. B., J. R. Webster, and T. F. Cuffney. 1982b. Stream detritus dynamics: regulation by invertebrate consumers. Oecologia (Berlin) 53:197–200.

Wallace, J. B., W. R. Woodall, Jr., and F. F. Sherberger. 1970. Breakdown of leaves by feeding of *Peltoperla maria* nymphs. Annals of the Entomological Society of America 63:562–567.

Waters, T. F. 1977. Secondary production in inland waters. Advances in Ecological Research 10:91–164.

Webster, J. R. 1977. Large particulate organic matter processing in stream ecosystems. Pages 505–526 *in* D. L. Correll, editor. Watershed research in eastern North America. Smithsonian Institution Press, Washington, D.C., USA.

Webster, J. R., E. F. Benfield, and J. Cairns, Jr. 1979. Model predictions of effects of impoundment on particulate organic matter transport in a river system. Pages 339–358 *in* J. V. Ward and J. A. Stanford, editors. The ecology of regulated streams. Plenum Press, New York, New York, USA.

Webster, J. R., and S. W. Golladay. *In press.* Seston transport in streams at Coweeta Hydrologic Laboratory, North Carolina, USA. Internationale Vereinigung für Theoretische und Angewandte Limnologie, Verhandlungen 22.

Webster, J. R., M. E. Gurtz, J. J. Hains, J. L. Meyer, W. T. Swank, J. B. Waide, and J. B. Wallace. *In press.* Stability of stream ecosystems. *In* J. R. Barnes and G. W. Minshall, editors. Testing general ecological theories in stream ecosystems. Plenum Press, New York, New York, USA.

Webster, J. R., and B. C. Patten. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecological Monographs 49:51–72.

Webster, J. R., and J. B. Waide. 1982. Effects of forest clearcutting on leaf breakdown in a southern Appalachian stream. Freshwater Biology 12:331–344.

Webster, J. R., J. B. Waide, and B. C. Patten. 1975. Nutrient cycling and the stability of ecosystems. Pages 1–27 *in* F. G. Howell, J. B. Gentry, and M. H. Smith, editors. Mineral cycling in southeastern ecosystems. Energy Research and Development Administration Symposium Series (CONF-740513), Washington, D.C., USA.

Winterbourn, M. J., and S. F. Davis. 1976. Ecological role of *Zelandopsyche ingens* (Trichoptera: Oeconesidae) in a beech forest stream ecosystem. Australian Journal of Marine and Freshwater Research 27:197–215.

Woodall, W. R., Jr. 1971. A comparison of aquatic insects in four different watersheds. Thesis. University of Georgia, Athens, Georgia, USA.

Woodall, W. R., Jr., and J. B. Wallace. 1972. The benthic fauna in four small southern Appalachian streams. American Midland Naturalist 88:393–407.

Wotton, R. S. 1978. Growth, respiration, and assimilation of blackfly larvae (Diptera: Simuliidae) in a lake-outlet in Finland. Oecologia (Berlin) 33:279–290.

Yalin, M. S. 1977. Mechanics of sediment transport. Pergamon, Oxford, England.

Young, S. A., W. P. Kovalak, and K. A. Del Signore. 1978. Distances travelled by autumn-shed leaves introduced into

a woodland stream. American Midland Naturalist **100**:217–222.

APPENDIX

Symbols used in the paper

G gradient (m/m)

x stream distance measured from the headwaters (m)

W bankfull stream width (m)

Q discharge (units vary)

T temperature (°C)

t time (units vary)

LF leaf fall ($g \cdot m^{-2} \cdot d^{-1}$)

BI blow-in ($g \cdot m^{-1} \cdot d^{-1}$)

S_F suspended FPOM concentration (mg/L)

S_C suspended CPOM concentration (mg/L)

B_F benthic FPOM standing crop (g/m²)

B_C benthic CPOM standing crop (g/m²)

S_{Fmax} maximum S_F for specified flow and gradient

E_F rate of FPOM entrainment (d^{-1})

S_{Cmax} maximum S_C for specified flow and gradient

E_C rate of CPOM entrainment (d^{-1})

I insect ingestion rate ($mg \cdot mg^{-1} \cdot d^{-1}$)

M_1 insect shredder standing crop (g/m²)

M_2 crayfish standing crop (g/m²)

M_3 collector-gatherer standing crop (g/m²)

M_4 collector-filterer standing crop (g/m²)

A assimilation efficiency

D stream depth (m)

V stream velocity (m/s)

F_1 litter fall and blow-in ($g \cdot m^{-2} \cdot d^{-1}$)

F_2 entrainment of CPOM ($mg \cdot L^{-1} \cdot d^{-1}$)

F_3 entrainment of FPOM ($mg \cdot L^{-1} \cdot d^{-1}$)

F_4 deposition of CPOM ($mg \cdot L^{-1} \cdot d^{-1}$)

F_5 deposition of FPOM ($mg \cdot L^{-1} \cdot d^{-1}$)

F_6 microbial breakdown and leaching of CPOM ($g \cdot m^{-2} \cdot d^{-1}$)

F_7 microbial shredding of CPOM ($g \cdot m^{-2} \cdot d^{-1}$)

F_8 microbial assimilation and leaching of FPOM ($g \cdot m^{-2} \cdot d^{-1}$)

F_9 shredder ingestion ($g \cdot m^{-2} \cdot d^{-1}$)

F_{10} shredder egestion ($g \cdot m^{-2} \cdot d^{-1}$)

F_{11} collector-gatherer ingestion ($g \cdot m^{-2} \cdot d^{-1}$)

F_{12} collector-gatherer egestion ($g \cdot m^{-2} \cdot d^{-1}$)

F_{13} collector-filterer ingestion ($g \cdot m^{-2} \cdot d^{-1}$)

F_{14} collector-filterer egestion ($g \cdot m^{-2} \cdot d^{-1}$)

S_{FT} average tributary and groundwater FPOM concentration (mg/L)

S_{CT} average tributary and groundwater CPOM concentration (mg/L)