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Freshwater Invertebrate Biology, Vol. 3, No. 4. (Nov., 1984), pp. 153-171.

Stable URL:
http://links.jstor.org/sici?sici=0738-2189%28198411%293%3A4%3C153%3APMOAHS%3E2.0.CO%3B2-L

Freshwater Invertebrate Biology is currently published by The North American Benthological Society.

FRESHWATER INVERTEBRATE BIOLOGY

VOLUME 3, NUMBER 4, NOVEMBER 1984

Pesticide Manipulation of a Headwater Stream: Invertebrate Responses and Their Significance for Ecosystem Processes[1]

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Abstract. The influence of macroinvertebrates on detrital processing was evaluated by excluding them from one of two small southern Appalachian streams. Exclusion in the treated stream was accomplished by periodic applications of 10 ppm of the insecticide methoxychlor. This caused massive invertebrate drift (>12,000 organisms/m^3 of discharge) during the initial treatment and reduced aquatic insect densities and biomass to <10% of the levels within the adjacent untreated reference stream. Community structure in the treated stream shifted from a system dominated by small numbers of large shredding insects (e.g., *Peltoperla, Pycnopsyche, Tipula*) with comparatively low reproductive rates, to one dominated by large numbers of small collector-gatherers and predators (e.g., Oligochaeta, Chironomidae, Turbellaria) with high reproductive rates. Non-insect invertebrate biomass and density became significantly higher in the treated stream than in the reference stream following initial methoxychlor treatment. We interpreted this response as a consequence of increased survivorship and growth of non-insect taxa associated with both insect predator removal and a potential increase in the food quality of fine particulate organic matter (FPOM). Total invertebrate density in the treated stream increased to that of the reference stream 117 days after the initial treatment, but total invertebrate biomass in the treated stream remained significantly lower throughout the study. Counts of fungal hyphae, respiration rates of conditioned leaf discs, and ATP content of coarse particulate organic matter (CPOM) were not affected by methoxychlor. However, ATP levels of FPOM were significantly higher in the treated stream than in the reference stream. Methoxychlor treatment reduced the concentration, the amount exported, and the median particle size of transported particulate organic matter (TPOM). Our study indicates that insects in forested headwater streams play a major role in both the generation and subsequent transport of FPOM to downstream reaches. Biological processes in headwater streams, where there

[1]We thank Drs. J. Douglass, W. Swank, J.W. Elwood, and T. Georgian for their invaluable assistance with numerous aspects of this work. A. Lingle, M. Freeman, J. Haefner, and S. Golladay assisted with the field and laboratory work. This work was supported, in part, by a sub-contract to J.B. Wallace, provided by a National Sciences Foundation grant to the Oak Ridge National Laboratory.

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is high physical retention of CPOM, produce and entrain small particles, whereas communities in downstream areas have evolved toward exploitation of these entrained particles.

Communities of small headwater streams of forested regions are based on allochthonous detritus and the streams retain most of their large seasonal input of coarse particulate organic matter (CPOM) (e.g., Fisher & Likens 1973; Otto 1975; Webster & Patten 1979) and export fine particulate (FPOM) and dissolved organic matter (DOM) (Naiman & Sedell 1979a; Webster & Patten 1979, Wallace, et al. 1982a). Feeding and behavioral activities of macroinvertebrates on CPOM (e.g., shredding, Cummins 1973) are thought to greatly enhance the rate of CPOM conversion to FPOM and DOM as well as aid in suspension and export of this material. The exported material becomes an important source of energy and nutrients for downstream deposit and filter-feeding organisms (Short & Maslin 1977; Anderson & Sedell 1979; Wallace & Merritt 1980). This downstream linkage of benthic communities has formed a basis for such theoretical considerations as the River Continuum Concept (Vannote, et al. 1980) and nutrient spiralling (Webster & Patten 1979; Newbold, et al. 1982).

Indirect evidence, such as low assimilation efficiencies, high ingestion rates, and comminution activities typically associated with shredding insects (McDiffett 1970; Golladay, et al. 1982), has been used to suggest that shredders can generate considerable quantities of FPOM and DOM from CPOM. However, little direct evidence has been offered to substantiate the existence, magnitude, and importance of the macroinvertebrate mediated CPOM-FPOM conversion process in streams, and alternative explanations of FPOM generation have appeared (Winterbourn, et al. 1981).

The effects of invertebrate removal on stream processes were previously outlined by Wallace et al. (1982b). The present paper concentrates on: 1) illustrating biological differences between methoxychlor treated and untreated streams, 2) detailing the relationships between leaf litter breakdown and the macroinvertebrate community, 3) characterizing drift patterns in the two streams, 4) changes in seston particle sizes, and 5) implications of our results on current interpretations of lotic ecosystem structure and function.

The Study Site. - The study was conducted at the U.S. Forest Service Coweeta Hydrologic Laboratory (CHL), Macon County, North Carolina, USA. Mean annual air temperature is 12.8°C, and precipitation averages about 203 cm/year. However, during our study, rainfall from 1 May 1980 to 30 April 1981 was only 65% (132.5 cm) of normal. This represents the second lowest annual rainfall of the 46-year record at Coweeta (W. Swank, pers. comm.).

Chemistry of the Coweeta Basin streams was summarized by Swank and Douglass (1975). Concentrations of most ions are usually low (<1 mg/liter). Nitrate concentrations in undisturbed watersheds average about 0.003 mg/liter, phosphate about 0.001-0.002 mg/liter, and pH is about 6.6 to 6.8.

The two streams selected for study drain adjacent mixed hardwood forest watersheds (Fig. 1) and are heavily shaded by canopy trees and riparian rhododendron. Physical characteristics of the two streams are very similar (Table 1). Monthly mean stream temperatures during the study period ranged from 6-17°C. Stream substrate consisted of outcrops of bedrock or cobble and boulders intermixed with organic debris accumulations often supported by woody litter. Each stream was equipped with a flume for continuous flow measurements. Prior to the severe summer-winter drought of 1980, base flow of each stream ranged from 1 to 2.5 liters/s. This was reduced to 0.03-0.17 liters/s during the drought period. Both streams discharge into a large fourth order-stream (Shope Fork) capable of diluting pesticide concentrations 100×.

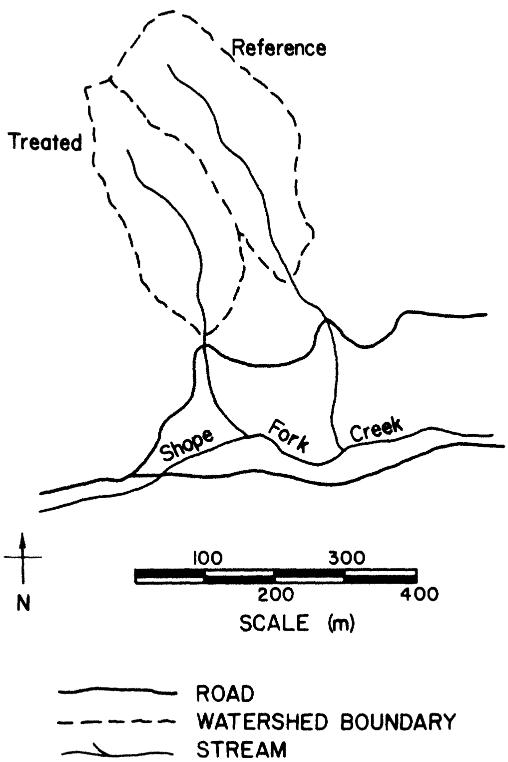

Fig. 1. Locations of the treated and reference streams and watersheds at Coweeta Hydrologic Laboratory, North Carolina, USA.

MATERIALS AND METHODS

Methoxychlor Application. - Prior to treatment, selected macroinvertebrates from Coweeta streams were exposed to various concentrations of methoxychlor [1,1,1-trichloro-2,2 bis (para methoxyphenyl) ethane] for 5-10 h in flow-through troughs. These pretreatment bioassays indicated that a dosage of 10 ppm methoxychlor killed most macroinvertebrates tested and this dosage was selected for the exclusion experiment. This dosage also insured that methoxychlor concentration would be well below lethal levels in Shope Fork.

Treatment was begun on 16 February 1980 when a 24% emulsifiable concentrate of methoxychlor was diluted and released at a rate, based on discharge at the flume, sufficient to yield a concentration of 10 ppm. This was accomplished by using both a stationary reservoir system near the headwaters that delivered a continuous 10 h metered release and a simultaneous 5 h, hand-sprayer release in leaf packs, stream margins, seeps, backwater areas, debris accunulations, and areas upstream to the source. Unfiltered stream water was collected at the discharge flume and methoxychlor concentrations determined using gas chromatography (Watt 1980). Supplementary 10 ppm (2-3 h) handsprayer releases were conducted on 10 May, 20 August, and 8 November 1980.

Animal Drift. - Prior to and following application of methoxychlor, animal drift was measured in each stream with a 230 μm mesh drift net placed at each flume to filter total stream flow. Nets were emptied hourly and samples were preserved in 5-8% formalin solution to which Phloxine B dye was added to facilitate sorting of organisms (Mason & Yevitch 1967). Animals were removed from drift samples by hand-picking samples under a dissecting microscope at 10X magnification. During the initial methoxychlor

TABLE I

Physical characteristics of the treated and reference streams.

	Treated Stream	Reference Stream
Watershed Area (ha)	5.2	4.2
Elevation (m)	829	841
Gradient (cm/m)	27	33
Wetted Channel Length (m)	135	140
Mean Wetted Channel Width (m)	0.535	0.490
Annual Accumulated Degree-days	4089	4039
% Rock Outcrop	30	20

application, drift densities in the treated stream were extremely high and a sample splitter, similar to that described by Waters (1969), was used to obtain estimates of drift. The smallest fraction sampled was 1/32 for chironomid larvae.

Leaf Bag and Benthic Invertebrates. - The invertebrates colonizing rhododendron (*Rhododendron maxima*), white oak (*Quercus alba*), red maple (*Acer rubrum*), and dogwood (*Cornus florida*) leaf litter were studied using plastic mesh bags. Fifty-one bags containing approximately 15 g dry mass of leaf material were constructed for each leaf species (i.e., a total of 204 leaf bags). Mesh sizes of the bag consisted of 85% 5 × 5 mm and 15% 1 × 3 mm mesh. These percentages are based on the surface area of the bag composed of each mesh size. Twenty-six (TS) and 25 (RS) replicates, consisting of one bag of each of the four leaf species, were placed in the streams on 16 February 1980 and collected at 8, 14, 49, 79, 117, 144, 207, 265, and 358 days (treated stream was not sampled at 8 days). All animals removed from leaf bags were preserved in 5-8% formalin, sorted, identified, and counted. Leaf material remaining in the bags was used to determine decomposition rates for each leaf species (see Wallace, et al. 1982b). Ash-free-dry-masses of representative organisms were used to determine biomass (mg AFDM) in each sample. Insects were assigned to functional groups (i.e., shredder, collector-gatherer, collector-filterer, or predator) following the classification scheme of Merritt and Cummins (1978) and our own knowledge of the fauna. Chironomids belonging to the Tanypodinae were regarded as predators, while all other chironomids, possibly including some collector-filterers such as *Rheotanytarsus*, were classified as collector-gatherers.

Surber samples (0.093 m^2, mesh = 250 μm) were collected from rock outcrop and cobble-boulder sections of each stream during April (1 outcrop, 3 cobble samples) and August (1 outcrop, 2 cobble samples). Cobble-boulder samples were collected to a depth of about 10 cm and preserved in 5-8% formalin solution dyed with Phloxine B. All samples were picked under a stereo microscope at a magnification of 10×.

Transported Particulate Organic Matter (Seston). - Particle size distributions of seston were determined using a modification of the wet-sieving technique described by Gurtz et al. (1980). Determinations of median seston particle size (i.e., particle size for which 50% of the AFDM resides in smaller sized particles) were made by linear interpolation.

Microbial Assays. - The effect of methoxychlor on respiration was evaluated in the laboratory using dogwood leaf discs (1.3 cm diameter) incubated in 15° C stream water for two weeks. Respiration rates were measured for 3 h, following equilibration, in ten Gilson respirometer flasks each containing two leaf discs. Methoxychlor was then added to five of the ten flasks to achieve a concentration of 10 ppm methoxychlor. All flasks were then allowed to re-equilibrate and respiration rates were again measured for 3 h. In addition, one-half of the unused incubated leaf discs were further conditioned for one week in a 10 ppm solution of methoxychlor. Respiration rates of these leaf discs were compared with discs similarly conditioned but not exposed to methoxychlor.

Direct microscopic counts of aquatic hypomycetes were made using red maple leaf discs collected from each stream during December 1980. Leaf discs were stained using lactophenol cotton blue and cleared with chloral hydrate (Shipton & Brown 1962). Fungi were enumerated as the mean number of hyphae intersecting reference ocular crosshairs in five random microscopic fields observed (125× magnification) on each leaf disc.

Adenosine triphosphate (ATP) content of benthic detritus in each stream was analyzed on 7 August 1980 by the luciferin-luciferase method. The ATP was extracted from benthic CPOM (i.e., pieces of leaf detritus >1 mm) using Lumac's nucleotide releasing agent (Mulholland et al., In press). Enzyme and ATP standards (Lumac) were analyzed on a Lumac M2010 photon counter.

RESULTS AND DISCUSSION

Drift: Initial Methoxychlor Treatment. - Methoxychlor was applied at a rate of 10 ppm to the treatment stream on 16 February 1980; however, concentrations of methoxychlor measured at the flume were well below (<33 ppb) this level, probably as a result of absorption by stream sediments, detritus, and microorganisms. These concentrations resulted in a dramatic increase in drift density commencing 2-3 h after initiation of treatment and peaking at 12,881 organisms/m^3 at 5-6 h (Fig. 2).

Drift density during the pesticide treatment exceeded pre-treatment levels (27-28 November 1979) by 10-10,000× (Fig. 2). Both drift density (number/m^3) and number of taxa composing the drift (number of taxa/m^3) remained significantly higher in the treated stream for as long as one week (23 February 1980) following application (Table 2), whereas neither differed significantly between the two streams prior to treatment. Increases in the number and diversity of drifting insects accounts for the differences observed in invertebrate drift during treatment periods (Table 3).

Drift patterns (e.g., time of initiation of drift and time to peak drift) were relatively uniform for most taxa with initiation into the drift occurring within 3 h and peak drift within 5-6 h of treatment (Table 4). This reflects the relationship between methoxychlor concentrations and drift density (Fig. 1) and implies that the effect of methoxychlor on the invertebrates was almost immediate. *Ectopria* and Oligochaeta were notable exceptions to this pattern since they did not peak until 22 h after treatment. Both taxa were poorly represented in the drift either because they occurred in very low abundance or were relatively resistant to methoxychlor.

About 336,000 organisms drifted out of the treated stream during the initial treatment. The taxa listed in Table 4, while representing only 50% of the taxa collected, composed almost 98% of the total number of drifting organisms. Chironomids composed 50.2%, followed by *Peltoperia* (18.0%), *Paraleptophlebia* (5.7%), *Nemoura* (4.7%), and *Leuctra* (4.4%). Biomass of drifting fauna, based on mean weights (mg AFDM) for each taxon in leaf bag samples, was estimated at 175.4 g during this period (Table 4). This represents 92% of the total biomass exported during the initial poisioning. *Peltoperla* composed 69.7% of the biomass, followed by *Paraleptophlebia* (7.2%), *Nemoura* (6.7%), and chironomids (3.6%). This represents about 29% and 131%, respectively, of the annual number and biomass of organisms estimated to drift out of a 2nd-order stream at CHL (O'Hop 1983) which has about 15 times the wetted channel area of the treated stream.

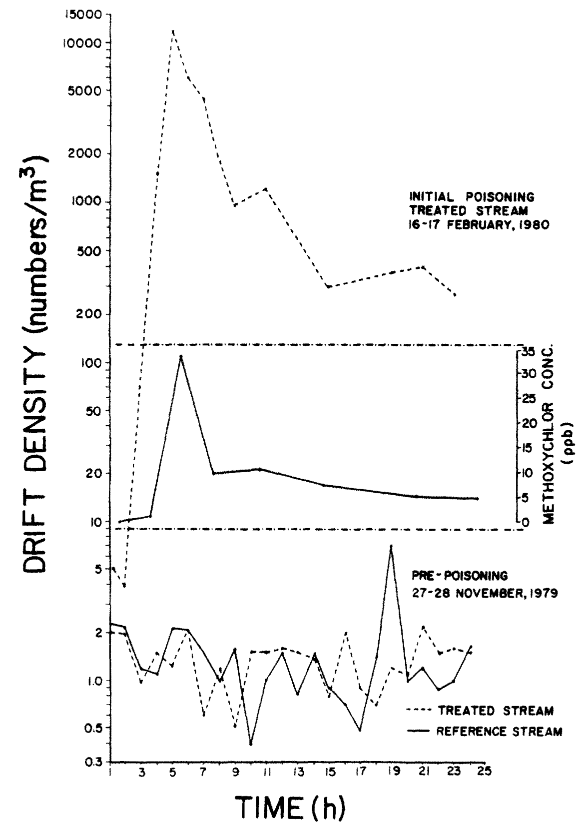

Fig. 2. Comparison of drift density before (27-28 November 1979) and during (16 February 1980) the initial poisoning of the treated stream. Methoxychlor concentrations are measurements made at the discharge flume.

TABLE II

Comparison of mean drift densities (number/m^3) and mean number of taxa drifting from the methoxychlor treated (TS) and reference (RS) streams. Data for 10 May 1980 has been divided into pre-treatment (I) and treatment (II) periods. Streams are compared using a paired t-test as outlined by Zar (1974).

Date	Mean Drift Density		Mean No. Taxa/m^3		n[1]	Elapsed Time	Total Volume Sampled (m^3)		Comments
	TS	RS	TS	RS			TS	RS	
27 Nov 1979	1.39	1.56(ns)	0.66	0.73(ns)	24	23.1	311.4	226.2	Prior to treatment
16 Feb 1980	2084.19	---	2.24	---	14	27.4	159.9	---	during 1st treatment
23 Feb 1980	51.95	3.95(*)	2.69	1.26(*)	6	12.7	56.6	34.9	7d after 1st treatment
4 Apr 1980	2.79	0.73(ns)	0.40	0.26(*)	4	7.7	117.6	83.6	between application
10 May 1980 I	6.05	4.76(ns)	1.05	1.32(ns)	3	2.8	24.2	13.7	prior to 2nd application
10 May 1980 II	1014.91	4.72(*)	2.30	1.11(*)	6	7.9	47.7	39.7	during 2nd application
11 Jun 1980	4.36	2.64(ns)	0.56	0.69(ns)	5	9.8	49.7	38.9	between application
20 Aug 1980	293.09	4.85(*)	3.24	2.31(ns)	5	20.0	27.7	24.5	during 3rd application
7 Nov 1980	713.00	0.48(a)	8.29	0.34(a)	2	4.5	4.1	2.9	during 4th application

*significantly different ($p<0.05$); ns, not significantly different; a, not tested due to insufficient sample size; [1]n = number of samples.

TABLE III

Comparison of taxa composing drift (no./m^3) in the treated (TS) and reference (RS) streams, before, during, and after application of methoxychlor.

Date	Copepoda		Oligochaeta		Other Non-Insects		Chironomidae		Other Insects	
	TS	RS	TS	RS	TS	RS	TS	RS	TS	RS
Before:										
27 Nov 79	0.26	0.14	0.03	0.18	0.10	0.32	0.26	0.41	0.74	0.51
During:										
16 Feb 79	8.34	---	2.08	---	2.08	---	1046.3	---	1027.5	---
10 May 80	526.74	0.64	296.35	0.46	30.45	1.76	138.03	1.63	24.35	0.45
20 Aug 80	150.94	1.10	33.41	0.54	28.14	0.11	73.27	1.05	7.62	2.05
7 Nov 80	327.98	0.48	1.43	0.00	12.12	0.00	331.55	0.00	39.93	0.00
After:										
23 Feb 80	3.84	0.66	0.16	0.26	2.03	1.37	29.04	0.79	16.88	0.87
4 Apr 80	0.40	0.03	0.09	0.22	0.65	0.01	1.03	0.31	0.62	0.17
10 May 80	2.53	0.64	0.46	0.29	1.52	1.76	0.79	1.63	0.74	0.45
11 Jun 80	0.99	0.63	1.52	0.20	0.52	0.00	1.06	1.27	0.27	0.54

Estimates of invertebrate density and biomass at the time of treatment can be calculated by dividing export figures by wetted channel area upstream of the flume (135 m × 0.54 m). This technique was used to calculate pretreatment densities in Table 5. These are minimum estimates of density and biomass since many drifting organisms may have been trapped in debris dams, leaf packs, and other retention devices before reaching the flume, and organisms with heavy cases such as the caddisflies *Fattigia, Psilotreta,* and *Pycnopsyche* may die without drifting. However, both estimated density (4600 organisms/m^2) and estimated biomass (2.62 g AFDM/m^2) approximate mean annual values reported for other Coweeta streams (Haefner 1980, Gurtz 1981) much more closely than might be expected. This may imply that: 1) retention devices on these small headwater streams are not effective in trapping dead or immobilized insects; 2) benthic densities in the winter are higher than mean annual densities; or 3) standard benthic sampling techniques underestimate standing stock.

Other Methoxychlor Treatments. - Drift densities and mean number of drifting taxa in the treated stream were significantly higher than in the reference stream (t-test, $P < 0.05$) during all treatments (Table 2). This indicated that no single treatment was effective in eliminating all insect fauna. During subsequent treatment periods (i.e., May, August, and November 1980), there was a marked decrease in the proportion of the drift composed of insects and an increase in the non-insect portion (Table 3). This was an expected consequence of the continued depletion of the benthic insect community in the treated stream (Table 5) that occurred with each pesticide application. What was not expected was the close similarity of drift densities between the treated stream and the reference stream during intervals between treatments (Tables 3 & 5). Insect drift densities, both chironomids and other insects, were surprisingly similar, considering that the drift sources in the treated stream have been reduced to about 10% of normal (Table 5). These similarities (Tables 3 & 5) implied that a higher proportion of the treated stream's benthic fauna (Table 5) was drifting as compared to the reference stream.

Several factors may have interacted to influence the rate at which organisms entered and left the drift in the two streams. These include: 1) the amount of reproduction, i.e., hatching of early instars, occurring in each stream, 2) the rate at which drifting organisms are removed from the water column by predators, i.e., net-spinning caddisflies, and 3)

TABLE IV

Characteristics of major fauna drifting during the initial methoxychlor application 16-23 February 1980. Peak density is no./m^3.

Taxa	Peak Density	Export Totals Number	Export Totals g AFDM
EPHEMEROPTERA			
Ephemerella	270.8	7,419	1.50
Paraleptophlebia	616.6	19,188	12.64
Stenonema	64.8	3,214	3.64
ODONATA			
Lanthus	5.5	72	0.44
PLECOPTERA			
Acroneuria	43.9	744	2.58
Alloperla	90.6	2,239	0.15
Isogenus	164.7	4,557	2.13
Leuctra	901.5	14,711	4.71
Nemoura	928.9	15,814	11.69
Peltoperla	3,137	60,538	122.35
COLEOPTERA			
Anchytarsus	11.0	170	0.08
Ectopria	2.1	82	0.04
Optioservus	44.0	1,743	0.81
TRICHOPTERA			
Diplectrona	90.6	3,390	0.73
Lepidostoma	22.0	1,246	0.57
Parapsyche	142.7	4,445	2.57
Pycnopsyche	6.9	104	0.12
Rhycophila	90.6	1,533	0.89
Wormaldia	45.3	937	0.60
DIPTERA			
Ceratopogonidae	87.8	3,326	0.12
Chironomidae	5,246	168,854	6.25
Dicranota	428.1	7,819	0.52
Dixa	32.9	947	0.04
Hexatoma	81.0	2,542	0.17
Nymphomyiidae	38.5	905	0.03
MISCELLANEOUS			
Oligochaeta	2.7	80	0.03
Copepoda	32.9	1,220	0.01
Acari	11.0	189	0.01
TOTAL		328,027	175.42

residual methoxychlor which may stimulate higher drift rates, in proportion to benthic density, in the treated stream. Any one, or combination of the above, may be responsible for the differences between benthic density and drift density in the two streams.

Leaf Bag Fauna. - Methoxychlor treatment drastically depleted the number of taxa, particularly insect taxa, available for colonization of leaf bags in the treated stream. Consequently, colonization in the treated stream stabilized more rapidly (ca. 14 days vs. 49 days) and with fewer taxa per leaf bag ($\bar{x}=4.8$) than in the reference stream ($\bar{x}=17.3$) (Fig. 3A). During the year following treatment, 55 of the 56 taxa known to occur in the two streams prior to treatment were recovered from the reference stream and 31 from the treated stream. Only Chironomidae, Ceratopogonidae, Copepoda, Oligochaeta, and Turbellaria were encountered with regularity in the treated stream. The remaining taxa, mainly insects, were encountered rarely and in very low abundances in the treated stream.

TABLE V

Comparison of invertebrate abundance, as percent composition, in outcrop, cobble, leaf bags, and drift samples from the reference stream (RS) versus the methoxychlor treated stream (TS). Initial density is based on drift losses from the treated stream during initial treatment (16 February 1980) divided by wetted channel area (see text).

Taxa	Outcrop RS	Outcrop TS	Cobble RS	Cobble TS	Leaf Bags RS	Leaf Bags TS	Drift RS	Drift TS	Initial Density
Chironomidae	35.0	3.2	47.6	4.6	31.9	5.4	27.9	38.9	50.4
Other Insects	49.0	1.8	27.0	2.2	43.1	2.2	24.5	26.9	49.2
Copepoda	0.5	6.4	12.3	43.2	4.7	10.6	19.1	24.5	0.4
Oligochaeta	9.5	59.8	11.5	37.2	14.0	68.3	8.9	8.0	1.0
Turbellaria	6.0	28.8	1.6	9.9	5.9	12.6	0.1	0.1	1.0
Other Invertebrates	0.0	0.0	0.1	3.0	0.3	0.9	19.6	1.7	1.0
Mean Density (No./m^2)	4,794	5,962	16,586	7,414	2,130	2,228	---	---	4,596

Density was initially suppressed in the treated stream but recovered within 117 days to equal or exceed that of the reference stream (Fig. 3B). This increase occurred despite the depauparate insect fauna and repeated applications of methoxychlor in the treated stream. Biomass in the treated stream, dominated by non-insects, did not show the same trends as did density (Fig. 3C). Instead, biomass remained significantly lower in the treated stream with the exception of the period of summer insect emergence (day 144 = July).

Both density (Fig. 4A) and biomass (Fig. 4C) of insects in the treated stream were greatly reduced. Insect density in the reference stream was bimodal, corresponding to hatching of summer (day 79 = May) and winter (day 265 = November) generations of insects (Fig. 4A). Insect biomass in the leaf bags (Fig. 4C) did not change significantly after about 44 days of colonization with about 80 mg AFDW/bag in the reference stream and about 4.5 mg AFDW/bag in the treated stream. This large difference resulted both from a decrease in density of insects in the treated stream, especially elimination of large long-lived insects such as *Pycnopsyche, Paraleptophlebia, Lepidostoma,* and *Peltoperla,* which were replaced by small short-lived species of Chironomidae and Ceratopogonidae.

Non-insect macroinvertebrate density was significantly higher in the treated stream than in the reference stream after about 79 days of colonization. We suspect that the reduction in insect predators in the treated stream was similarly responsible for the difference observed in non-insect density between the two streams. Decreased competition with insects for food resources and a higher quality food resource (see following sections) may also have contributed to increases in non-insect taxa.

Insect density, insect biomass and non-insect density differed more between streams than non-insect macroinvertebrate biomass (Fig. 4D) with the exception of data for 144 days (July 1980) and 358 days (February 1981). Oligochaeta and Turbellaria dominated the non-insect taxa (Table 6) and accounted for about 86-99% of the density and biomass of the non-insect macroinvertebrates after 44 days of colonization (April 1980) in both streams. Copepoda contributed a significant proportion of the non-insect fauna only in the 7 November 1980 samples. However, the mesh size (250 μm) used to collect the leaf bag samples probably did not adequately retain smaller copepods. Consequently the values are underestimated.

Methoxychlor treatment also altered the structure of the invertebrate community. The affect can be summarized as an elimination of insect fauna with relatively long life cycles (i.e., univoltine or semivoltine) and a subsequent increase in invertebrate fauna, particularly Oligochaeta, Turbellaria, and Chironomidae with short life cycles. This altered the functional characteristics of the community by virtually eliminating shredders and collector-filters while increasing the relative importance of collector-gatherers (Fig. 5). Invertebrate drift data from the initial poisoning emphasized the magnitude of the loss of shredders from the treated stream. Four of the top five taxa drifting during this period were shredders, *Peltoperla, Paraleptophlebia, Nemoura,* and *Leuctra.* Collectively, they represented a minimum loss of over 2 g AFDW/m^2.

Comparisons of Leaf Bags and Benthic Fauna. - Drift samples collected from the treated stream during periods of pesticide treatment gave the most complete taxonomic characterization of the stream fauna with 52 taxa drifting. Leaf bags and Surber samples consistently underestimated benthic taxa because of the limited number of microhabitats sampled. Surber samples taken in rock outcrop and cobble-boulder habitats of each stream on 5 April and 20 August 1980 followed trends similar to leaf bags (Table 5). That is, the community in the treated stream shifted from one dominated by insects to one dominated by non-insects (Oligochaeta, Turbellaria, and Copepoda) while the reference stream was dominated by insects.

Microbial Comparisons. - Addition of 10 ppm methoxychlor did not inhibit microbial respiration on conditioned leaf discs compared to that of controls (t-test, P > 0.10).

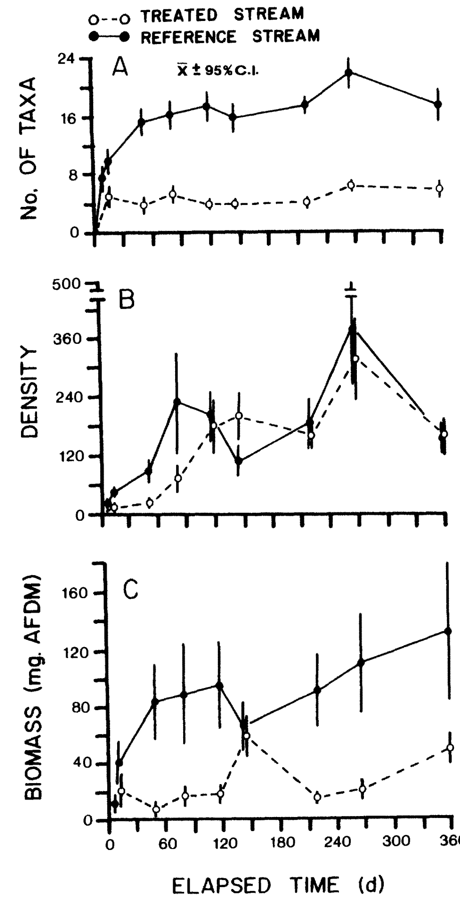

Fig. 3. Development of macroinvertebrate fauna on leaf bags of the treated and reference streams. Figure A represents the number of taxa colonizing the leaf bags; B represents density per leaf bag (0.072 m^2); and C represents biomass per leaf bag. All values are means of 12 leaf bags.

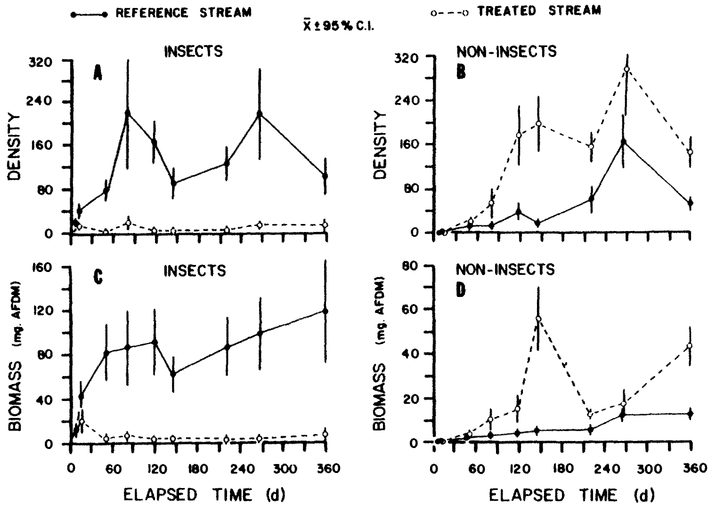

Fig. 4. Development of insect and non-insect fauna on leaf bags of the treated and reference streams. A and C represent the insect fauna and B and D represent the non-insect fauna. Density and biomass values are means of 12 leaf bags. Error bars are 95% confidence intervals.

Similarly, leaf discs did not show any significant changes in respiratory rates from those of control discs following one week of exposure to 10 ppm methoxychlor (t-test, $P > 0.10$). Direct microscopic counts of fungal hyphae on 20 red maple leaf discs collected from the treated and reference streams were not significantly different (t-test, $P > 0.10$). There was no significant difference (t-test, $P > 0.10$) in ATP levels associated with CPOM between the two streams based on the limited number of samples analyzed on 7 August 1980 (4.24 vs. 5.30 μg ATP/g AFDM). We conclude, based on respiration, fungal, and ATP data, that methoxychlor had no significant inhibitory effect upon microbial activity.

Higher ATP levels on the FPOM from the treated stream are difficult to interpret but may be the result of bacterial and protozoan populations being released from insect grazing. Laird (1958) obtained similar results in simple laboratory infusions containing mosquito larvae and exposed to DDT. Death of the mosquito larvae resulted in rapid bacterial growth which in turn stimulated protozoan populations even though the species composition of the microflora and microfauna was not altered by DDT treatment.

Organic Matter Export. - Wallace et al. (1982b) found that reduction of macroinvertebrates caused a significant reduction in non-storm TPOM export from the treated stream. Non-storm export during the post-treatment period averaged 3.9× higher in the reference stream despite higher average discharge in the treated stream during a prolonged drought. Typically, storms cause significant increases in TPOM concentrations, expecially during rising hydrographs (e.g., Bilby & Likens 1979, Gurtz et al. 1980, Wallace et al. 1982a). Only one small storm (16 June 1980) was sampled during this study. This storm increased discharge about 2.45× (1 to 2.45 liters/s) in the treated stream and 2.5× (0.6 to 1.5 liters/s) in the reference stream (Fig. 6). Whereas the number of samples were limited, they do show large increases in TPOM concentrations. The highest concentration of TPOM observed during this storm was about 15× higher in the reference stream (180 mg AFDM/liter) than that of the treated stream (12.1 mg AFDM/liter) (Fig. 6).

Typically, maximum concentrations of transported matter occur prior to or at peak discharge (Bilby & Likens 1979; Paustian & Beschta 1979; Webster et al. 1983). This peak may have been missed on either stream (between 1940 and 1950 h), especially in the

TABLE VI

Comparison of the twelve most important taxa ranked by their percent abundance and biomass in all litter bags from the reference stream versus the methoxychlor treated stream.

Rank by Percent Abundance				Rank by Biomass			
RS		TS		RS		TS	
Taxa	Percent	Taxa	Percent	Taxa	AFDM mg	Taxa	AFDM mg
Chironomidae	31.9	Oligochaeta	68.3	*Hexatoma*	1496	Oligochaeta	1573
Oligochaeta	14.1	Turbellaria	12.6	*Pycnopsyche*	1319	Turbellaria	293
Leuctra	11.0	Copepoda	10.6	*Peltoperla*	1312	*Lanthus*	243
Turbellaria	6.0	Chironomidae	5.4	*Tipula*	611	*Tipula*	89
Copepoda	4.8	*Lepidostoma*	1.0	*Lanthus*	597	*Lepidostoma*	79
Peltoperla	4.4	Nematoda	1.0	*Fattigia*	520	*Cordulegaster*	47
Lepidostoma	3.8	*Lanthus*	0.4	*Lepidostoma*	407	Chironomidae	35
Hexatoma	3.5	*Cordulegaster*	0.1	Oligochaeta	327	*Acroneuria*	20
Wormaldia	3.0	Ceratopogonidae	0.1	Chironomidae	292	*Stenonema*	18
Paraleptophlebia	3.0	Sphaeriidae	0.1	*Diplectrona*	241	*Peltoperla*	16
Ceratopogonidae	2.2	*Hexatoma*	0.1	*Leuctra*	168	Copepoda	14
*Diplectrona**	2.0	*Stenonema**	0.1	*Acroneuria*	157	*Diplectrona*	7
Totals	89.7%		99.6%		7447**		2434**
Non-insects	24.9%		92.6%		327 (4.4%)		1880 (77.3%)

*Note - twenty additional taxa were found in the RS above the 0.05% level abundance of *Stenonema* in the TS.
**Total biomass of RS bags fauna = 8,494 mg AFDM; TS = 2457 mg (n = 96 bags/stream).

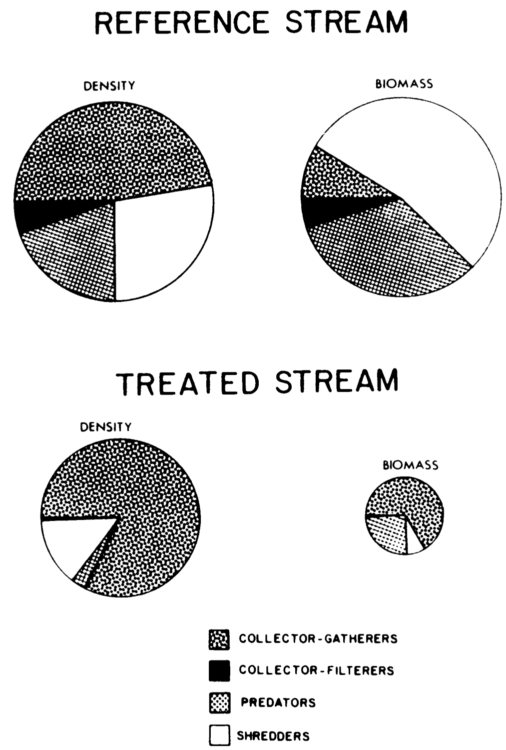

Fig. 5. Relative composition of the fauna of the treated and reference streams. Percentage composition (wedge area) is based on sums of density and biomass from all leaf samples. Size of the circles representing the treated stream indicate the density and biomass relative to the reference stream.

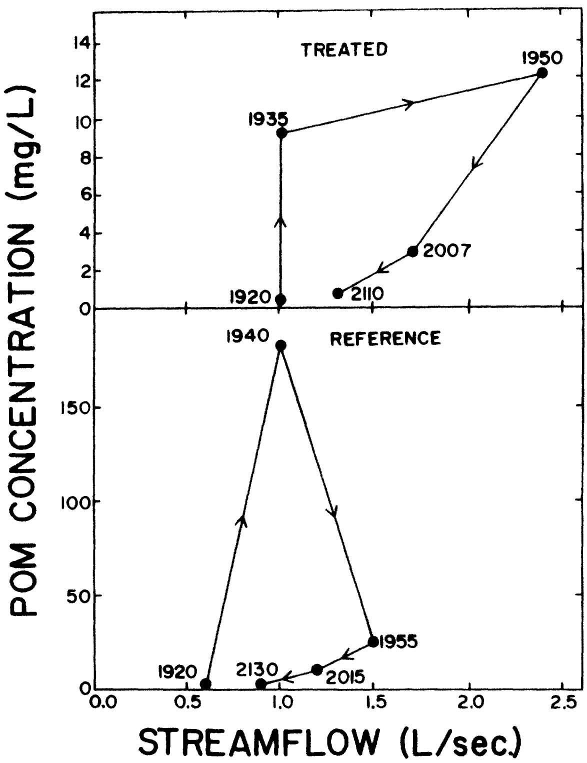

Fig. 6. Changes in transported particulate organic matter concentrations from the treated and reference streams caused by a small storm (16 June 1980). Numbers with the data points are the times when the samples were taken.

treated stream. Notwithstanding that peak discharge may have been missed, both streams had the typical hysteresis associated with storms, i.e., higher particulate concentrations on the rising limb of the hydrograph than on the falling limb. Similar results have been well documented for storms in other streams (e.g., Bilby & Likens 1979; Paustain & Beschta 1979; Gurtz et al. 1980; Wallace et al. 1982a; Webster et al. 1983).

The storm data indicate that reduction of the macroinvertebrate community altered the magnitude of the response but not the manner in which the stream responded to storms. We interpret the difference in response between streams as due to the accumulation of a large amount of macroinvertebrate-produced FPOM ($<$ 1 mm) (Wallace et al. 1982b) in the reference stream which was easily entrained during rather small increases in discharge. Greater CPOM breakdown in the reference stream, resulting in lower CPOM and a higher FPOM standing crop (compared to that of the treated stream), may represent another potential factor in seston export since CPOM may retain FPOM (e.g., Short & Ward 1981).

Median TPOM particle size was significantly smaller in the treated stream following methoxychlor application (paired t-test, $P < 0.05$; Fig. 7). The lower median TPOM particle size and reduced TPOM concentrations in the treated stream (Wallace et al. 1982b) may be directly related to the loss of large insect shredders. Loss of shredders reduced the production of medium-sized, readily transportable particles by reducing both the production of medium to large fecal pellets (234-900 μm; Ladle & Griffiths 1980; O'Hop 1983) and orts which result from leaf shredding and ingestion. Activities of microphagous species (e.g., Oligochaeta, Chironomidae, Turbellaria) produce much

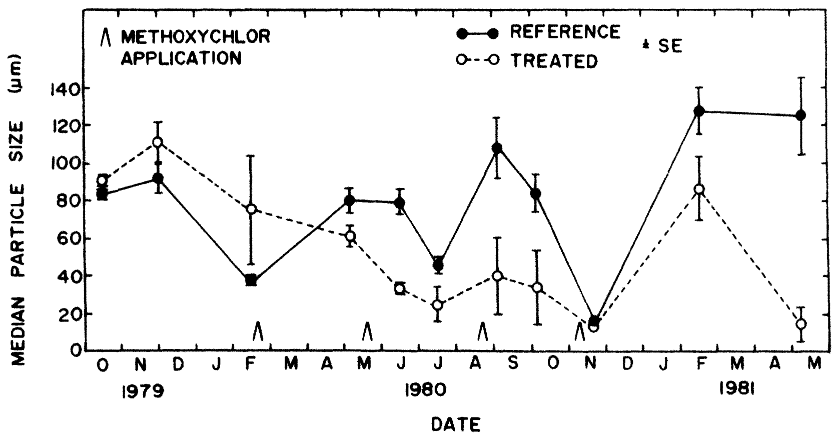

Fig. 7. Median particle sizes of transported particulate organic matter in the treated and reference streams. Error bars are ± one standard error of the mean.

smaller fecal pellets (ca. 50 μm, Ladle & Griffiths 1980) and do not result in the comminution of very large particles (e.g., whole leaves) into smaller, easily transportable particles. Furthermore, non-feeding activities (i.e., locomotion, burrowing, etc.) of the insect community may entrain particles that are trapped in benthic debris.

Significance of Invertebrates in Litter Processing. - Based on an examination of three detritus (> 1 mm) categories (woody, whole leaves, and other detritus), Wallace et al. (1982b) found that only the standing crop of 'other' detritus varied significantly between the treated and reference streams (TS > RS). This 'other' detritus consisted primarily of partially decomposed leaf fragments. The difference between 'other' detritus in the two streams represents CPOM (primarily leaves) retained within the study area (i.e., not respired or transported) and emphasizes the importance of the insect community in accelerating both the comminution of CPOM inputs and transport of FPOM to downstream areas. Accumulations of partially decomposed leaves (i.e., 'other' detritus) in the treated stream may also filter out smaller particles of detritus and thereby reduce seston transport below levels predicted from differences in leaf breakdown rates. Therefore, both the higher standing crop of 'other' detritus and the potentially higher microbial activity (e.g., ATP measured on benthic FPOM) suggest that microbial processing may have been greater in the treated stream. We have insufficient data to estimate the magnitude of this difference. Standing crops of whole leaves and woody detritus did not show a response to insect elimination because leaves had not been in the stream long enough for significant processing to have occurred (i.e., newly fallen leaves) while the processing rate of wood is so slow (Anderson et al. 1978; Triska & Cromack 1980) as to preclude detection of standing crop differences in an experiment of one year's duration.

We suggest that insects primarily function in litter fragmentation whereas litter decomposition, or chemical deterioration, occurs primarily through microbial action. Consequently, though exploitation of the energy and nutrients in litter may be much less for stream invertebrates than for bacteria and fungi, the actions of invertebrates in 'fragmenting' litter and making it available to microbes for chemical degradation is a major rate limiting step in litter decomposition. Similar conclusions have been reached for the role of invertebrates in terrestrial litter decomposition (Edwards et al. 1970; Whitkamp 1971).

Acceleration of litter fragmentation by invertebrates also increases the probability of leakage (i.e., transport) of energy and nutrients to downstream areas.

This may be viewed either as decreasing the efficiency of the system when defined in a narrow sense (i.e., as a small segment of channel length) or as an important source of 'communication' linking upstream and downstream sections into a sequence of overlapping communities (i.e., a continuum *sensu* Vannote et al. 1980). Elimination of insects may increase processing efficiency in the sense defined above if litter is converted to CO_2 with minimal downstream displacement (e.g., microbial processing). However, this would substantially limit the degree to which upstream and downstream systems are linked and may have important consequences on the form and timing of organic inputs from upstream regions. Elimination of invertebrates from upstream reaches would tend to weaken this upstream to downstream linkage.

Pesticides and Ecosystem Production. - Pesticide treatment altered community structure, but effects of the treatment on production are more difficult to assess. Undoubtedly, the high catastrophic drift resulting from methoxychlor application produced an immediate short-term depression in production within the treated stream. Total faunal biomass in leaf bags of the reference stream (8.49 g AFDM) was about 3.4× that of the treated stream (2.46 g AFDM). Thus the P/B (production/biomass) ratio would have to be about 3.5 × higher in the treated stream for similar production in each stream. These higher P/B ratios may exist in the treated stream since there was a shift in biomass from univoltine or semivoltine insects to Oligochaeta, Turbellaria (Planariidae), Copepoda, and Chironomidae, which have shorter life cycles. Oligochaete taxa found in Coweeta streams, including Glossoscelecidae, Lumbriculidae, and Naididae (*Pristina* sp. and *Nais* sp.), are known to exhibit high P/B ratios. Naidids have been reported to produce a new individual every 2-3 days under favorable conditions (Pennak 1978; Bonomi & DiCola 1980; Brinkhurst & Cook 1980). Turbellarians (Planariidae) can divide as frequently as every 5-10 days under favorable conditions (i.e., temperatures above 10°C) (Boddington & Mettrick 1977; Hay & Ball 1979; Ball & Reynoldson 1981). Temperatures of our study streams exceeded 10°C for over 5-6 months of the year. Annual P/B's of 15-20, corrected for annual temperature regimes, have been reported for laboratory rearings of the dominant copepod (*Bryocamptus zschokkei*) at Coweeta (O'Doherty, pers. com.). The latter is 3-4× that of the P/B for univoltine insects (Benke 1979; Waters 1979). Thus, shifts in population structure toward smaller organisms with shorter generation times, higher P/B's, and a capacity for asexual reproduction may well have resulted in increased turnover rates in the treated stream.

Increased production of non-insects such as Oligochaeta, Turbellaria, and Copepoda may also have resulted from enhanced survivorship in the treated stream. We suspect that the increase in abundance of many non-insects in the treated stream was attributable primarily to the removal of large insect predators. Insect predator biomass was 5.7× higher among the taxa recovered from the reference stream leaf bags (1.83 g AFDM) than among the taxa of the treated stream (0.33 g AFDM). Predaceous insects represented 21.3% of the total leaf bag animal biomass in the reference vs. 12.8% in the treated stream. These estimates are probably conservative since *Hexatoma* are shredders in early instars and predators in their later instars and we considered only one-half of their biomass as predator biomass. Thus, potentially enhanced survivorship, resulting from insect predator removal, appears to be a viable explanation for the increase in non-insects in the treated stream. This assumes that potential competition among prey species was not increased by predator removal. Complicating this interpretation is the role played by triclads in controlling oligochaete densities. Evidence for triclad predation on oligochaetes is quite convincing (e.g., Ball & Reynoldson 1981; Boddington & Mettrick 1979; Hay & Ball 1979).

Another potential influence on production in the treated stream was increased food quality as suggested by ATP measurements of the FPOM sediments. Ward and Cummins (1979) found growth of the chironomid *Paratendipes albimanus* was positively related to detrital ATP levels. The significantly higher ATP levels of the FPOM sediments in the treated stream may have resulted in increased growth rates of FPOM deposit feeders such as oligochaetes and copepods. Increased growth rates could have resulted in increased production and shorter generation times (Cohort production interval: Benke 1979; Waters 1979) within deposit feeding species, although survivorship may have been similar in each stream.

Pesticide treatment resulted in lower standing stock biomass, shifts in population structure from uni- or semivoltine insects to other invertebrates with higher annual P/B ratios, increased survivorship resulting from large insect predator removal, and, possibly increased growth rates resulting from higher food quality of FPOM sediments; these may all have increased production of non-insects in the treated stream to levels higher than that suggested by biomass alone. The relatively rapid increase in non-insect biomass in the treated stream (Fig. 4) does suggest that these animals may have higher annual P/B ratios than commonly recognized, and under 'normal' situations (i.e., reference stream) they may compose a more important component of the diet of carnivores than would be suggested by their biomass. However, if the production of these other non-insect invertebrates is important in these systems, their feeding activities are probably associated with FPOM and associated microflora rather than direct CPOM processing.

In conclusion, our application rate of methoxychlor was about 10× higher and 20-30× longer than the 1 ppm for 30 minutes recommended for larval blackfly control (Jamnback 1973). However, lower application rates are known to induce similar invertebrate drift responses in larger streams (e.g., Wallace & Hynes 1975; Flannagan et al. 1979, Yasuno et al. 1982). In addition to purely toxicological effects, applications of chemical control methods for larval blackfly control may influence patterns of energy and nutrient flow within stream ecosystems. Such direct effects of pesticides, or any other perturbation which upsets the structure of invertebrate communities, deserve more careful consideration.

Stream ecosystems display continuous changes in physical and chemical characteristics from their source to mouth which may influence the composition and function of the biological communities along this continuum (Vannote et al. 1980). Small 1st- and 2nd-order headwater streams (ca. 73% of the total stream length in the U.S.; Leopold et al. 1964) have maximal interface with the terrestrial environment implying a significant role for these streams in the accumulation, processing, and transfer of organic matter from terrestrial to downstream areas (Vannote et al. 1980). Such headwater streams in forested regions are characterized by both numerous physical retention devices, which restrain the downstream transport of CPOM (e.g., Naiman & Sedell 1979a,b; Bilby & Likens 1980; Wallace et al. 1982b; Minshall et al. 1983), and by an invertebrate fauna which processes this retained CPOM more effectively than downstream communities (Cummins 1975; Vannote et al. 1980). In our previous publication (Wallace et al. 1982b), we showed that the invertebrate fauna of headwater streams influenced both the processing of CPOM and subsequent export of FPOM to downstream reaches.

CPOM breakdown and FPOM export by macroinvertebrates in headwater streams is enhanced by the physical characteristics of these systems (e.g., low stream power, Leopold et al. 1964; higher roughness, Chow 1959; and shallow, narrow channels which are readily subject to obstruction) which increase CPOM retention (Sedell et al. 1978; Naiman & Sedell 1979b; Bilby & Likens 1980, Wallace et al. 1982a; Minshall et al. 1983). Conversely, in larger streams with greater power, less roughness, and fewer channel obstructions, physical characteristics favor entrainment and transport of particulate organic matter. The importance of macroinvertebrates as regulators of downstream organic matter movement is probably less important in these areas. This implies that in headwater streams where there is high physical retention, biological processes favor entrainment (i.e., through their processing of CPOM to FPOM), whereas fauna of downstream areas have evolved toward exploitation of these entrained particles (i.e., collector-gatherers and filter-feeders).

If we define 'ecosystem efficiency' as the ability of an ecosystem to convert reduced organic carbon to CO_2, then the role of macroinvertebrates in the efficiency of headwater streams depends on how they are viewed in time and space. Biological communities of natural streams have been postulated to assume processing strategies which involve minimum energy loss to downstream areas (Webster 1975; Vannote et al. 1980). Our previous data suggest that macroinvertebrates increase export of organic matter and energy loss and therefore lower efficiency of headwater streams when viewed for short time periods and not considering downstream areas (Wallace et al. 1982b). Without macroinvertebrates, CPOM storage increases in headwater streams and decomposition would probably be primarily limited to microbial activity. However, benthic CPOM storage may be subject to infrequent major storms which might quickly move large amounts of materials through downstream reaches. Such storms could lead to lower efficiency in both the headwater and downstream areas since storm-transported materials may pass rapidly through a given reach of stream with little utilization by either microbes or higher consumers. Therefore, headwater macroinvertebrates, by mediating a continuous downstream supply of organic matter, probably increase efficiency when the entire river continuum is considered. The regulation of organic matter supply to downstream areas potentially influences the structure and function of downstream communities which have been postulated to depend on 'leakage' or inefficiency of upstream processing for a considerable portion of their energy (Fisher & Likens 1973, Cummins 1974; Vannote et al. 1980). The results of our study do not conform to the suggestion, which has been made for New Zealand streams, that benthic macroinvertebrates, especially insect shredders, are of minor importance in the production of FPOM (Winterbourn et al. 1981). However, in some of these streams, where physical retention of allochthonous organic matter is high, the pattern may be quite similar to that observed in the headwater streams of Coweeta (e.g., Rounick & Winterbourn 1983).

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