

Recovery of a headwater stream from an insecticide-induced community disturbance

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Abstract. Faunal assemblages, leaf litter processing rates, and seston export were followed in two streams two years after one was altered with an insecticide.

Two years after treatment ended, the macroinvertebrate trophic structure of the treated stream (TS) community had recovered and was similar to that of the reference stream (RS); however, major differences in taxonomic composition persisted. Some taxa, e.g., *Diplectrona metaqui* and *Pseudostenophylax*, which were rare or absent in TS before treatment became locally abundant during recolonization. Other taxa (e.g., *Peltoperla*, *Pycnopsyche*, *Diplectrona modesta*, and *Fattigia*), which were known to be abundant in TS before treatment, remained absent or rare in TS and common in RS.

Recovery of shredder functional group biomass in TS was accompanied by restoration of leaf litter processing rates, seston concentrations, and export. These had all decreased significantly in TS, relative to RS, during the treatment period. Despite the recovery of the shredder functional group biomass, the taxa dominating this group remained strikingly different from RS and pretreatment conditions in TS. Biomasses of some shredders (e.g., *Lepidostoma* spp. and *Tipula*) were twice as high in TS as in RS, while others (e.g., *Peltoperla*, *Fattigia*, and *Pycnopsyche*) were low or absent in TS.

Although taxonomic differences still existed between TS and RS, trophic structure was similar between streams. Restoration of shredder biomass, leaf litter processing, and organic seston concentrations in TS supports the concept that stream ecosystems are resilient to disturbance. Thus recovery of trophic function may occur in a fashion not recognizable solely by taxonomic criteria.

Key words: invertebrates, stream, disturbance, insecticide, recovery, trophic, taxonomic, leaf processing, seston.

Allochthonous inputs, primarily autumn-shed leaves, greatly exceed autochthonous production in small headwater streams of forested watersheds (Cummins et al. 1983, Fisher and Likens 1973, Webster et al. 1983). These streams retain coarse particulate organic matter (CPOM) (Bilby and Likens 1980, Cummins et al. 1983, Minshall et al. 1983, Naiman and Sedell 1979a, Sedell et al. 1978, Wallace et al. 1982a) and export primarily fine particulate organic matter (FPOM) and dissolved organic matter (DOM) (Minshall et al. 1983, Naiman and Sedell 1979b, Wallace et al. 1982a, Webster and Patten 1979). The exported FPOM and DOM may represent an important source of energy and nutrients to the downstream fauna, especially those adapted for deposit- and filter-feeding (Anderson and Sedell 1979, Short and Maslin 1977, Wallace and Merritt 1980), and account for a large proportion of the annual FPOM flux to downstream

reaches (Fisher 1977). This upstream to downstream linkage has formed the basis for theoretical concepts such as nutrient spiraling (Newbold et al. 1982a, 1982b, Webster and Patten 1979) and the river continuum (Minshall et al. 1983, Vannote et al. 1980).

Within headwater reaches, macroinvertebrates feeding on CPOM, or "shredding" (sensu Cummins 1973), convert CPOM to FPOM (Boling et al. 1975, Cummins 1973) and DOM (Meyer and O'Hop 1983), forming a link between storage and export of organic matter. Insect shredders generally have low assimilation efficiencies and high ingestion rates, suggesting that they might play an important role in the conversion of CPOM to FPOM (Golladay et al. 1983, Grafius and Anderson 1979, McDiffett 1970) and DOM (Meyer and O'Hop 1983). The ability to generate large quantities of small particles that become available for microbial colonization and degradation is probably far more important than the shredders' degradation of organic material directly by metabolic respiration. The latter is generally

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considered to represent an insignificant (<1%) portion of the annual flux of organic matter through headwater streams (Fisher and Likens 1973). Little direct evidence is available to quantify macroinvertebrate production of FPOM from CPOM in streams (e.g., Merritt et al. 1984), and for some zoogeographical regions, insect shredders may have little influence on FPOM generation (Winterbourn et al. 1981).

In 1980–1981, we used an insecticide to eliminate over 90% of the aquatic insect abundance and biomass from a headwater stream. This treatment caused massive invertebrate drift, changes in benthic community structure, significant reductions in leaf breakdown rates, and significant reductions in FPOM export to downstream reaches compared with an adjacent reference stream (Cuffney et al. 1984, Wallace et al. 1982b).

The objectives of the present study were to compare the insecticide-treated stream and the reference stream in the second year following insecticide treatment, with major emphasis on the following: (1) litter breakdown rates in the two streams in 1982–1983 compared with rates obtained previously; (2) seston concentration and export; (3) invertebrate community structure in litter bags; and (4) functional feeding groups in relation to taxonomic groups.

Study Sites

The 1st order study streams drain Catchments 53 (Treated Stream TS) and 54 (Reference Stream RS) within Coweeta Hydrologic Laboratory (CHL), a 1625-ha drainage basin in the Blue Ridge Province of the Southern Appalachian Mountains. CHL has a 50-year history of hydrologic and climatological monitoring. Winters are mild and summers cool with a mean annual air temperature of 12.8°C. Stream temperatures range from 4 to 17°C with annual accumulated degree days differing <7% between the two streams. Concentrations of most ions are usually low (<1 mg/L), and pH averages ca. 6.6–6.8 (Swank and Douglas 1977).

Mean annual precipitation varies from 170 cm to 250 cm at lower (ca. 700 m) and upper (>1600 m) elevations, respectively, and is rather evenly distributed throughout the year with at least 7 cm falling each month. Precipitation varied considerably during the period of 1980

to 1984. Expressed as percent of normal precipitation (50 year annual mean = 182.3 cm), the values for the years of study are: 1980=105%; 1981=69% (lowest annual precipitation in 40 years); 1982=95%; 1983=112%; and 1984=113%. Less than 5% of the annual precipitation is snow. Stream discharge is highest and most variable in late winter, lowest and most stable in autumn, and overland flow rarely occurs. Normal baseflow discharge of the two streams studied was 0.2–2.3 L/s.

Early use of the CHL forest was described by Johnson and Swank (1973). Oaks (*Quercus* spp.) and hickories (*Carya* spp.) dominate the study watersheds, and stream margins are heavily shaded by dense growths of rhododendron. Since 1924, no timber cutting or forest fire has occurred on the two study watersheds. Both streams drain into a much larger 4th order stream (Shope Fork), have southern aspects, similar elevations (ca. 830 m), and drain adjacent catchments of 5.2 (TS) and 4.2 (RS) ha. Additional descriptions of these streams can be found in Wallace et al. (1982b) and Cuffney et al. (1984).

Methods

Treatment

Applications of methoxychlor (1,1,1-trichloro-2,2 bis [paramethoxyphenyl] ethane) to the TS were made on each of four dates in 1980 (Cuffney et al. 1984, Wallace et al. 1982b). Initial treatment on 16 February 1980 consisted of a continuous 10-hr metered release of the insecticide supplemented with a 5-hr hand sprayer release to stream margins, leaf packs, backwater areas, and seeps upstream to the source. Subsequent 5-hr hand sprayer treatments were conducted on 10 May, 20 August, and 8 November 1980. Metered and hand sprayer releases were adjusted to deliver methoxychlor at a rate of 10 ppm, based on stream discharge at the flume. The TS has not been treated with insecticide since November 1980.

Leaf litter breakdown

Leaves of rhododendron (*Rhododendron maximum* L.), white oak (*Quercus alba* L.), red maple (*Acer rubrum* L.), and dogwood (*Cornus florida* L.) were placed in litterbags (36 × 20 cm with 5-mm mesh). Each bag contained about 15 g

dry mass. Thirty-six bags of each of the four leaf species were placed in each stream on 20 February 1982 in the same locations as those used in the 1980-1981 study begun on 16 February 1980 (Cuffney et al. 1984, Wallace et al. 1982b). Four bags of each leaf species were collected from each stream 8, 22, 56, 123, 185, 225, 260, 323, and 385 days after introduction. Leaf litter remaining in the bags was processed and analyzed as described by Wallace et al. (1982b) to obtain % of original ash free dry mass (AFDM) remaining.

Stream seston

Replicated ($n=3$ to 11 per collection) grab samples (1-6 L) of stream water were collected at the flume and used to measure organic seston. All samples were collected on pre-ashed, glass fiber filters (Gelman type AE) and organic seston concentrations were measured by drying (50°C) and ashing (500°C) to obtain mg AFDM/L (Gurtz et al. 1980). Instantaneous export (=mg AFDM/s) was calculated as mean concentration \times discharge for each sample date.

Invertebrates colonizing litterbags

Sediments, detritus, and invertebrates were washed from litterbags and retained on a 250- μ m sieve. Invertebrates were also hand-picked from material that remained in the bag. Invertebrates were subsampled ($\frac{1}{8}$ to $\frac{1}{16}$ of original sample) using a sample splitter (Waters 1969), hand-picked at 10 \times magnification, and preserved in 7% formalin. Subsamples of representative size classes of each taxon were used to estimate AFDM by determining mean individual mass for >100 individuals (e.g., Copepoda, Collembola) or regressing head width or body length against mass. Insects were assigned to functional feeding groups (i.e., shredder, collector-gatherer, collector-filterer, or predator) following the scheme of Merritt and Cummins (1984) or our own knowledge of the CHL fauna. Tanyptodinae were regarded as predators whereas all other Chironomidae, oligochaetes, and copepods were regarded as collector-gatherers. We realize some taxa included in this scheme may employ feeding modes other than those to which they were assigned. However, further refinement of functional feeding groups within these taxa was not practical.

Invertebrate abundances and biomasses were compared between years and between streams using proportional similarity (Whittaker 1975):

$$PS = 1 - 0.5 \sum |p_a - p_b| = \sum \min(p_a \text{ or } p_b)$$

where p_a and p_b are the average decimal importance values (either abundance or biomass) of a given taxon in community a or b. We calculated the percent contribution of each taxon to total invertebrate densities and biomass in litterbags for the 1980-1981 (Cuffney et al. 1984) and 1982-1983 studies (total samples per stream = 96 in 1980-1981 and 144 in 1982-1983).

The sample splitter used in our 1982-1983 study greatly facilitated the recovery of small invertebrates; consequently, in both streams we recovered more Nematoda, Copepoda, Acarina, Collembola, and early instars of Ceratopogonidae and Chironomidae than in the 1980-1981 study (Cuffney et al. 1984, Wallace et al. 1982b). These taxa were therefore omitted from our between-year comparisons of abundances. Proportional similarities of functional group biomass were compared between years with all taxa. We have used annual means $\pm 95\%$ CI for the entire study period as a means of distinguishing differences between streams in the 1982-1983 study. This approach incorporates considerable temporal variation and tends to maximize estimates of variance; thus, our analyses represent a conservative measure of differences between streams. Our study, like most ecosystem-level manipulations, involves pseudoreplication. Therefore, differences between RS and TS cannot be attributed strictly to treatment effects (Hurlbert 1984); hence, the reader should use discretion in making such attributions.

We assessed pretreatment community structure of TS at the time of original treatment by counting total macroinvertebrates lost as drift from the catchment during the initial insecticide treatment. Estimates of pretreatment abundances and biomasses were then obtained by dividing total drift by wetted stream area. These values approximate those obtained for other Coweeta streams (4600 organisms/m², 2.62 g AFDM/m²) (e.g., Haefner 1980, Woodall 1971) and are very conservative estimates because many case-making caddisflies died without drifting (Cuffney et al. 1984). This whole system "harvesting" technique provides pre-

TABLE 1. Exponential breakdown rates, k (day^{-1} , $\pm 95\%$ CI), of four leaf species, calculated by regressing \ln (% AFDW remaining) on time for leaves placed in the reference stream (RS) and treatment stream (TS). Study periods were 16 February 1980 to 8 February 1981 and 20 February 1982 to 12 March 1983. The far right column is the ratio of k values within each stream for the two study periods.

Leaf species	Stream	1980-1981 ^a			1982-1983			k (1982-1983): k (1980-1981)
		k	95% CI	r^2	k	95% CI	r^2	
Dogwood	RS	0.0208	± 0.0022	0.96	0.0316	± 0.0048	0.91	1.52
Dogwood	TS	0.0105	± 0.0017	0.88	0.0229	± 0.0025	0.94	2.18
Red Maple	RS	0.0138	± 0.0016	0.93	0.0141	± 0.0024	0.81	1.02
Red Maple	TS	0.0054	± 0.0010	0.82	0.0119	± 0.0024	0.75	2.20
White Oak	RS	0.0106	± 0.0009	0.95	0.0105	± 0.0011	0.91	0.99
White Oak	TS	0.0037	± 0.0006	0.86	0.0110	± 0.0013	0.90	2.97
Rhododendron	RS	0.0049	± 0.0009	0.81	0.0057	± 0.0016	0.59	1.16
Rhododendron	TS	0.0013	± 0.0002	0.90	0.0086	± 0.0025	0.56	6.62

^a Expanded and modified from Wallace et al. (1982b) to include 8 February 1981 samples. Calculations of breakdown coefficients were restricted to litterbags which retained $\geq 5.0\%$ of the original AFDW.

treatment data for TS. These data support the hypothesis that the difference between streams is attributable to the treatment and not to natural between-stream variation in the region. Proportional similarity is used to make comparisons between our estimate of original community structure (Cuffney et al. 1984, Wallace et al. 1982b) and subsequent litterbag faunal abundances and functional group biomasses in both the TS and RS communities.

Results

Leaf litter breakdown

Leaf litter breakdown rates (k) in each stream during 1982-1983 followed the same leaf species patterns described by previous workers at CHL (Wallace et al. 1982b, Webster and Waide 1982); dogwood > red maple > white oak > rhododendron. Dogwood broke down significantly faster in RS than in TS, whereas breakdown rates of red maple, white oak, and rhododendron were not significantly different between streams (Table 1). These results contrast with the 1980-1981 study (Wallace et al. 1982b) in which all four leaf species broke down more slowly ($p < 0.05$) in TS than in RS.

The ratios of breakdown rates (k) in RS between the 1980-1981 and 1982-1983 study were similar, ranging from 0.99 for white oak to 1.52 for dogwood (Table 1). Dogwood was the only leaf species in RS with significantly faster breakdown in 1982-1983 than in 1980-1981.

Breakdown rates for all four leaf species in TS were significantly higher during the 1982-1983 study than in the earlier one. The ratios of k values for TS between the two studies range from 2.18 for dogwood to 6.62 for rhododendron leaves (Table 1) indicating that processing rates in TS increased most for the more refractory species and least for the more labile (rhododendron > white oak > red maple > dogwood).

Seston concentration

Seston concentrations in the TS and RS did not differ systematically before treatment (Wallace et al. 1982b), although sample sizes were too small for proper statistical tests. During treatment and early recovery periods (Sample Period 1, Table 2), seston concentrations in TS were consistently lower than in RS. This difference in seston concentrations was sustained for 30 months after the last pesticide application (Sample Period 3), indicating that recovery was slow. Seston concentrations in TS approximated those of RS about 3.5-4 yr (Sample Period 4) after treatment ended.

During the summer and early winter of 1981 (Sample Period 2), discharge declined because of a severe drought which showed more pronounced effects in RS than in TS (minimum flows were 0.03 and 0.17 L/s, respectively). Despite lower discharge in RS, seston concentrations remained higher there than in TS. With the return of more normal discharges (Table 2,

TABLE 2. Comparison of seston concentrations (mg AFDM/L) and export (mg AFDM/s) during the four sampling periods. Period 1 is the pretreatment period (Oct. 1979–Feb. 1980). Period 2 is the initial study period (Feb. 1980–May 1981) and covers both the treatment period and the first 6 months of recovery. Period 3 is 17–25 months (April 1982 to Jan. 1983) after insecticide treatment ended. Period 4 is 36–50 months (Nov. 1983–Feb. 1985) after treatment. TS is the treated stream and RS is the reference stream. Means for each sample date were used to test for significant differences in concentration and export within each Sample Period by a Randomization Test for Matched Pairs (Siegel 1956) at the 0.05 level of significance. Export values represent the means of instantaneous values obtained during non-storm periods. Export was calculated as concentration \times discharge (=mg AFDM/s) for each sample date.

Sample Period	Seston Concentration			Seston Export		
	n	Mean (\pm 95% CI)		n	Mean (\pm 95% CI)	
		TS	RS		TS	RS
1	3	1.11 (1.83) ^a	1.03 (1.16)	3	1.70 (1.70) ^a	1.38 (2.30)
2	11	0.17 (0.13) ^b	1.10 (0.67)	11	0.22 (0.67) ^b	0.81 (0.91)
3	7	0.89 (0.49) ^b	2.08 (0.92)	—	— ^c	—
4	9	0.90 (0.22) ^d	0.99 (0.36)	7	0.80 (0.73) ^d	1.22 (0.92)

^a Insufficient sample size for statistical analysis.

^b Significantly different.

^c No discharge records available.

^d Not significantly different.

Sample Period 3), seston concentrations increased in both streams. However, the proportional increase in seston was higher in TS (ca. 5 \times) than in RS (ca. 2 \times), perhaps due to increased discharge and the reappearance of the invertebrate fauna in TS (see following sections).

Organic matter export

The average export (concentration \times discharge = mg AFDM/s) dropped by 16.4 \times (1.9 mg AFDM/s versus 0.1 mg AFDM/s) in TS during the treatment period (Feb. 80–Nov. 81) (Table 2). Whereas discharge declined more in RS, export in this stream dropped by only 2.8 \times (1.3 versus 0.5 mg AFDM/s) during the same period. Despite higher discharges in TS, average non-storm export during the post-treatment period was ca. 3.9 \times higher in RS.

Invertebrates colonizing litterbags

Mean invertebrate abundances and biomasses (\pm 95% CI) in TS litterbags (1087 \pm 190 individuals/bag; 42.52 \pm 4.72 mg AFDM/bag) were not significantly different from those of RS (815 \pm 115 individuals/bag; 48.84 \pm 5.81 mg AFDM/bag) during the period of February 1982 to March 1983. Shredder taxa accounted for most of the biomass of invertebrates in each stream during 1982–1983. Although total

shredder biomass did not differ significantly between streams, taxonomic differences did exist (Table 3). Biomasses of seven of the eight most abundant shredder taxa were significantly greater in one stream than the other. The plecopteran shredders, *Peltoperla* (Peltoperliidae), *Leuctra* (Leuctridae), and Nemouridae, constituted about 25% of the total shredder biomass in RS versus less than 2% in TS. Nemourids constituted a minute fraction of total shredder biomass in both streams and were the only shredders with similar biomasses in each stream. Early instars of nemourids were difficult to identify and most later instars were *Amphinemura wui* (Claassen) in RS and *Soyedina carolinensis* (Claassen) in TS. *Peltoperla*, Nemouridae, and *Leuctra* peaked at over 18 mg AFDM/bag in RS. This was attributable primarily to *Peltoperla*, which was absent or extremely rare in TS until late in the study.

Trichopteran shredders represented about 54% of total shredder biomass in RS and 60% in TS. *Pycnopsyche gentilis* (McLachlan) (Limnephilidae) contributed 52% of biomass of shredding caddisflies in RS compared to only 3.5% in TS. Conversely, *Lepidostoma* spp. (Lepidostomatidae) constituted 33.5% of caddisfly shredder biomass in RS and 86% in TS. *Pseudostenophylax uniformis* (Betten) (Limnephilidae) was found only in TS while *Fattigia pele* (Ross) (Sericostomatidae), which is common in

TABLE 3. Mean biomass (mg AFDM \pm 95% CI) per litterbag for the major shredder taxa in the reference and treatment streams during 1982–1983. These samples were taken 477 to 854 days after the last insecticide application to the treatment stream in early November 1980. An asterisk denotes that the biomass of that taxon was significantly higher in that stream. Total shredder biomass did not differ significantly between streams (RS = 27.96 ± 4.32 and TS = 24.65 ± 3.44 mg AFDM/bag).

Taxon	Reference Stream	Treatment Stream
<i>Pycnopsyche</i>	*7.750 (± 2.823)	0.517 (± 0.463)
<i>Peltoperla</i>	*5.338 (± 1.629)	0.115 (± 0.063)
<i>Lepidostoma</i>	5.042 (± 1.062)	*12.646 (± 2.028)
<i>Tipula</i>	4.096 (± 1.117)	*8.744 (± 2.531)
<i>Fattigia</i>	*2.214 (± 0.536)	0.000
<i>Leuctra</i>	*0.932 (± 0.233)	0.098 (± 0.040)
Nemouridae	0.251 (± 0.081)	0.231 (± 0.065)
<i>Pseudostenophylax</i>	0.000	*1.556 (± 1.342)

RS and all undisturbed streams at CHL, was not found in TS during 1982–1983. Together, *Tipula* (Diptera: Tipulidae) and *Lepidostoma* maintained a high, continuous, shredder biomass in the litterbags of TS throughout this study.

Biomasses of predominant non-shredding taxa are summarized in Table 4. The collector-gathering insects, Collembola, Chironomidae (all non-Tanypodinae), and Ephemeroptera (*Paraleptophlebia* [Leptophlebiidae], *Stenonema* [Heptageniidae], and *Ephemerella* [Ephemerellidae]), had significantly greater biomasses in RS than TS. However, total biomass of the collector-gatherer functional group did not differ significantly between streams.

Diplectrona metaqui Ross (Trichoptera: Hydroptychidae) was the only filter feeder with significantly greater biomass in TS (Table 4). During the initial treatment of TS in 1980, *D. modesta* was over $9 \times$ more abundant than *D. metaqui* in the drift. However, throughout the 1982–1983 study only *D. metaqui* was taken from TS litterbags and only *D. modesta* from RS litterbags. Biomass of *D. modesta* in RS (0.6 mg/bag) exceeded that of *D. metaqui* in TS (0.04 mg/bag) until the summer of 1982 after which *D. metaqui* in TS (3.1 mg/bag) exceeded that of *D. modesta* in RS (1.2 mg/bag).

Total invertebrate predator biomass did not differ significantly between streams. Based on biomass, *Lanthus* near *vernalis* Carle (Odonata: Gomphidae) was the dominant invertebrate predator in each stream. *Lanthus* was the only large insect predator that survived repeated pesticide treatments in TS (Cuffney et al. 1984). *Hexatoma* (Diptera: Tipulidae), *Acronuria* (Plecoptera: Perlidae), *Isoperla* (Plecoptera: Perlod-

idae), and *Rhyacophila* spp. (Trichoptera: Rhyacophilidae) had significantly higher biomasses in RS than TS (Table 4). Reappearance of plecopteran predators in TS was not evident until the late summer 1982. Tanypodinae were the only predators whose biomass was significantly higher in TS than in RS.

Taxonomic versus trophic recovery

Initial treatment resulted in massive invertebrate drift: $>320,000$ organisms during the first week of treatment (Cuffney et al. 1984, Wallace et al. 1982b). The composition of this drift (i.e., pretreatment community structure) was more similar to taxa colonizing litterbags of RS in 1980–1981, 1982–1983, and TS in 1982–1983 than to litterbags of TS in 1980–1981 (Table 5). Furthermore, both abundances and biomasses of taxa in litterbags were much more similar between study years in RS than in TS. Abundances of taxa were slightly more similar between RS and TS in 1982–1983 than between years in RS. In contrast, biomasses were much more similar between years in RS. These differences are largely attributable to the abundance of early instars during recolonization of TS, especially during the summer through autumn of 1982. These early instars contributed more to abundance than to biomass similarities. In spite of the relatively high similarity in abundances between RS and TS in 1982–1983, large differences still exist in important groups which contribute significantly to biomass (Tables 3 and 4).

Initial treatment produced large disparities in the distribution of functional feeding groups

TABLE 4. Mean biomass (mg AFDM \pm 95% CI) per litterbag for the major collector-gatherer, collector-filterer, and predator taxa in the reference and treatment streams during 1982-1983. An asterisk denotes that the biomass of that taxon was significantly higher in that stream.

Taxon	Reference Stream	Treatment Stream
Collector-gatherers		
Chironomidae ^a	*4.686 (\pm 0.880)	2.956 (\pm 0.473)
Copepoda	0.851 (\pm 0.146)	*2.801 (\pm 0.741)
Oligochaeta	1.265 (\pm 0.247)	1.337 (\pm 0.285)
Collembola	*1.892 (\pm 0.457)	0.857 (\pm 0.221)
<i>Paraleptophlebia</i>	*0.359 (\pm 0.086)	0.023 (\pm 0.021)
<i>Stenonema</i>	*0.311 (\pm 0.152)	0.012 (\pm 0.017)
<i>Ephemerella</i>	*0.035 (\pm 0.016)	0.000
Collector-filterers		
<i>Diplectrona metaqui</i>	0.000	*1.734 (\pm 0.603)
<i>Diplectrona modesta</i>	*0.767 (\pm 0.200)	0.000
<i>Wormaldia moesta</i>	0.099 (\pm 0.030)	0.067 (\pm 0.034)
<i>Dixa</i>	*0.225 (\pm 0.061)	0.092 (\pm 0.042)
<i>Simulium</i>	*0.023 (\pm 0.022)	0.000
Predators		
<i>Lanthus</i>	4.280 (\pm 1.020)	3.083 (\pm 2.206)
Chironomidae ^b	0.654 (\pm 0.097)	*1.893 (\pm 0.273)
Ceratopogonidae	1.062 (\pm 0.265)	1.016 (\pm 0.285)
<i>Hexatoma</i>	*1.591 (\pm 0.364)	0.023 (\pm 0.016)
<i>Acroneuria</i>	*0.963 (\pm 0.518)	0.059 (\pm 0.089)
<i>Pedicia</i>	0.175 (\pm 0.137)	0.745 (\pm 0.508)
<i>Rhyacophila</i>	*0.681 (\pm 0.272)	0.064 (\pm 0.065)
Turbellaria	0.471 (\pm 0.103)	0.697 (\pm 0.212)

^a Includes all non-Tanypodinae.

^b Tanypodinae.

between TS and RS, especially with respect to shredders and collector-gatherers (Fig. 1). Pre-treatment trophic composition of TS, based on biomasses of functional feeding groups in the drift, was much more similar to that of litterbag fauna of RS during 1980-1981, 1982-1983, and TS in 1982-1983 than to that of TS in 1980-1981 (Fig. 1 and Table 6). More than 1200 shredders/m² of wetted stream area drifted from the TS during the initial application of pesticide on 16 February 1980. Most of the shredder biomass in the TS litterbags of 1980-1981 was collected before the second application of methoxychlor on 10 May 1980. Thereafter (May 1980 to February 1981), litterbags in this stream were colonized primarily by oligochaetes (Cuffney et al. 1984). Functional group abundances and biomasses were much more similar between years in RS than in TS. Considerable trophic similarity (Fig. 1 and Table 6) (see *Invertebrates colonizing litterbags*, above) had been restored in TS by 1982-1983. Restoration of lit-

ter breakdown rates (Table 1) coincided with recovery of shredder biomass in TS despite differences which persisted among individual shredder taxa (Table 3).

Discussion

Restoration of leaf litter processing rates and organic seston concentrations in TS coincided with recolonization by shredding taxa such as *Lepidostoma*, *Pseudostenophylax*, and *Tipula* (Table 3) implying that these insects are the causative agents. However, other factors such as physical abrasion, microbial maceration, and invertebrate activities (bioturbation) must also be considered. Physical abrasion does not appear to be a reasonable mechanism for the between-year differences observed for leaf breakdown rates in TS because litter processing rates in RS were similar between years. Furthermore, between-year extremes in discharge were greater in RS than in TS. Microbial maceration

TABLE 5. Top: proportional similarity of litterbag taxa and 1980 drift from the treatment stream (TS) during initial insecticide application based on abundances. Bottom: the same based on mean biomass of individual taxa in litterbags. Small invertebrates, i.e., Copepoda, Hydracarina, Collembola, and Nematoda, were excluded from the analyses of abundances (see text); these invertebrates represented 20 to 59 percent of total abundances but <7 percent of total biomass. The 1980-1981 litterbag and drift data are expanded from Cuffney et al. 1984.

Proportional Similarity Based on Abundances				
	Litterbags			
	RS 1980-1981	RS 1982-1983	TS 1980-1981	TS 1982-1983
Litterbags RS 1982-1983	0.626			
Litterbags TS 1980-1981	0.306	0.140		
Litterbags TS 1982-1983	0.572	0.673	0.177	
TS Drift in 1980 ^a	0.563	0.626	0.071	0.562

Proportional Similarity Based on Biomass				
	Litterbags			
	RS 1980-1981	RS 1982-1983	TS 1980-1981	
Litterbags RS 1982-1983	0.750			
Litterbags TS 1980-1981	0.242	0.249		
Litterbags TS 1982-1983	0.374	0.483	0.250	

^a Used to estimate pretreatment community structure (see text).

may also enhance the breakdown rate of leaf litter (Suberkropp and Klug 1980). However, we have evidence suggesting that the reduced breakdown rates of leaves during the initial study were not the result of lower microbial activity during and following methoxychlor treatment. Laboratory respiration studies of conditioned leaf litter in 10 ppm methoxychlor failed to show any reduction in microbial activity (Wallace et al. 1982b). During the initial treatment, ATP measurements were similar for CPOM (leaf detritus) in both streams, and levels of ATP associated with FPOM sediments were higher in TS than in RS (Cuffney et al. 1984). Likewise, during the second year of recovery, ATP, INT dehydrogenase activity, and bacterial cell counts (epifluorescent direct counts using acridine orange) were all higher in FPOM sediments of TS than in RS (Vogel 1984). Non-feeding, locomotive activities of invertebrates may enhance export of FPOM by dislodging particles that are in benthic storage. Headwater streams are retentive (e.g., Cummins et al. 1983) and large amounts of FPOM, up to 3 kg AFDM/m² (T. F. Cuffney and J. B. Wallace, unpublished data) are stored in these systems. Consequently, we feel that the combination of CPOM shredding and bioturbation by inver-

tebrates is the most important factor leading to restoration of litter processing rates and export.

Restoration of the biomass of filter-feeders in TS (primarily by *D. metaqui* during the summer of 1982) followed that of the shredding taxa suggesting a link between FPOM generation (Table 2, TS seston of Period 3) and activities of shredders and other recolonizing invertebrates. This linkage between invertebrates and seston supports concepts of headwater stream ecosystems which suggest that they operate in a serial configuration (sensu O' Neill and Reichle 1980), implying that shredders and/or microbes must process CPOM to FPOM before it can be used by collectors (i.e., Cummins 1974, Vannote et al. 1980). Hence, our results do support an important role for invertebrates in upstream to downstream linkages in retentive headwater streams.

Recolonization of the TS was slow (>2 years) with early instars of many species reappearing during the summer and early autumn of 1982. In contrast, studies elsewhere report rapid colonization by drift of invertebrates from upstream sources (Gore 1982, Sheldon 1984, Williams and Hynes 1976, 1977). Drift cannot be a major mechanism or source of insect recolonization.

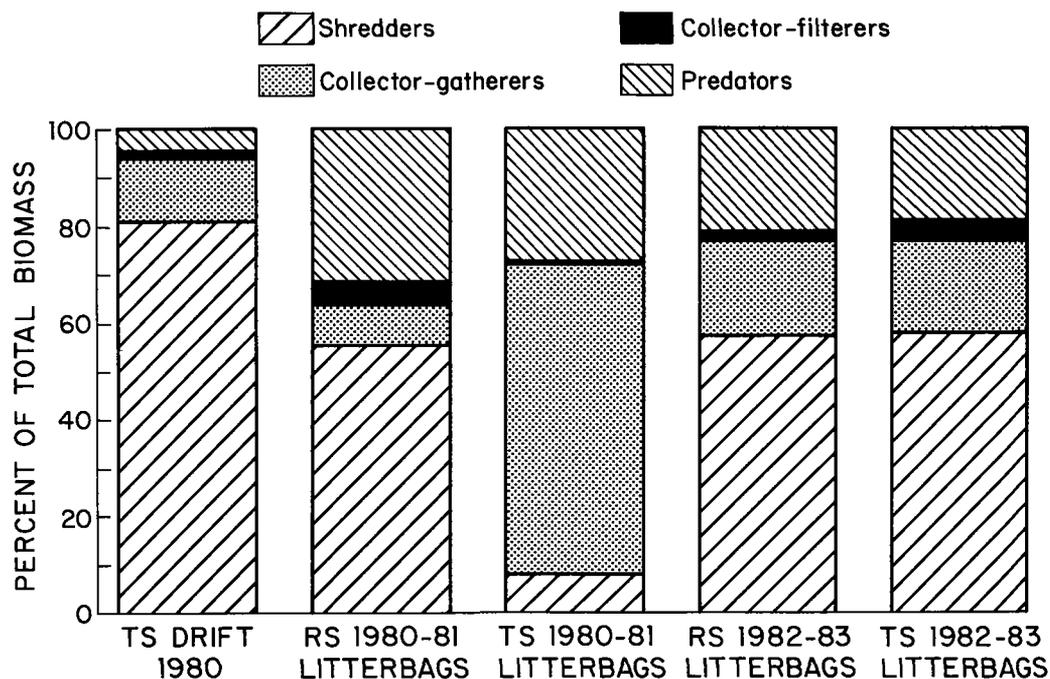


FIG. 1. Percent composition based on total biomass by functional feeding group of all macroinvertebrates. The TS pretreatment data are based on the composition of the drift during the initial pesticide treatment in February 1980 (see text). Litterbag fauna represents that recovered from reference stream (RS) and treatment stream (TS) in 1980-1981 and 1982-1983. Litterbag samples include annual means per litterbag for all invertebrates.

zation in this headwater stream because the insecticide was applied up to the source. Some taxa, e.g., *Diplectrona metaqui*, *Pseudostenophylax*, and *Lepidostoma* spp. are possibly exceptions as they may have occurred in small seepage areas overlooked during treatments. Upstream movements, within either the water column or substrate, are unlikely routes for recolonization because the lower 150 m of TS, between the flume and the junction of TS with Shope Creek,

has a steep gradient (>0.4 m per m) and a series of small waterfalls flowing over granitic bedrock. The flume also represents a barrier to such upstream migrations. Ovipositing aerial adults appear to be the main source of insect recolonization in TS based on the first reappearance of early instars of many Ephemeroptera, Plecoptera, and Trichoptera during the summer and early autumn of 1982.

The slow return of many taxa is probably at-

TABLE 6. Proportional similarity by functional feeding group biomass including all invertebrates collected in litterbags from the reference stream (RS) and treatment stream (TS) on all dates and total invertebrate drift from TS during the initial insecticide treatment in February 1980.

	Litterbags			
	RS 1980-1981	RS 1982-1983	TS 1980-1981	TS 1982-1983
Litterbags RS 1982-1983	0.869			
Litterbags TS 1980-1981	0.447	0.500		
Litterbags TS 1982-1983	0.868	0.971	0.472	
TS Drift in 1980 ^a	0.704	0.758	0.258	0.768

^a Used to estimate pretreatment community structure (see text).

tributable to long life cycles and poor dispersal abilities. Many taxa have restricted adult flight periods and some apparently have poorer dispersal abilities (e.g., some stoneflies) than others (e.g., some Trichoptera and Diptera). For example, plecopterans such as *Peltoperla*, which dominated pretreatment shredder populations in TS based on drift obtained during the initial treatment in 1980 ($>1000/m^2$ or 1.9 g AFDM/ m^2 of wetted stream area), showed little evidence of return by 1982-1983 (Table 3).

This slow reappearance of taxa contrasts with the rapid recovery observed in warm desert streams, where unpredictable and catastrophic flooding may eliminate up to 95% of the insect taxa. These desert species have short life cycles which ensure rapid recolonization by adults from adjacent riparian areas (Fisher et al. 1982, Gray 1981, Gray and Fisher 1981). Although headwater streams at CHL are subject to frequent spates, disruptive effects are tempered by stable substrate, debris dams, and invertebrate species that are adapted to these modest disturbances. In contrast, the application of insecticide to TS constituted a severe, rare anthropogenic disturbance for which no historical equivalent is known. Thus, without prior exposure to such a disturbance there is no evolutionary basis upon which either a specific or community response can be framed (e.g., life history or physiological resistance). Prior exposure, frequency, and the nature of the disturbance influence species composition and the response of a given community to the disturbing force. Our results apply to situations where the original disturbance is removed, i.e., cessation of pesticide treatment, and not to conditions such as long-term acidification of freshwaters.

Other stream studies at CHL, which have focused on the response of stream biota and processes to catchment disturbance, e.g., clearcutting (Gurtz and Wallace 1984, Haefner and Wallace 1981, Webster and Patten 1979, Webster et al. 1983), have emphasized functional characteristics rather than community structure (Webster et al. 1983). Watershed disturbances such as clearcutting alter both the physical environment and energy inputs to the system. For these disturbances, the traditional view of stability as the return of a disturbed community to some original predisturbance configuration may not be feasible without ex-

tremely long-term studies. Such disturbances may influence retention characteristics for decades (e.g., Likens and Bilby 1982), resulting in long-term physical alterations which influence community structure and thereby confound measurements relating solely to stability or persistence of fauna through time. Compared to clearcutting, insecticide treatment is a disturbance that does not alter either physical structure or energy inputs and offers an excellent means for examining system recovery in a relatively short time. The recovery of shredder biomass following the initial massive loss from TS, restoration of leaf litter processing rates, and increase in organic seston concentrations in TS relative to RS, without corresponding taxonomic recovery, support the concept that stream ecosystems are resilient to disturbance, i.e., have the ability to absorb change and resume behavior and function similar to those of undisturbed systems (Holling 1973). Although, on recovery, large differences still existed between RS and TS with respect to certain taxa, trophic structure was similar between streams. Thus, restoration of function may occur in a manner not recognized solely by taxonomic criteria.

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