

First-year benthic recovery of a headwater stream following a 3-year insecticide-induced disturbance

M.R. WHILES AND J. BRUCE WALLACE

Department of Entomology, University of Georgia, Athens, Georgia 30602 U.S.A.

SUMMARY

1. A headwater stream (C54) was treated seasonally (twelve times from December 1985 to October 1988) with the insecticide methoxychlor for 3 years, resulting in 72 and 75% reductions of insect abundances and biomass, respectively. Following treatment, monthly benthic abundances and biomass were measured in the treated stream and a nearby reference stream (C55) in order to assess recovery. Seasonal average abundances and biomass were calculated from samples taken from December 1988–December 1989, the first post-treatment year of C54.
2. Non-insect abundances and biomass were higher in the recovering stream during the winter + spring and summer periods, but were similar to the reference stream by autumn. Abundances and biomass of collector–filterers, scrapers, and shredders were all lower in the recovering stream during winter + spring; however filterers and scrapers were similar to reference stream values by the end of the recovery year. No distinct differences were seen between collector–gatherers and predators throughout the year.
3. Univoltine and multivoltine taxa, along with treatment-resistant taxa, were the most important contributors to recovery of C54. Taxa with longer generation times, life histories which were more vulnerable to timing of treatments, and/or poor dispersal abilities were poorly represented during first-year recovery.
4. Abundance data alone were not sufficient for a complete analysis of recovery. Biomass estimates reflected differences in taxonomic composition and developmental stages between streams after 1 year of recovery.

Introduction

Studies of ecosystem disturbance and subsequent recovery provide insight into mechanisms of community structure (Hurlbert, 1975; Gray, 1981; Gray & Fisher, 1981; Wallace *et al.*, 1989), as well as information on the resistance and resilience of individual systems (Molles 1985; Grimm & Fisher, 1989). For these reasons, disturbance studies have become an important component of stream ecosystem research (Resh *et al.*, 1988).

Patterns of recovery (e.g. recolonization of macroinvertebrate communities) in lotic systems following disturbance are dependent upon the nature of the disturbance. Bender, Case & Gilpin (1984) distinguished press and pulse disturbances as the two major disturbance types. Press disturbances are chronic disturbances which may affect the physical

structure of the stream involved, as opposed to pulse disturbances which are limited in temporal scope and do not involve changes to the physical structure of the stream or catchment. In general, press disturbances are associated with longer recovery periods than pulse disturbances (Niemi *et al.*, 1990). Disturbances of either type can vary greatly both spatially and temporally, however, substantially affecting rates and patterns of recovery (see Wallace, 1990 and Yount & Niemi, 1990 for reviews).

Once recovery is initiated, a variety of factors involving the disturbed system, as well as the colonizing organisms, influence the process. Niemi *et al.* (1990) examined several aquatic case studies and concluded that the most important factors influencing recovery, independent of the specific taxa involved, related to the overall nature (press or pulse) and timing of the disturbance, the presence of refugia,

barriers to dispersal, and the proximity of sources for colonists. Characteristics of the resident taxa that affect recolonization include generation times and vagility of influenced populations (see review by Wallace, 1990). Gray (1981) and Fisher *et al.* (1982) demonstrated that, in a Sonoran Desert stream, frequent and unpredictable spates have favoured an invertebrate community capable of rapid recolonization following reductions of up to 95% of invertebrate densities. These observations suggest that the taxonomic composition of a given stream may be a product of the disturbance regime within that system.

Studies of post-disturbance recovery often examine only the presence and abundances of taxa (Niemi *et al.*, 1990). In some cases, disturbances can actually lead to increases in densities of certain taxa, as a result of a reduction in predation and/or competition for resources (Hurlbert, 1975). Immediately following disturbance, smaller taxa with faster generation times may colonize rapidly, resulting in high total invertebrate densities, despite taxonomic differences from pretreatment or reference system communities (Wallace, Vogel & Cuffney, 1986; Lugthart & Wallace, 1992). In a study examining the effects of insecticide treatment on the invertebrate community in a headwater stream, Lugthart & Wallace (1992) demonstrated that estimates of biomass and secondary production were preferable to density data alone.

The objectives of this study were to examine benthic macroinvertebrate community recovery in a headwater stream following repeated applications of insecticide (a pulse disturbance). Abundance and biomass data were used to examine the recovery of the benthic macroinvertebrate community for 1 year following a 3 year period of seasonal insecticide treatments. Furthermore, both functional and taxonomic recovery were assessed by comparisons to pretreatment and reference stream conditions.

Study site

The two streams studied are located at the Coweeta Hydrologic Laboratory (U.S. Forest Service) in Macon county, North Carolina. The entire Coweeta drainage basin is 1625 ha and is located in the Blue Ridge Province of the southern Appalachian Mountains. Both streams are first order and drain catchments (C) 54 and 55. Riparian vegetation at Coweeta con-

sists of oak (*Quercus* spp.) and hickory (*Carya* spp.) dominated mixed hardwoods. Low-order streams are heavily shaded by dense rhododendron (*Rhododendron* spp.) growth throughout the year. Physical characteristics of both study streams are summarized in Table 1.

The predominant substratum in the study streams was a mixture of sand, gravel, pebble and cobble, which is referred to as mixed substratum here. Mixed substrata composed 65 and 87% of the length of the treated (C54) and reference (C55) streams, respectively. The remaining substratum in each stream was bedrock outcrop. Due to high streambed roughness, both streams retain large amounts of woody debris and leaf litter (Lugthart & Wallace, 1992). Additional information on the study streams is given by Cuffney & Wallace (1988) and Cuffney, Wallace & Lugthart (1990). Detailed information on the Coweeta basin, including stream chemistry, can be found elsewhere (Swank & Crossley, 1988).

Prior to this study, C54 was treated seasonally for 3 consecutive years (1986–1988) with the insecticide methoxychlor(1,1,1-trichloro-2,2-bis[*p*-methoxyphenyl] ethane; CAS no. 72-43-5) (see Wallace, Huryn & Lugthart, 1991). Hand sprayers were used to treat the entire length of the stream channel from the flume to the spring seep at a rate of 10 mg l^{-1} , based on flume discharge. Insecticide treatment induced

Table 1 Physical characteristics of the study streams. Elevations were measured at the gauging flumes

	C54	C55
Catchment		
Area (ha)	5.5	7.5
Elevation (m a.s.l.)	841	810
Channel		
Length (m)	260	170
Gradient (cm m^{-1})	33	20
Substrate		
Bedrock outcrop (%)	35.2	13.1
Mixed substrates (%)	64.8	86.9
Discharge		
Average 1989 (l s^{-1})	1.97	2.34
Temperature ($^{\circ}\text{C}$)		
Average (1986–1990)	12.0	12.1
Min. (1986–1990)	1.1	1.6
Max. (1986–1990)	19.6	19.5
Annual degree days	4402	4464

massive invertebrate drift (Wallace *et al.*, 1989). Annual average abundances, biomass, and production of insects during the first year of treatment were reduced by 72, 75, and 80%, respectively (Lugthart & Wallace, 1992). In contrast, non-insect abundances and production increased by 35 and 40%, respectively. Non-insect biomass decreased by approximately 40%, as a result of the loss of decapods. Seasonal treatment of C54 continued for 3 consecutive years, with the final treatment in October 1988. Recovery sampling began in December 1988, corresponding with what would have been the winter insecticide application.

During one of the 1985–1988 treatment years of C54 (1986), record drought conditions prevailed (55 years of record) (Coweeta Hydrologic Laboratory, unpublished). In contrast, the 1989 recovery sampling year was the wettest on record.

Methods

Monthly benthic samples were collected from the treated stream (C54) for a 1 year period beginning in December 1988. The reference stream (C55) was sampled during alternate months over the same time period. Four mixed substrate, and three bedrock outcrop samples were collected on each sampling date. Sampling sites within each stream were randomly selected prior to each sampling date.

Mixed substratum samples were taken with a 400 cm² coring device from areas of the stream where the substratum consisted of various combinations of sand, gravel, pebble and cobble. All material in the corer was removed to a depth of approximately 10 cm or until bedrock was contacted. Bedrock outcrop habitats were sampled by scraping and brushing all associated material from a 15 × 15 cm area into a plastic bag held against the rock surface at the bottom edge of the sampled area.

All organic material in the samples was elutriated from inorganic substrates and passed through 1 mm and 250 μm nested sieves. Samples were preserved in a 6–8% formalin solution containing Phloxine B dye. Animals in the >1 mm fraction were removed by hand sorting under a dissecting microscope using ×15 magnification. The <1 mm >250 μm fraction of each sample was subsampled ($\frac{1}{4}$ to $\frac{1}{64}$ of sample) using a sample splitter (Waters, 1969), prior to removal of animals under a dissecting microscope.

Animals were identified, counted and measured

(total body length) with a dissecting microscope equipped with a graduated stage. Insects were identified to genus and species whenever possible, except for chironomids which were identified as Tany-podinae or non-Tany-podinae. Most non-insect taxa were identified only to order. Biomass estimates (ash free dry mass [AFDM]) for all insect taxa and large non-insect taxa were made using length–weight regressions derived from animals in the study streams, other streams at Coweeta (Huryn, 1986), or other North Carolina streams (Smock, 1980). Biomass estimates for small non-insect taxa (e.g. Copepoda, Hydracarina) were obtained by determining mean individual biomass from >50 individuals in each size class.

All taxa were assigned to a functional feeding group based on Merritt & Cummins (1984), or our knowledge of local fauna. Crayfish numbers and biomass were divided among shredders (1/2), collector–gatherers (1/4), and engulfing predators (1/4) (Huryn & Wallace, 1987).

Monthly and seasonal (winter + spring, summer, autumn) averages of biomass and density were calculated for each taxon in each stream. Habitat-weighted [(bedrock outcrop total × % bedrock outcrop) + (mixed substratum total × % mixed substratum)], as well as average abundances and biomass on each substratum were also calculated for each taxon. In most cases, standard deviations were proportional to mean values, necessitating log [$\log(x + 1)$] transformations of mean values (Zar, 1984). Confidence intervals (95%) for transformed mean values were calculated when comparisons between the two streams were made (Zar, 1984). Differences between mean values were considered significant ($P < 0.05$) when 95% confidence intervals did not overlap, a conservative test for differences (Zar, 1984).

Results

Yearly comparisons: pretreatment, treatment, and recovery

Annual average abundances (habitat-weighted) of insect taxa increased from 9807 ind. m⁻² during treatment to 20 176 ind. m⁻² during the recovery year (Fig. 1a). Non-insect taxa, which increased in abundance during treatment, remained abundant during the recovery period (Fig. 1b), resulting in higher over-

all invertebrate densities in the treated stream during the recovery year (74 992 ind.m⁻²) than the pretreatment (69 532 ind.m⁻²) or treatment (61 324 ind.m⁻²) periods (Fig. 1c). Insect biomass increased from 441 mg m⁻² during treatment to 987 mg m⁻² during the recovery year. Despite greater abundances in the treated stream, total invertebrate biomass was well below that of pretreatment conditions, and reflects the small size of most non-insect taxa (Fig. 1c).

Invertebrate community comparisons: treated v reference

No significant differences in seasonal average abundances (habitat-weighted) of total invertebrates or total insects in the recovery and reference streams were evident during the recovery year (Table 2). Insect biomass was significantly lower ($P < 0.05$) in the recovering stream during the winter + spring period. With the exception of the summer period, total invertebrate and total insect biomass remained slightly lower than that of the reference stream.

Abundances (habitat-weighted) of non-insect taxa in C54 were significantly higher than in the reference stream during initial recovery months (winter + spring). Despite decreases, non-insect abundances in C54 remained slightly higher than in the reference stream throughout first-year recovery (Table 2). Non-insect biomass was also significantly greater during the winter + spring period in the recovering stream, but declined through the year and was slightly less than that of the reference stream by autumn (Table 2).

The relative contribution of insects and non-insects to total invertebrate abundances and biomass differed greatly between streams (Table 2). Insect abundance in the reference stream decreased during the summer, but accounted for a larger proportion of invertebrate abundance than in the recovering stream throughout the year. Insects in the reference stream accounted for over 90% of total invertebrate biomass during the winter + spring period (Table 2). This proportion decreased through the year, largely because of the contribution of decapods to non-insect biomass. The contribution of insect taxa to total invertebrate biomass in the recovering stream was less than that of the reference stream early in the recovery year, but greater during summer and autumn (Table 2).

Dipterans, particularly Chironomidae and Cera-

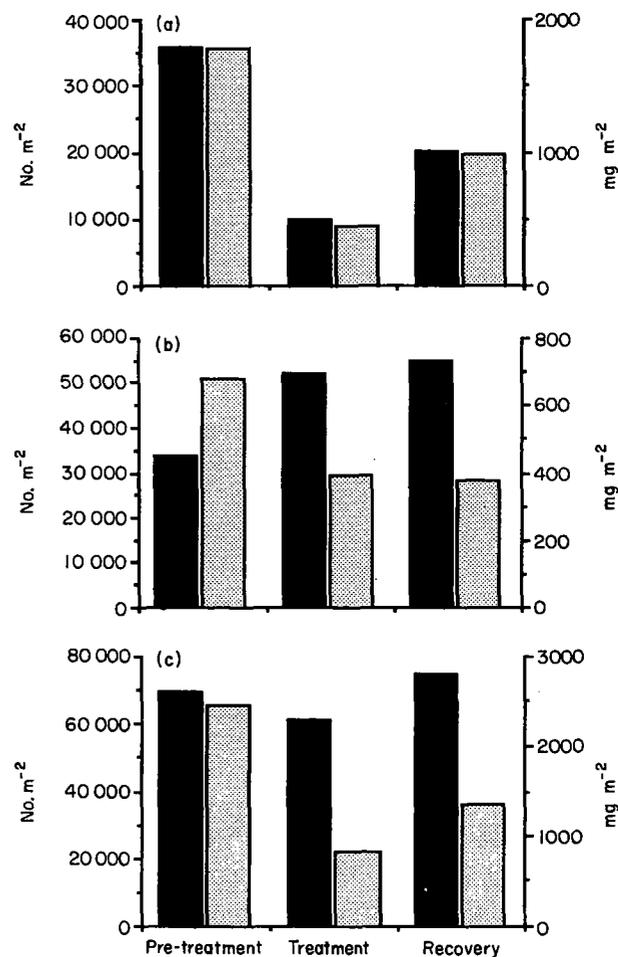


Fig. 1 Average annual habitat-weighted abundances (no. m⁻²) and biomass (mg AFDM m⁻²) of (a) insects, (b) non-insects, and (c) total invertebrates in C54 pretreatment, during treatment, and during first year recovery. Note different axis for abundance and biomass. Pretreatment and treatment data from Lughart & Wallace (1992). ■, abundances;▨, biomass.

topogonidae, dominated the insect communities of both streams, accounting for 94 and 88% of the habitat-weighted annual averages of insect abundances in the recovery and reference stream, respectively (Table 3). Dipterans also constituted approximately 45% of insect biomass in both streams. With the exception of odonates, abundances and biomass of exopterygote taxa (Ephemeroptera, Plecoptera), as well as Trichoptera and Coleoptera were all lower in the recovering stream (Table 3).

Copepods, nematodes, oligochaetes, and Hydra-carina dominated non-insect abundances in both streams (Table 3). Habitat-weighted abundances of

Table 2 Habitat-weighted average abundance (no. m⁻² ± SE) and biomass (mg AFDM m⁻² ± SE) of invertebrates (IN, insects; NI, non-insects) in the treated (C54) and reference (C55) streams during December 1988–April 1989 (winter + spring), May 1989–September 1989 (summer), and October 1989–December 1989 (autumn). * non-overlapping 95% confidence intervals between [log(x + 1)] transformed seasonal values

Group	Winter + Spring		Summer		Autumn	
	C54 (n = 35)	C55 (n = 21)	C54 (n = 35)	C55 (n = 14)	C54 (n = 21)	C55 (n = 14)
Abundances						
IN	23557 ± 4516	29316 ± 9277	19712 ± 3379	9678 ± 2173	17260 ± 3004	17998 ± 3727
NI	77507 ± 11937*	26668 ± 9936*	54109 ± 8118	14336 ± 3731	32834 ± 9136	19907 ± 7316
%IN	23%	52%	27%	40%	34%	47%
Biomass						
IN	1251 ± 326*	1641 ± 199*	889 ± 139	736 ± 173	815 ± 158	1011 ± 231
NI	551 ± 90*	140 ± 61*	425 ± 97	536 ± 454	153 ± 39	922 ± 646
%IN	69%	92%	68%	58%	84%	52%

Table 3 Invertebrate community composition in the treated (C54) and reference (C55) streams during 1989. Values are mean annual habitat-weighted abundances, and ash-free dry mass

Taxa	Abundance (no. m ⁻²)		Biomass (mg m ⁻²)	
	C54	C55	C54	C55
Insects				
Ephemeroptera	179	297	21	40
Odonata	82	43	306	168
Plecoptera	305	1022	45	167
Trichoptera	589	646	164	249
Coleoptera	63	143	7	29
Diptera	18 958	16 843	444	564
Insect total	20 176	18 994	987	1217
Non-insect taxa				
Oligochaeta	7266	3240	302	113
Nematoda	7524	5561	6	4
Turbellaria	572	137	19	5
Cladocera	1036	37	2	<1
Copepoda	32 851	9795	33	10
Ostracoda	202	45	<1	<1
Acari	5365	1495	14	4
Decapoda	0	3	0	418
Total non-insects	54 816	20 313	376	554
Total invertebrates	74 992	39 307	1363	1771

all non-insect taxa were considerably higher in the recovering stream than in the reference stream. Decapods, which constituted 75% of the non-insect biomass in the reference stream, were not found in the recovering stream during the recovery year. Excluding decapods, non-insects accounted for 28

and 8% of total invertebrate biomass in the recovery and reference stream, respectively (Table 3).

Functional group comparisons: treated v reference

Habitat-weighted abundances and biomass of shredders, collector-filterers, and scrapers were initially all significantly lower ($P < 0.05$) in the recovering stream (winter + spring) (Table 4). Except for decapods, insects were the only representatives of these functional groups in the study streams. Collector-gatherers and predators, functional groups which contain large numbers of non-insect taxa and dipterans, showed no significant differences between the two streams, although abundances of both were somewhat higher in the recovering stream until autumn (Table 4). During the summer and autumn, there were no significant differences in functional group abundances and biomass between the two streams, although values for shredders remained somewhat lower in the recovering stream (Table 4).

Relative abundances of functional groups in each stream were similar throughout the study period. Patterns of invertebrate functional group abundance in both streams during 1989 were collector-gatherers > predators > shredders > collector-filterers > scrapers (Table 5). Despite similarities in relative abundances, functional-group biomass differed between streams. Shredders dominated biomass in the reference stream, followed by predators > collector-gatherers > collector-filterers > scrapers. In contrast, biomass in the treated stream was dominated by

Table 4 Habitat-weighted average abundance (no. $m^{-2} \pm SE$) and biomass (mg AFDM $m^{-2} \pm SE$) of invertebrate functional groups (CF, collector-filterer; CG, collector-gatherer; PR, predator; SC, scraper; SH, shredder) in the treated (C54) and reference (C55) streams during December 1988–April 1989 (winter + spring), May 1989–September 1989 (summer), and October 1989–December 1989 (autumn). * non-overlapping 95% confidence intervals between $[\log(x + 1)]$ transformed seasonal values

Group	Winter + Spring		Summer		Autumn	
	C54 (n = 35)	C55 (n = 21)	C54 (n = 35)	C55 (n = 14)	C54 (n = 21)	C55 (n = 14)
Abundance						
CF	53 ± 51*	130 ± 56*	429 ± 133	263 ± 120	348 ± 163	280 ± 97
CG	86 494 ± 11 716	46 799 ± 16 999	62 438 ± 9 165	19 430 ± 4 774	39 180 ± 9 403	31 636 ± 9 700
PR	14 080 ± 2 607	6 852 ± 1 977	10 024 ± 1 885	3 479 ± 978	9 620 ± 2 770	4 580 ± 1 020
SC	4 ± 2*	125 ± 45*	258 ± 188	233 ± 135	147 ± 105	203 ± 76
SH	438 ± 238*	2 079 ± 462*	674 ± 178	608 ± 141	802 ± 217	1 205 ± 313
Biomass						
CF	3 ± 2*	89 ± 33*	97 ± 41	25 ± 10	161 ± 56	85 ± 26
CG	708 ± 130	294 ± 77	541 ± 107	256 ± 128	253 ± 49	412 ± 177
PR	749 ± 194	695 ± 132	473 ± 89	427 ± 149	298 ± 85	433 ± 193
SC	1 ± 1*	34 ± 15*	15 ± 10	23 ± 12	30 ± 14	11 ± 4
SH	340 ± 112*	670 ± 104*	188 ± 42	541 ± 308	225 ± 79	991 ± 351

Table 5 Invertebrate functional group composition of the treated (C54) and reference (C55) streams during 1989. Values are mean annual habitat-weighted abundance, and ash-free dry mass

Functional group	Abundance (no. m^{-2})		Biomass (mg m^{-2})	
	C54	C55	C54	C55
Collector-filterer	276	225	87	66
Collector-gatherer	62 703	32 623	502	322
Predator	11 240	4 972	508	624
Scraper	136	188	15	24
Shredder	637	1 299	251	735
Total	74 992	39 307	1 363	1 771

collector-gatherers > predators > shredders > collector-filterers > scrapers (Table 5).

Taxonomic comparisons: treated v reference

Between-stream differences in taxonomic composition were more pronounced than those of functional groups. Taxa richness in the recovering stream during the first month of recovery was less than half that of the reference stream (Fig. 2). First appearances of most taxa in C54 occurred during the spring and summer months, but taxa richness never equalled that of the reference stream during 1989 (Fig. 2), or C54 pretreatment conditions (Lugthart & Wallace,

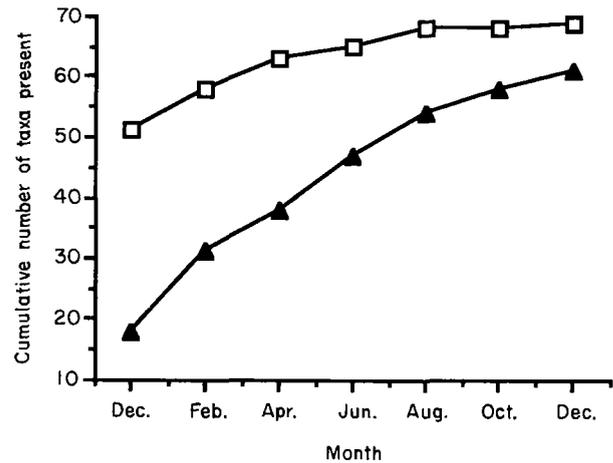


Fig. 2 Cumulative taxa richness in the treated (C54) and reference (C55) stream during the 1989 recovery year. ▲, C54; □, C55.

1992). Some taxa (e.g. *Beloneuria* [Plecoptera], *Fattigia*, *Psilotreta* [Trichoptera]) were not collected in the recovering stream during 1989, although they were present in the reference stream and C54 pretreatment. Other taxa (e.g. *Baetis* [Ephemeroptera]) colonized C54, but were not collected in the reference stream.

Many non-insect taxa persisted in C54 during the treatment period (Lugthart & Wallace, 1992; Wallace *et al.*, 1991a), and some (e.g. *Oligochaeta*, *Turbellaria*) increased in numbers during insecticide treatments

(Lugthart & Wallace, 1992). Abundances of oligochaetes (Fig. 3e), turbellarians (Fig. 3f), and most other non-insect taxa declined in C54 during the recovery year.

Odonates (*Lanthus*, *Cordulegaster*) and some Dipterans (e.g. *Tipula*) were apparently resistant to the repeated insecticide treatments and exhibited growth during treatments of C54 (Wallace *et al.*, 1991). Abundances of *Tipula* (Fig. 3d) and other resistant taxa were similar in both streams during the recovery year.

Abundances of some multivoltine insect taxa (e.g. collector-gatherer Chironomidae) (Diptera) were similar to those of the reference stream at the onset of the recovery period (Fig. 3c). In contrast, most univoltine insect taxa were not present in the treated stream at the onset of recovery, but appeared during the spring and summer. Appearances of these taxa in the recovering stream corresponded with known flight and oviposition periods at Coweeta

(Figs 3b, 4a, b, e, f). Semivoltine insect taxa either recolonized in low densities (e.g. Peltoperlidae) [Plecoptera] (Fig. 4c), or failed to recolonize during first-year recovery (e.g. *Beloneuria*, *Fattigia*).

Discussion

Mechanisms for recolonization of C54 during this study were limited by certain aspects of the stream, as well as the disturbance itself. Drift from undisturbed upstream reaches is often a major pathway for rapid recolonization of invertebrate communities (Gore, 1982; Sheldon, 1984; Williams & Hynes 1976, 1977). This study involved pesticide treatment of a headwater stream and its source, eliminating drift from upstream reaches as a pathway for recolonization. Upstream migration as a possible recolonization pathway (Soderstrom, 1987) was also prevented by the presence of a flume at the downstream end of the treated reach of stream. Because of these limi-

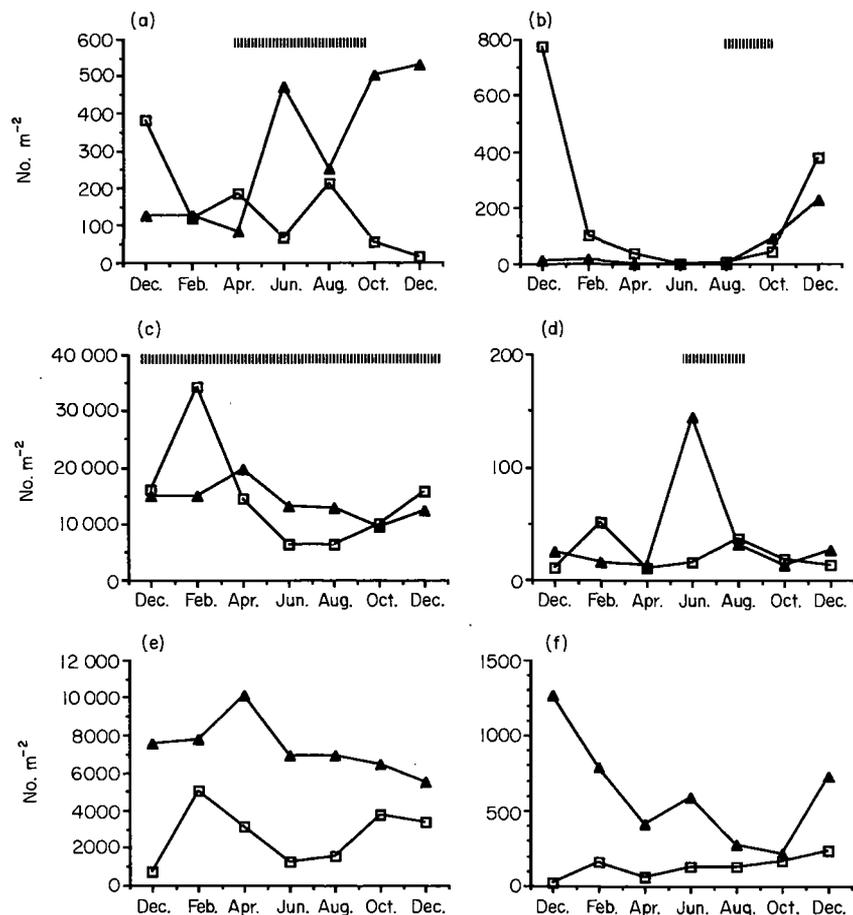


Fig. 3 Bi-monthly habitat-weighted abundance (no. m^{-2}) of (a) *Lepidostoma* and (b) *Pycnopsyche* (Trichoptera), (c) collector-gatherer chironomidae and (d) *Tipula* (Diptera), (e) Oligochaeta, and (f) Turbellaria in the treated and reference stream during the 1989 recovery year. Dashed lines indicate known flight periods at Coweeta (see text). \blacktriangle , C54 treated stream; \square , C55 reference stream.

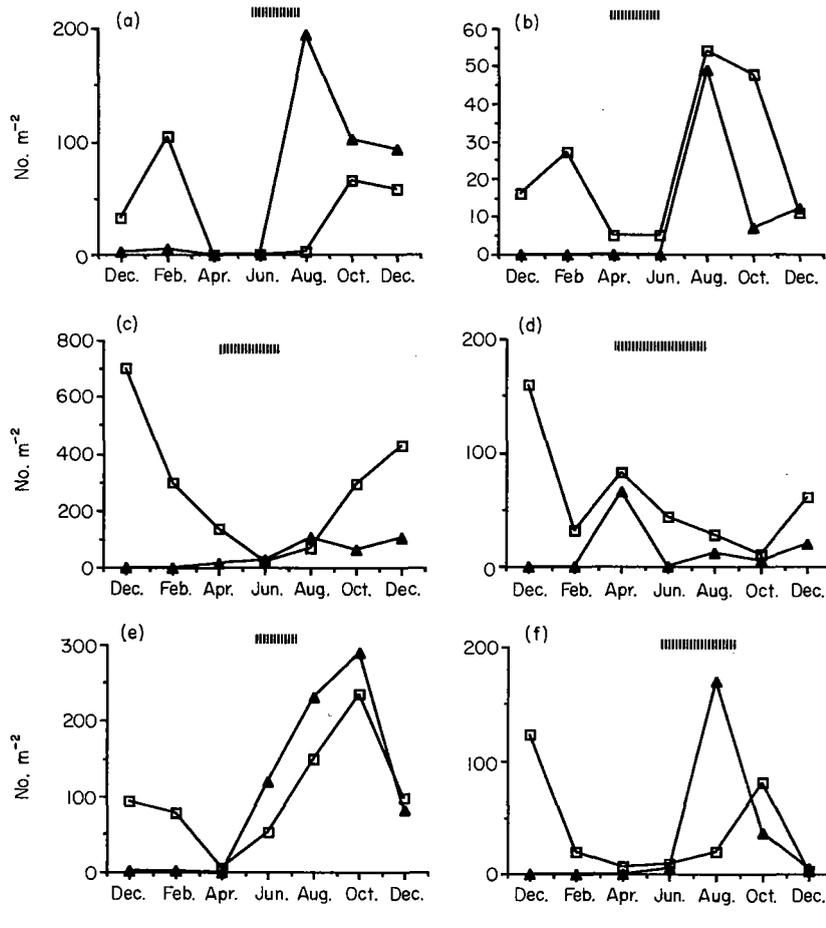


Fig. 4 Bi-monthly habitat-weighted abundance (no. m⁻²) of (a) *Serratella* and (b) *Stenonema* (Ephemeroptera), (c) Peltoperlidae and (d) *Isoperla* (Plecoptera), and (e) *Diplectrona modesta* Banks and (f) *Parapsyche cardis* Ross (Trichoptera) in the treated and reference stream during the 1989 recovery year. Dashed lines indicate known flight periods of adults at Coweeta (see text). ▲, C54; □, C55.

tations, the major pathway for recolonization of C54 was adult oviposition (Wallace *et al.*, 1991a).

The size classes present, and their temporal appearance patterns during recovery support the scenario of predominately aerial colonization by ovipositing adults. Source areas for colonizing adults at Coweeta are abundant, unlike many xeric regions where streams are often isolated (Cushing & Gaines, 1989). Polyvoltine taxa, such as collector-gatherer chironomids (Huryn, 1990), were undoubtedly present as aerial adults or resistant eggs during many of the treatments, enabling rapid recolonization.

The invertebrate community inhabiting C54 during treatment was dominated by small taxa with relatively short life cycles such as copepods, oligochaetes, and chironomids, and taxa which appeared to be resistant to treatment, such as the odonates and *Tipula* (Lugthart & Wallace, 1992; Wallace *et al.*, 1991a). Many univoltine (e.g. *Pycnopsyche*, *Lepidostoma*, *Diplectrona* [Trichoptera], *Isoperla*

[Plecoptera], *Ectopria* [Coleoptera]) and some semi-voltine (e.g. Peltoperlidae) taxa recolonized C54 between treatments, but were eliminated by subsequent treatments (Wallace *et al.*, 1991a). Compared with the pretreatment year, total invertebrate abundances during treatment of C54 were relatively unchanged (Fig. 1c). Lugthart & Wallace (1992) suggested that increases in abundances of many non-insect taxa may have been a result of lower predation pressure in the treated stream. Other studies conducted in aquatic systems have also demonstrated an increase in prey densities corresponding with a decrease in predatory macrofaunal densities (Heckman, 1981; O'Doherty, 1981).

Decreases in abundances of taxa which had previously increased with treatment (e.g. Copepoda), corresponded with the recovery of many predaceous insect taxa, suggesting that predation does influence community structure in these streams. With the exception of odonates, many predators, especially

those with longer generation times, were completely eliminated during treatment of C54. Estimates of secondary consumption of total invertebrate production decreased during the treatment period by approximately 30% (Lugthart & Wallace, 1992). Triclad (Turbellaria) increased in density and became the dominant predator on bedrock outcrops during treatment of C54 (Lugthart & Wallace, 1992). Some triclad species can prey heavily on oligochaetes (Reynoldson & Davies, 1970; Armitage & Young, 1990) which also increased in density during treatment. Both triclad (Fig. 3e) and oligochaete (Fig. 3f) densities were high in C54 at the onset of recovery, and decreased with the appearance of other predaceous taxa (e.g. *Rhyacophila* [Trichoptera], *Isoperla* [Plecoptera], *Hexatoma* [Diptera]).

Wallace *et al.* (1986), in a study examining litter processing during second-year recovery from insecticide treatment, observed functional recovery (abundances and biomass) of invertebrates in litterbags by the end of the second year; however, distinct taxonomic differences between the recovering stream and a nearby reference stream persisted. In the current study, the relative abundances of functional groups were similar in the treated and reference streams after the first year of recovery. However, differences in functional group biomass reflected continued taxonomic differences. A co-dominance of shredders, collector-gatherers, and predators was evident in both C54 and C55 prior to treatment of C54 (Lugthart & Wallace, 1992). During treatment, functional structure in C54 was dominated by collector-gatherers, while numbers of predators declined and shredders decreased substantially. The largest discrepancies in functional group biomass after first-year recovery were also attributable to shredders (Table 5).

Many shredder taxa rapidly colonized C54 during their known flight periods at Coweeta. However, some shredder taxa with similar life histories exhibited differences in colonization abilities. *Fattigia*, a semivoltine (Huryn & Wallace, 1988) shredder present in C54 before treatment (Lugthart & Wallace, 1992), as well as in the reference stream during recovery, was not encountered in C54 during first-year recovery. Peltoperlidae, which are also semivoltine at Coweeta (O'Hop, Wallace & Haefner, 1984), displayed weak colonization during first-year recovery and did not reach pretreatment (Lugthart,

Wallace & Huryn, 1991) or reference stream densities (Fig. 4c). Leaf shredding *Lepidostoma* spp. were extremely successful colonizers, achieving densities substantially higher than in C54 before treatment (Lugthart & Wallace, 1992) and in the reference stream, whereas *Pycnopsyche* spp. displayed poor colonization during first-year recovery (Fig. 3a, b). *Lepidostoma* spp. and *Pycnopsyche* spp. were equally abundant in C54 prior to treatment (Lugthart & Wallace, 1992). Wallace *et al.* (1991) observed early instars of *Pycnopsyche* drifting during the final treatment (October 1988) of C54. At Coweeta, the recruitment period of *Pycnopsyche* begins in late summer and is shorter than that of *Lepidostoma* (Huryn & Wallace, 1988) (Fig. 3a, b). Because most members of the 1988 cohort had been eliminated, *Pycnopsyche* larvae were rare in C54 until October 1989. An apparent difference in *Lepidostoma* abundances between December 1988 and December 1989 in the reference stream was most likely a result of sampling at different times of the month. Egg hatching of at least one species of *Lepidostoma* in Coweeta streams occurs from October to January (Huryn & Wallace 1988).

The decapod, *Cambarus bartonii* (Fabricius), accounted for a large portion of the shredder biomass in C54 before treatment and in the reference stream. *Cambarus bartonii* is undoubtedly limited in its ability to colonize new habitats because of the absence of an aerial adult stage adapted for dispersal. *Cambarus bartonii* was eliminated from C54 during treatment (Lugthart & Wallace, 1992; Wallace *et al.*, 1991a) and was not observed in C54 during the recovery year. Furthermore, 5 years after insecticide treatment of an adjacent stream (C53), only one *C. bartonii* was collected in an annual series ($n = 84$) of benthic samples (Lugthart & Wallace, 1992).

Rapidly colonizing species such as *Lepidostoma* contributed to recovery of shredder densities in C54, but did not compensate for the loss of biomass. One shredder, *Tipula*, was at least partially resistant to treatment (Lugthart & Wallace, 1992; Wallace *et al.*, 1991), and was the main contributor to shredder abundance and biomass before recolonization by taxa eliminated during treatment (Fig. 3d).

Collector-gatherer abundances and biomass displayed the least change during treatment, because of increased contributions by many non-insect taxa (e.g. Oligochaeta, Copepoda) which compensated for decreases and loss of insects in this functional

group. Many non-insect taxa in Coweeta streams exhibit short generation times (O'Doherty, 1988) and may be resistant to the pesticide used during treatment. Collector-gatherer chironomids, the dominant group of insect collector-gatherers in these streams, decreased in abundance during treatment, but persisted in relatively high densities (Lugthart, Wallace & Huryn, 1991). Twenty-four genera of collector-gatherer Chironomidae were collected in drift samples during treatments of C54. Of these, only one genus, *Microspecta*, was significantly reduced in proportional abundance (Wallace *et al.*, 1991a). Collector-gatherer chironomid densities remained similar in both streams during recovery of C54 (Fig. 3c).

Other studies have shown that chironomid larvae are among the first colonists following disturbance (Gray & Fisher, 1981; Molles, 1985). Further, in streams subjected to frequent disturbance, chironomids and taxa with similarly short generation times are favoured (Gray, 1981; Gray & Fisher, 1981; Fisher *et al.*, 1982). Most collector-gatherer taxa that had increased in abundance during treatment (non-insects) decreased during recovery. Subsequently, collector-gatherer taxa reduced during treatment, e.g. *Serratella* (Fig. 3a) and *Paraleptophlebia* (Ephemeroptera) increased in abundance during recovery.

Generation time, dispersal abilities of individual taxa, and the timing of treatments in relation to life-history characteristics, influenced recovery of the benthic community in C54. Abundance data alone suggest that recovery of invertebrate groups was fairly rapid and nearly complete by autumn 1989. However, biomass differences between the reference stream, C54 pretreatment, and the recovery year reflect differences in taxonomic composition and developmental stages after 1 year of recovery.

Recovery of macroinvertebrate communities is a vital component of system recovery, because of the importance of macroinvertebrates to ecosystem level processes in headwater streams such as C54 (Cuffney, Wallace & Lugthart, 1990). For example, recovery of organic matter processing has been linked to the recovery of macroinvertebrate communities in small headwater streams (Wallace *et al.*, 1991b; Wallace, Vogel & Cuffney, 1986). The results of this study suggest that important ecosystem processes associated with macroinvertebrates were still affected 1 year after termination of disturbance in C54.

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