Colonization of a headwater stream during three years of seasonal insecticidal applications

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Abstract

We investigated recolonization by insects of a small headwater stream in the southern Appalachian Mountains that was treated along its entire length with an insecticide (methoxychlor). Initial treatment (December 1985) resulted in massive insect drift. Applications continued seasonally for three years, and drift was measured during each treatment. Taxonomic composition of the drift indicated several responses: (1) Some taxa were eliminated. (2) A number of taxa occurred only sporadically following initial treatment. (3) Early instars for some taxa showed seasonal occurrences which closely paralleled known life cycles and flight periods of adults. Groups which provided strong evidence for aerial recolonization included several Ephemeroptera, Plecoptera (Peltoperlidae and *Isoperla* spp.), and Trichoptera (*Parapsyche cardis, Diplectrona modesta, Pycnopsyche* spp., and *Lepidostoma* spp.). (4) Some long-lived taxa survived and exhibited distinct growth through several treatment periods. These include Odonata (*Lanthus* and *Cordulegaster*), some Ephemeroptera, and some Diptera (Tipulidae, Ceratopogonidae, and Tanypodinae). (5) Some taxa which were not present at the time of initial treatment appeared during the experiment. Chironomidae dominated the drift in all samples, and the number of genera did not decrease during the three-year treatment period. Of the 27 chironomid genera identified, only *Micropsectra* decreased in proportional abundance during treatment. In contrast, several genera (*Corynoneura, Meropelopia, Parametriocnemus*, and *Tvetnia*) showed little change in relative abundance. *Larsia* (Tanypodinae) increased in proportional abundance during the treatment period.

Introduction

The capacity of invertebrate populations to inhabit severely disturbed streams is dependent upon many factors, including their survival abilities, colonization abilities, and life history traits. The presence of life cycle stages or propagules which survive disturbances may contribute to early, or sustained, colonization by certain taxa (Ide, 1967; Cushing & Gaines, 1989). Although the presence of nearby source populations for recolonization is of obvious importance (Cairns & Dickson, 1977; Gore, 1982; Sheldon, 1984; Cushing & Gaines, 1989), the relative vagility of organisms, through aerial transport, drift, and upstream and hyporheic movements, is of primary importance (Williams & Hynes, 1976; Gore, 1985). Length of life cycle is also an important

factor influencing the rate at which recolonization may occur (Cairns & Dickson, 1977; Neuhold, 1981; Gray, 1981; Gray & Fisher, 1981; Molles, 1985).

Frequently disturbed habitats may be characterized by species which colonize, grow rapidly, and recover between disturbances (Connell & Sousa, 1983). Although severe flash flooding may eliminate most insects in warm desert streams, recovery can occur within 2 months. Chronic exposure to flooding, combined with warm thermal regimes, has apparently selected for life history traits which promote high resilience, such as rapid development, continuous emergence, diapausing eggs, and drift from undisturbed upstream areas (Gray, 1981; Gray & Fisher, 1981; Fisher et al., 1982). In contrast, recovery from flooding in more temperate regions may require longer periods (>4 months to several years) (Thorup, 1970; Hoopes, 1974; Molles, 1985; Minshall et al., 1983; Cushing & Gaines, 1989). In cool temperate streams where most insects possess distinctly seasonal life cycles, recolonization by aerial adults within a single year may vary greatly depending on the relationship between the temporal pattern of disturbance and flight periods of adult insects.

In a previous study, we showed that application of insecticide to a headwater stream resulted in massive invertebrate drift and drastically reduced or eliminated populations of many aquatic insects (Wallace et al., 1989). The composition of drifting invertebrate populations during three-years of subsequent seasonal treatments was quite different from that of the initial treatment. In this paper, the taxonomic composition of invertebrate drift during subsequent insecticide treatments is used to document colonization of the stream during each seasonal interim. The objectives of this paper are to examine recolonization and persistance of specific taxa as related to their life histories and the temporal distribution of insecticide treatments.

Study site

The study was conducted on a first-order stream draining a 5.5 ha catchment (Catchment 54 = [C 54]) at the Coweeta Hydrologic Laboratory in the Blue Ridge Province of the southern Appalachian Mountains (Macon County, North Carolina). The catchment is steep and rugged and the stream has a gradient of 33 cm m^{-1} and elevation at the flume is 841 m a.s.l. Vegetation consists primarily of mixed hardwood forest, and rhododendron forms a dense riparian canopy which results in heavy year-round shading. The stream is equipped with an H-flume and a FW-1 stage recorder to measure discharge (mean discharge = 0.93 L s^{-1}, range = 0.05 to 22.8 during the study interval). Annual precipitation averages about 180 cm yr^{-1} (54 year average); however, during the period of this study precipitation was below normal, ranging from 139 to 153 cm yr^{-1}. Streamflow is dominated by groundwater which moderates the thermal regime (Table 1). Substratum composition was estimated at 1 m intervals along the 282 m long stream in August 1988 as ca. 35% rock outcrop, 4% boulder, 17% cobble, 12% pebble, and 32% sand, woody debris, and accumulated detritus. Additional site descriptions can be found in Cuffney & Wallace (1988), Wallace et al. (1989), and Cuffney et al. (1990).

Materials and methods

Treatment
On 12 December 1985, a 25% emulsifiable concentrate of the insecticide methoxychlor (1,1,1-trichloro-2,2-bis[p-methoxyphenyl] ethane, CAS No. 72-43-5) was applied to the stream for 4 h at the rate of 10 mg L^{-1} based on discharge at the flume. The emulsion was applied using two hand sprayers in order to treat all stream margins, seeps, leaf packs, and debris dams from the flume to the headwater seeps of the stream. Methoxychlor treatments (10 mg L^{-} for 2–3 hr) were repeated seasonally from March 1986 to October 1988 (Table 1). Additional details on treatment,

Table 1. Insecticide treatment schedule for Catchment 54. Initial treatment was on 12 December, 1985. Average daily temperature is indicated for each time interval.

Date	Elapsed days	Avg. daily temp. (°C)
12 December, 1985	0	7.1
12 March, 1986	90	12.2
19 June, 1986	189	16.6
9 October, 1986	301	11.9
27 December, 1986	380	8.8
8 April, 1987	482	14.1
2 July, 1987	567	16.4
10 October, 1987	667	9.7
24 January, 1988	773	8.1
16 April, 1988	856	13.4
24 July, 1988	955	15.0
24 October, 1988	1,047	

methoxychlor concentrations in stream water, and residues in stream sediments are given by Wallace *et al.* (1989).

Invertebrate drift

During the initial treatment, animal drift was measured by 234 μm mesh drift nets which filtered the entire stream at 5 locations. During subsequent treatments, drift samples (3–8 h during and following treatment) were collected at the flume (March 1986 to January 1988) or, in addition to the flume, at midway channel length and near the headwaters (April 1988 to October 1988). All drift samples were preserved in a 6–8% formalin solution containing a small amount of Phloxine B dye. In the laboratory, drift samples were washed through nested 1 mm and 125 μm mesh sieves. The original samples were fractioned ($\frac{1}{2}$ to $\frac{1}{64}$ of the original volume using a device as described by Waters [1969]), and animals were removed from each fraction by hand picking at 15 × magnification. For additional details see Wallace *et al.* (1989). In most cases, identifications were to the generic or species level. However, the presence of only early instars of many species necessitated the use of family-level identifications. Larvae of Chironomidae obtained in the flume samples were mounted on slides for generic identification. Proportional similarities of chironomid taxa were calculated using the method described by Whittaker (1975). The initial treatment was conducted in the winter while subsequent treatments were carried out in all seasons and sampling effort (number of drift nets) varied among treatments. Therefore, absolute numerical comparisons between the two periods are inappropriate. Our use of these data is intended to show only the relative recolonization success and seasonal patterns of colonization by various taxa.

Body lengths of most insect taxa were measured to the nearest mm in order to estimate biomass from length-weight regressions. All lengths were converted to ash dry mass (AFDM) using taxa specific length-weight regressions from nearby Coweeta streams (Huryn 1986, and O'Hop, unpublished).

Results

Many taxa present during the initial treatment (December 1985) recurred in the drift during one or more of the eleven subsequent seasonal treatments (Tables 2–5). During the treatment period, only total abundances of *Cordulegaster* and *Lanthus* (Odonata), *Lepidostoma* spp. (Trichoptera) and several chironomid genera exceeded those of initial treatment. Diptera, Trichoptera, and Ephemeroptera were the most numerous drifting insects during subsequent treatments while Coleoptera and Plecoptera occurred at relative abundances that were generally much lower than during initial treatment. Several different patterns of occurrence in the drift were evident for various taxa during the subsequent treatment periods, including: (1) taxa eliminated or nearly eliminated from the stream, (2) those displaying sporadic occurrences, (3) distinctly seasonal occurrences during subsequent treatments, (4) survivors – taxa that persisted as larvae and exhibited distinct growth, and (5) taxa which were not present at the time of initial treatment. Chironomidae are discussed separately, since individual genera in this family displayed diverse trends.

Table 2. Insect taxa which displayed sporadic recolonization during the three years of seasonal insecticide treatment. Values represent total number of individuals drifting during initial treatment *versus* all subsequent treatments. Values in parentheses are mean individual weights (mg AFDM) of drifting animals during initial treatment and during all subsequent treatments. Letters in parentheses following each taxon indicate insect order, as follows: E = Ephemeroptera, P = Plecoptera, T = Trichoptera, and D = Diptera.

Taxon	Initial treatment numbers & (mean ind. wt.)	March 1986–October 1988 treatments	
		Numbers & (mean ind. wt.)	Subsequent change versus initial
Epeorus (Iron) sp. (E)	5,632 (0.074)	275 (0.014)	− 20.5 X
Baetis sp. (E)	101 (0.04)	643 (0.06)	+ 6.4
Leuctra spp. (P)	51,895 (0.23)	601 (0.16)	− 86.3 X
Pseudogoera singularis (T)	2,044 (0.014)	128 (0.005)	− 16.0 X
Polycentropus sp. (T)	374	31	− 12.1 X
Wormaldia sp. (T)	8,690 (0.169)	1,333 (0.081)	− 6.5 X
Rhyacophila spp. (T)	1,429 (0.20)	268 (0.007)	− 5.3 X
Hexatoma spp. (D)	18,125 (0.176)	204 (0.562) .	− 88.8 X
Molophilus spp. (D)	3,691 (0.087)	288 (0.059)	− 12.8 X
Dicranota spp. (D)	5,202 (0.058)	154 (0.107)	− 33.8 X
Pericoma sp. (D)	179	20	− 9.0 X
Glutops sp. (D)	7	1	− 7.0 X
Thaumalea thornburghae (D)	152	58	− 2.6 X
Empididae (D)	4,172 (0.019)	439 (0.018)	− 9.5 X

Eliminated or nearly eliminated taxa

Several taxa decreased to <1% of their initial abundances over the 1047 d experimental period. These included, *Beloneuria* sp. and *Amphinemura wui* (Claassen) (Plecoptera), *Anchytarsus bicolor* (Melsheimer) and Elmidae (Coleoptera), *Dolophilodes major* (Banks), *Lype diversa* Banks, *Fattigia pele* (Ross), *Psilotreta* spp., and *Molanna* sp. (Trichoptera), and Nymphomyiidae and *Bradysia* (Diptera).

Sporadic taxa

Many taxa occurred sporadically during the three year treatment period (Table 2). *Epeorus (Iron)* spp. were absent during the first year of treatment, present in moderate numbers (<300) in the summer of 1987 and rare in 1988. *Baetis* spp. occurred sporadically during the summers of 1986 and 1987 and in the winter of 1988, their drift abundances exceeded those of the initial treatment. The odontocerid, *Pseudogoera singularis* Carpenter, occurred in the drift only once during the 3-yr period, during late summer 1988. Other taxa which exhibited sporadic occurrences

includes *Rhyacophila* spp., *Polycentropus* sp., and *Wormaldia* sp. (Trichoptera); and *Thaumalea thornburghae* Vaillant, *Hexatoma* spp., *Dicranota* spp., *Molophilus* spp., *Pericoma* sp., *Glutops* sp., and Empididae (Diptera).

Seasonal taxa

Early instars of some taxa appeared during the experiment, indicating seasonal recruitment. Since recruitment occurs predominantly in summer and autumn at Coweeta, weights of individual insects are normally low during the late-autumn early winter period as reflected in collections during the initial treatment (December 1985) (Tables 2–4). However, later treatments (March 1986 through October 1988) often yielded smaller individuals than were obtained during the initial treatment, indicating recruitment of early instars. Many of these taxa exhibited distinct seasonal abundances that coincide with their known flight and recruitment periods within the Coweeta Basin (Table 3). Some examples are discussed below.

Peltoperlidae have a two year life cycle with late spring flight periods. Early instars of peltoperlids

Table 3. Insect taxa which displayed seasonal recolonization during the 3-yr treatments. Letters in parentheses following each taxon indicate insect order, as follows: P = Plecoptera, C = Coleoptera, T = Trichoptera, and D = Diptera. See Table 2 for additional explanation.

| Taxon	Initial treatment numbers & (mean ind. wt.)	March 1986–October 1988 treatments	
		Numbers & (mean ind. wt.)	Subsequent change versus initial
Peltoperlidae (P)	43,830 (0.16)	1,352 (0.02)	– 32.4 X
Sweltsa spp. (P)	4,462 (0.22)	382 (0.14)	– 11.7 X
Isoperla spp. (P)	4,470 (0.127)	464 (0.011)	– 9.6 X
Ectopria thoracica (C)	696 (0.113)	140 (0.075)	– 5.0 X
Pycnopsyche spp. (T)	5,152 (0.158)	888 (0.06)	– 5.8 X
Diplectrona modesta (T)	8,260 (0.373)	2,145 (0.129)	– 3.9 X
Diplectrona metaqui (T)	82 (0.891)	26 (0.938)	– 3.2 X
Parapsyche cardis (T)	3,224 (0.347)	2,531 (0.141)	– 1.3 X
Lepidostoma spp. (T)	2,006 (0.022)	3,519 (0.021)	+ 1.8 X
Dixa sp. (D)	10,360 (0.008)	537 (0.010)	– 19.3 X
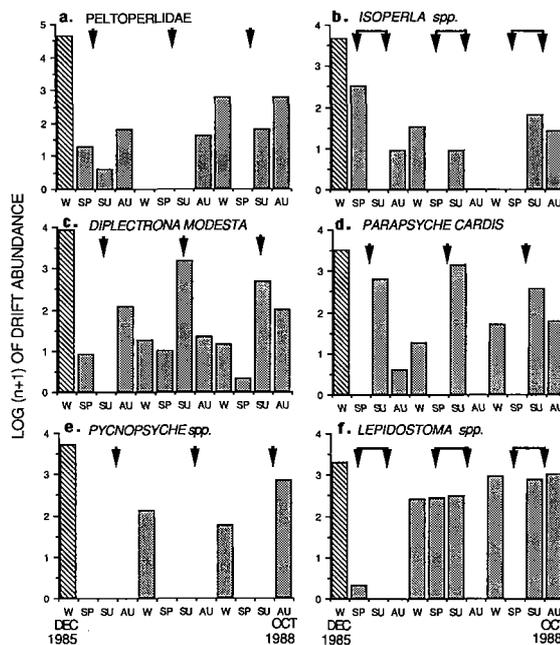
Fig. 1. Drift abundances during initial and subsequent treatments of Catchment 54 based on log (n + 1) of number of individuals drifting on each treatment date (Table 1) for a, Peltoperlidae; b, *Isoperla* spp.; c, *Diplectrona modesta*; d, *Parapsyche cardis*; e, *Pycnopsyche* spp.; and f, *Lepidostoma* spp. Arrows denote the known flight times within the Coweeta Basin (see text). The diagonally striped bar represents initial treatment abundances and the shaded bars are abundances during each subsequent treatment.

were abundant in the seasonal drift during summer, autumn, and winter, coinciding with apparent delayed hatching at Coweeta (O'Hop *et al.*, 1984) (Fig. 1a). The average body weight of a peltoperlid during the initial treatment was about 7 × greater than that obtained during the treatment period. Even medium sized ($\geq$ 3–6 mm) nymphs were absent during all seasonal treatments, indicating that no individuals survived into the second year of development.

Isoperla spp. are univoltine at Coweeta with flight periods extending from spring through summer and apparent extended hatching (Huryn and Wallace, 1987). During the treatment period, early instars were found during either summer or autumn months of all years (Fig. 1b). There was no evidence that any *Isoperla* successfully completed life cycles within the treatment stream, as the average weight of drifting specimens was lower than that during initial treatment (Table 3).

Ectopria thoracica (Ziegler) (Coleoptera: Eubriidae) was the most abundant coleopteran following initial treatment (Table 3) as other beetles were nearly eliminated. *Ectopria* were not present in the drift until the second year of treatment and were most abundant in 1988.

Parapsyche cardis Ross and *Diplectrona modesta* Banks (Trichoptera: Hydropsychidae) were pre-

sent as early instars in late spring and summer treatments. This coincides with their late spring (*Parapsyche*) and summer (*Diplectrona*) flight and recruitment periods (Figures 1c and 1d). Based on mean weights of drifting larvae, a few specimens of *Parapsyche* and *Diplectrona* larvae must have survived at least one or more treatments. Some *Parapsyche cardis* persisted in the stream and grew through the winter in both 1987 and 1988 (Fig. 2a). However, *Parapsyche* were not collected during any April treatments, and there is no evidence that larvae completed development within this stream. *Diplectrona modesta* declined with each successive treatment following peak abundance in summer of each year. *Diplectrona modesta* showed distinct growth patterns until the spring of 1987, however, only one early instar larva was recovered from the drift during the spring of 1988 (Fig. 2b). *Diplectrona metaqui* Ross larvae also showed evidence of growth through successive treatments; however, their abundances

were too low (Table 3) to discern distinct patterns. The above three taxa were the only trichopterans that exhibited any evidence of surviving treatments.

Pycnopsyche spp. and *Lepidostoma* spp. recruited during the experimental period. *Pycnopsyche* spp. are univoltine at Coweeta, and only early instars (1st- and 2nd-) were recovered during the treatment period. Larvae were recovered only from either winter (1986 and 1987) or autumn (1988) treatments (Fig. 1e). These correspond with known flight and recruitment periods (late-summer to early autumn) for *Pycnopsyche* at Coweeta (Huryn & Wallace, 1988). At least two species of *Lepidostoma* (*L. griseum* (Banks) and *L. lydia* Ross) were present in C 54. However, despite their abundances in the drift during the treatment period (Fig. 1f), only early instars were collected and growth was not evident. Total abundances of *Lepidostoma* during the treatment period exceeded those of the initial treatment (Table 3).

No information is available on flight periods of *Dixa* sp. (Diptera) at Coweeta. The consistent presence of early instars during summer and autumn treatments suggests flight and oviposition during the late spring-early autumn periods.

Survivors

Based on changes in mean weight of drifting animals with successive seasonal treatments, there is evidence that several taxa survived repeated insecticide applications and exhibited measurable growth during the treatment period (Table 4). For some taxa with 1.5-yr + life cycles, such as *Lanthus*, different cohorts could be separated (Fig. 2c). *Lanthus* has an 18 month cohort development time in this stream (Wallace *et al.*, 1987). Therefore, the largest *Lanthus* in cohort 1 would have survived at least 8–9 insecticide treatments (June or October 1986 to July 1988, Fig. 2c). Our data suggest that *Cordulegaster* require two to four years to complete development. Life cycles of *Cordulegaster* spp. are poorly known, and abundances of the larger size classes of *Cordulegaster* were insufficient to support any firm conclusions. However, other investigators
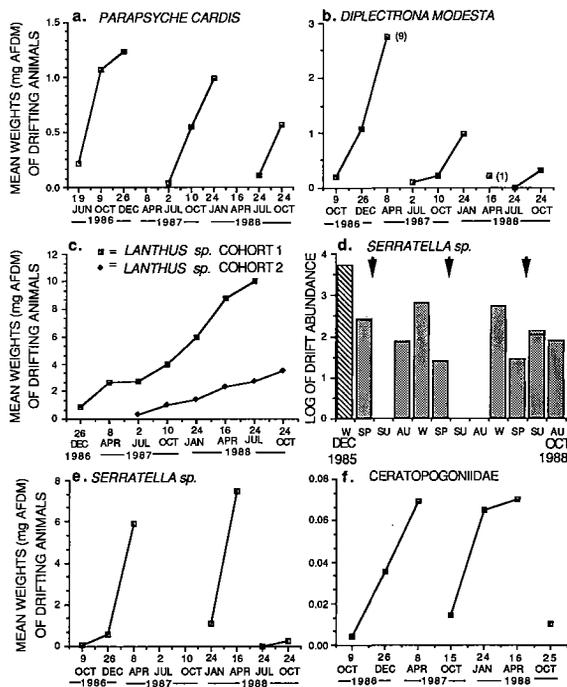

Fig. 2. Mean individual weights of drifting specimens during successive seasonal treatments for: a, *P. cardis*; b, *D. modesta*; c, *Lanthus* sp.; d, same as Fig. 1 for *Serratella* sp.; e, mean weights of drifting *Serratella* sp.; and f, Ceratopogoniidae.

Table 4. Insect taxa which survived successive treatments during the treatment period. Letters in parentheses following each taxon indicate insect order, as follows: O = Odonata, E = Ephemeroptera, and D = Diptera. See Table 2 for additional explanation.

Taxon	Initial treatment numbers & (mean ind. wt.)	March 1986–October 1988 treatments	
		Numbers & (mean ind. wt.)	Subsequent change versus initial
Lanthus sp. (O)	212 (0.23)	338 (0.88)	+ 1.6 X
Cordulegaster sp. (O)	265 (0.41)	599 (2.05)	+ 2.3 X
Leptophlebiidae (E)	9,399 (0.10)	1,461 (0.10)	− 6.4 X
Stenonema spp. (E)	9,649 (0.14)	1,901 (0.06)	− 5.1 X
Serratella sp. (E)	5.298 (0.08)	1,729 (0.34)	− 3.1 X
Ceratopogonidae (D)	51,625 (0.027)	10,621 (0.029)	− 4.9 X
Pedicia spp. (D)	1,998 (0.161)	819 (0.423)	− 2.4 X
Tipula spp. (D)	396 (5.52)	365 (6.76)	− 1.1 X
Limonia spp. (D)	462 (0.08)	460 (0.31)	1.0 X

have suggested a long (3 to 4-yr) development time (Brigham et al., 1982).

Several of the Ephemeroptera exhibited similar changes in mean weights through successive treatments. These include Stenonema (see Wallace et al., 1989), Leptophlebiidae (Habrophlebia and Paraleptophlebia), and Serratella sp. Serratella were present in the drift during all seasons except three (summer 1986 and summer and autumn of 1987, Fig. 2d). Despite their absence in drift during two seasons of 1987, some individuals apparently completed development in the stream during 1987–1988 by surviving repeated treatment. Serratella sp. exhibited the most distinct growth patterns of any mayfly during the treatment period (Fig. 2e). Early instars were present during the autumn treatments of 1986, 1987, and 1988, and exhibited increases in body weight throughout the winter and early spring of 1987 and 1988.

Several dipterans grew through successive treatments. Medium to full grown larvae of several taxa were collected during the treatment period: Tipulidae (Hexatoma, Dicranota, Pedicia, Limonia, and Tipula), Ceratopogonidae, and Chironomidae. The Ceratopogonidae were present in late summer and autumn of 1986, 1987, and 1988 and growth was evident until the early spring during both 1987 and 1988 (Fig. 2f). Tipula spp. displayed univoltine growth patterns with recruit-

ment occurring during the summer and early autumn (Fig. 3a). By spring, all larvae were in larger size classes, with most emergence occurring between the spring and summer treatments.

Chironomidae

Although treatments reduced the overall abundance of the Chironomidae, the number of genera did not show any marked decrease with time. On many subsequent treatment dates, generic richness was higher than that of the initial treatment (Fig. 3b). Eleven genera, not encountered in subsamples during the initial treatment, were collected during subsequent treatments (Table 5). Of the twenty-seven taxa collected, only Micropsectra (Chironominae) displayed a large decrease in proportional abundance during the seasonal treatment period. In contrast, Larsia (Tanypodinae) showed a large increase in relative abundance following initial treatment. Other taxa, e.g., Meropelopia (Tanypodinae), Corynoneura, Parametriocnemus and Tvetnia (Orthocladiinae), displayed little change (Table 5). The average proportional similarity (PS) among chironomids between the initial treatment and all subsequent treatments was 0.643. However, when the winter samples are compared (chosen for comparison with the season of initial treatment), the average PS for the initial treatment and subsequent winter treatments was 0.749. Most of this disparity was

Table 5. Percent contribution of various chironomid taxa to total chironomid drift during initial treatment, all subsequent treatments (March 1986 to October 1988) and during only winter subsequent treatments (December 1986 and January 1988) based on flume drift samples. Asterisks denote taxa that were not encountered during the initial treatment. The abbreviations in parentheses following genera indicate subfamily and/or tribe of each genus, as follows: CC = Chironominae, Chironomini; CT = Chironominae, Tanytarsini; D = Diamesinae; O = Orthocladiinae; P = Podonominae; and, T = Tanypodinae.

Taxon	Percent contribution to chironomid drift		
	Initial treatment	All subsequent treatments	Winter subsequent treatments
Corynoneura (O)	39.4	25.4	37.5
Micropsectra (CT)	19.1	1.2	<0.05
Meropelopia (T)	13.8	14.7	14.8
Parametriocnemus (O)	10.5	15.2	11.7
Tvetnia (O)	6.8	4.3	6.0
Stilocladius (O)	2.5	2.4	1.3
Eukiefferiella (O)	1.8	2.0	4.6
Brillia (O)	1.8	10.6	3.6
Microptendipes (CC)	1.6	0.05	<0.05
Heleniella (O)	1.2	2.1	0.6
Larsia (T)	0.9	9.0	11.4
Brundiniella (T)	0.6	0.8	0.7
Pseudorthocladius (O)	*	<0.05	0.1
Demicryptochironomus (CC)	*	0.1	<0.05
Orthocladius? (O)	*	<0.05	<0.05
Diamesa (D)	*	0.06	<0.05
Borochleus (P)	*	2.0	2.8
Polypedilum (CC)	*	4.0	2.7
Krenosmittia (O)	*	0.1	0.1
Tribelos (CC)	*	<0.05	<0.05
Cricotopus? (O)	*	<0.05	<0.05
Constempellina (CT)	*	0.4	<0.05
Rheocricotopus (O)	*	1.6	1.7
Paratrichocladius? (O)	*	1.4	0.1
Synorthocladius (O)	*	1.3	<0.05
Chaetocladius? (O)	*	0.2	<0.05
Rheotanytarsus (CT)	*	0.5	0.1

attributable to the decline in *Micropsectra* which was apparently susceptible to methoxychlor or not as vagile as other taxa.

Most Tanypodinae at Coweeta are univoltine, and larvae were abundant in the drift throughout the treatment period (Fig. 3c). Tanypodinae survived treatments and grew from autumn to summer months. At least three genera of Tanypodinae (*Brundiniella*, *Larsia* and *Meropelopia*) were present and displayed seasonal increases in size and weight. Mean individual weights of Tanypodinae were lowest in autumn and highest in summer

(Fig. 3d). Most Tanypodinae hatched in late summer and early autumn as there were significant differences among size-frequency distributions of larger summer and smaller autumn larvae (X^2 = 487.5, d.f. = 5, $p < 0.001$).

Chironomidae other than Tanypodinae were by far the most abundant insects during the treatment period (Fig. 3e). Pretreatment benthic samples (1984–85) indicate that abundances of non-Tanypodinae chironomids were about 2 to 3 × greater than those of the first year of treatment (1986) (Lugthart *et al.*, in press). Size-
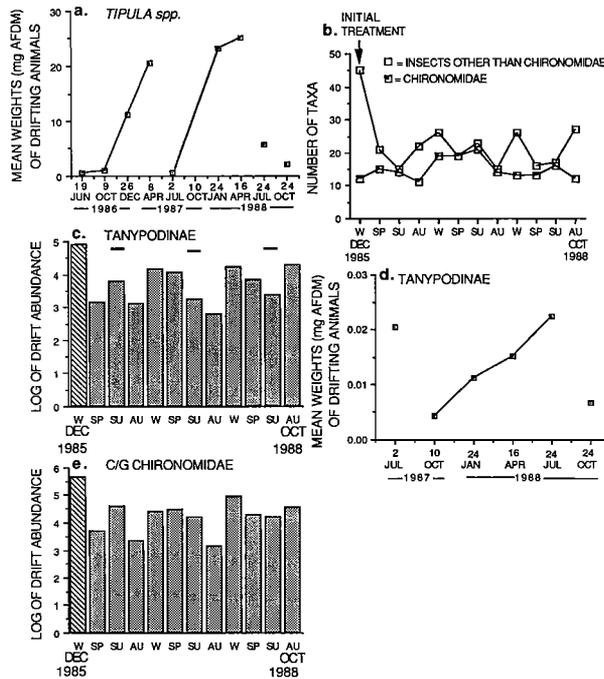
Fig. 3. Mean individual weights of drifting specimens during successive seasonal treatments for a, *Tipula* spp.; b, number of insect taxa (non-chironomids) versus the number of chironomid taxa on each treatment date; c, same as Fig. 1 for Tanypodinae (bars at top indicate periods of maximum abundances of pupae); d, mean weights of drifting Tanypodinae; and e, same as Fig. 1 for non-Tanypodinae Chironomidae.

frequency distributions of larvae did not differ significantly between initial treatment and all subsequent treatments. This similarity in size distribution and the presence of larger size classes throughout the treatment period indicates that some non-Tanypodinae either (1) exhibited continual growth, recruitment, and emergence throughout the treatment period, or (2) had rapid recolonization and growth between seasonal treatments (see below).

Taxa not present during initial treatment

Pseudostenophylax uniformis (Betten) (Trichoptera) and Simuliidae (Diptera) were absent during the initial treatment but appeared in the drift during subsequent treatments. In addition,

eleven genera of Chironomidae not present during the initial treatment occurred in one or more seasonal samples during the 3-yr treatment period (see above and Table 5).

Discussion

The flume and a 6 m waterfall, that is located immediately below the flume, serve as a barrier for non-aerial upstream movement. Furthermore, since upstream populations as sources for drift do not exist, and since appearance of early instars coincided with known flight periods, immigration of aerial adults is probably the predominant mechanism of recolonization for many insect taxa in this stream. Yasuno *et al.* (1982b) reached similar conclusions following treatment of two adjacent headwater tributaries in Japan with an insecticide. One entire stream was treated, whereas only the lower half (ca. 200 m) of a second stream was treated. Yasuno *et al.* found similar recovery times of 4 months for each stream although untreated upper reaches of the second stream provided a potential source area for drift. The study of Yasuno *et al.* was restricted to the summer months when aerial adults would be active.

Studies of the flight directions of adult lotic insects (upstream vs. downstream) yield conflicting results (Muller, 1982; Bird & Hynes, 1981; Flecker & Allan, 1988; Jones & Resh, 1988). However, strict quantitative interpretations of upstream-downstream movements may be somewhat misleading since a few successful gravid females may lay several hundred to several thousand eggs, thereby compensating for a considerable amount of downstream drift. Vagility of adults obviously varies greatly, even within orders. Poor vagility decreases predictability of recolonization by aerial sources. For example, no evidence of recolonization over a 3-year period exists for some Trichoptera, e.g. *Dolophilodes major*, *Lype diversa* and *Fattigia pele*, while the pattern exhibited by *Pseudogoera singularis* is indicative of apparently fortuitous recolonization during one of the three years. In contrast, others such as *Para-*

psyche cardis, *Diplectrona modesta*, *Pycnopsyche*, and *Lepidostoma* showed consistent colonization during each of the three years.

Seasonality of disturbance and flight periods of ovipositing adults may introduce an unpredictable element into recolonization. For those taxa that depend on aerial adults as immigrants, colonization may be delayed depending on the timing of treatment (or disturbance) relative to flight periods (Figs. 1a and 1e). The ability to colonize only in discrete annual periods undoubtedly has a profound influence upon the rate of recolonization. In cool, temperate streams where many insects have very seasonal life cycles, disturbances which occur shortly after hatching or recruitment of univoltine and semivoltine species relying on aerial adults for colonists may eliminate any possibility of recovery for that year. For example, without upstream source populations, late autumn or early winter disturbances, which eliminate taxa such as Peltoperlidae or *Pycnopsyche* (Figs. 1a and 1e), would postpone recolonization until the following year; although potential source populations may be located only a few hundred meters away in adjacent drainage systems. In contrast, in warm desert streams rapid recovery (<2 months) of aquatic invertebrates following severe flash flooding caused by localized thunderstorms may be due to factors such as rapid development, continuous emergence (with adults in adjacent riparian vegetation), diapausing eggs, and downstream drift (Gray, 1981; Gray & Fisher, 1981; Fisher *et al.*, 1982). However, Molles (1985) and other authors (Thorup, 1970; Minshall *et al.*, 1983; Cushing & Gaines, 1989) found recolonization required much longer for species with longer life cycles in more temperate areas.

Non-Tanypodinae chironomids constituted 47 to 74% (mean = 65%) of all insect drift during the seasonal treatments. At Coweeta, many exhibit characteristics of relatively rapid growth and continuous emergence, which are some of the same attributes found among fauna in warm desert streams (Gray & Fisher, 1981). Chironomid growth and development have been studied in several Coweeta streams which differ in

elevation, aspect, and thermal regime (Huryn, 1989). Life cycles of non-Tanypodinae in an adjacent stream (C 53) ranged from bivoltine (for larger taxa) to polyvoltine with more than 12 cohorts per year (for small *Corynoneura*) (Huryn, 1989). Thus, following rare unpredictable disturbances as well as relatively frequent disturbances such as our pesticide treatments, there may be aerial adults or unhatched eggs present which can quickly re-establish populations. This may explain why chironomids from a diverse array of lotic habitats are frequently among the first colonizers following disturbance (Iversen *et al.*, 1978; Gray & Fisher, 1981; Smith & Distler, 1985; Yasuno *et al.*, 1982a; Molles, 1985; Victor & Ogbeibu, 1986).

This study has addressed recolonization in a mesic area where source populations (nearby streams) are abundant and in close proximity (<500 m). In more arid areas with fewer source populations and greater spatial distances between habitats, e.g. cool endorheic desert streams, recolonization may be prolonged and species diversity reduced, which results in unpredictable long-term faunal changes following major flooding (Cushing & Gaines, 1989). In contrast, in the southern Appalachians there is evidence to support a return to predisturbance community structure. In 1980, a similar (but shorter, 1-yr) treatment of an adjacent stream (C 53) produced comparable changes in community structure. Many of those insect taxa which dominated biomass during the 2nd-year recovery in C 53 (Wallace *et al.*, 1986) showed either substantial recolonization abilities or the ability to survive repeated treatments during the present study. By 1985, benthic samples indicated that biomass and taxonomic composition in C 53 closely resembled that of C 54 prior to treatment (Lugthart *et al.*, unpublished).

The Coweeta Basin has a high drainage density with many streams in close (300 m to 1 km) proximity, and a high degree of faunal similarity exists within the basin. Unlike the isolated cool desert streams studied by Cushing & Gaines (1989), the close proximity and abundance of nearby habitats and the dispersal abilities of most

taxa ensures recolonization by taxa common to the basin. Furthermore, our results strongly suggest that aerial adults represent an extremely important mechanism for recolonization of this headwater stream.

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