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Temporal variability of stream macroinvertebrate abundance and biomass following pesticide disturbance

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Abstract. We determined the extent of macroinvertebrate recovery in a former pesticide-treated stream (FTS) relative to a reference stream (RS) by examining macroinvertebrates colonizing red maple (*Acer rubrum* L.) litter bags between 5 to 10 y following pesticide treatment. Mean abundance and biomass, variability in abundance and biomass (using the coefficient of variation [CV]), and assemblage structure were compared both within and among years to assess recovery. The 5 y of study included 3 drought years followed by 2 wet years. Mean total abundance and biomass of macroinvertebrates, and that of most functional feeding groups (FFG) did not significantly differ between streams during this study, nor did within-year variability of these means, indicating macroinvertebrates in FTS had recovered relative to RS. Some exceptions to the above patterns (shredder abundance and mean annual gatherer biomass) resulted from the dynamics of a single taxon in each group (*Leuctra* and *Paraleptophlebia*, respectively). Macroinvertebrate assemblage structure in litter bags was similar between streams throughout the study as shown by their similar ordination scores; hence, assemblage structure had also recovered. In each stream, mean annual abundance and biomass of total macroinvertebrates and of each FFG, aside from shredder abundance, differed significantly among years. However, assemblage structure was generally similar among years. Among-year CVs were usually lower than within-year CVs because macroinvertebrate abundance and biomass fluctuated more during a year than it did from year to year, and different processes apparently contributed to the variation observed at these 2 time scales. For example, juvenile development time influenced within-year CVs, indicating that life-history characteristics affected temporal variability of macroinvertebrate abundance and biomass. Examination of both the means and their variances was useful for determining the extent of recovery and how macroinvertebrates responded to natural environmental variability. The detailed analysis of temporal dynamics at different time scales afforded by the CV supported our contention that FTS had recovered from the pesticide application relative to RS.

Key words: long-term recovery, within-year variability, among-year variability, coefficient of variation, life history, cohort production interval.

The ability of stream macroinvertebrate assemblages to recover from disturbance depends on many factors, including 1) life-history characteristics of organisms, 2) timing of the disturbance, 3) presence of survivors within disturbed sites, 4) distance of source populations for recolonization, and 5) nature of the disturbance (Gore and Milner 1990, Wallace 1990, Yount and Niemi 1990, Mackay 1992, Milner 1994). For example, species that have high vagility or that survive disturbances can recolonize disturbed areas rapidly, often in a stochastic manner largely dependent on the timing of the disturbance relative to their life-cycle stage (e.g., Gray and Fisher 1981, Fisher et al. 1982, Wallace et al. 1986, Whiles and Wallace 1992, 1995). Subsequent changes in a recovering macroinvertebrate assemblage may result from further recolonization and biotic interactions, but also depend on the natural disturbance regime of the area (Fisher 1983).

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Disturbances can generally be categorized as either pulse or press type (sensu Bender et al. 1984). Pulse disturbances are short term and cause relatively instantaneous alterations to population densities or community structure, whereas press disturbances are long term and cause a sustained alteration of these parameters. Distinguishing between disturbance type can promote understanding of recovery mechanisms of lotic macroinvertebrate assemblages because recovery is affected both by direct effects of the disturbance on organisms and long-term physical changes to habitats (Resh et al. 1988, Yount and Niemi 1990). For example, logging activities can alter both habitat quality and the energy base of streams. Recovery of stream macroinvertebrates following catchment logging, then, is linked to recovery of the riparian vegetation and substrate characteristics of the stream bed (Webster et al. 1983, Stone and Wallace 1998). In such cases, it is hard to separate the response of macroinvertebrates to the actual disturbance from their ability to recover from residual physical alterations to the stream. In contrast, pulse disturbances caused by some pollutants, such as pesticides, affect stream biota without inducing any significant changes in the physical environment (Wallace 1990, Milner 1994).

Here, we report results of a study comparing macroinvertebrate colonization of litter bags in a stream that had been treated with pesticide 5 y prior with that in an untreated reference stream. Seasonal applications of a pesticide (methoxychlor) to this headwater stream removed animals from the stream without significantly changing the physical habitat or energy sources, such as leaf litter and associated microbes (Cuffney et al. 1984, 1990). This arrangement allowed us to assess the recovery from disturbance within the context of natural fluctuations in populations. Natural variability in macroinvertebrate assemblage structure, abundance, and biomass is a product of both within-year, and among-year changes associated with factors such as life cycles, availability of resources, and climate (Resh and Rosenberg 1989). Detecting changes in the magnitude of natural fluctuations in animal populations following disturbance is essential, yet often neglected (Underwood 1994). In our analyses, we examine these fluctuations using measures of both mean values and variance because analyses of means alone may hide important ecological information about recovery and long-term population dynamics (Underwood 1991, 1994, Palmer et al. 1997).

Wallace et al. (1986) previously examined the recovery of the pesticide-treated and reference streams for 2 y and found that trophic recovery (i.e., functional feeding group [FFG] abundance and biomass) had occurred, but not taxonomic recovery. We examined these same streams for 5 y to examine whether trophic recovery persisted and whether taxonomic recovery occurred. Many studies of recovery are limited to <1 y so our study provided a valuable opportunity to examine a relatively long-term recovery sequence. Furthermore, because the streams were sampled throughout the year, we were able to compare recovery patterns within and among years. Little is known about the relative amount of variation between these 2 temporal scales because simultaneous comparisons of variability are rare.

Our specific objectives were 1) to compare the means of total macroinvertebrates and FFG abundance and biomass colonizing litter bags in a pesticide-disturbed stream and a nearby reference stream to determine the extent of recovery relative to a previous short-term study (Wallace et al. 1986), 2) to compare the variability of these means at within- and among-year temporal scales to help determine recovery and describe patterns of variability, and 3) to compare assemblage structure within and between these streams.

Study Site

The study was conducted at the Coweeta Hydrologic Laboratory (CHL), a 1626-ha drainage basin in the Blue Ridge Province of the southern Appalachian Mountains (lat 35°03'N, long 83°25'W). The 2 first-order streams used in this study drain Catchments 53 and 55. These streams have predominately mixed-substrate beds (a heterogeneous mixture of cobbles, pebbles, gravel, sand, and silt), and are similar in elevation, size, slope, aspect, and thermal regime (Table 1). The dominant riparian vegetation of these systems is also similar, and includes the deciduous red maple (*Acer rubrum* L.), tulip poplar (*Liriodendron tulipifera* L.), red oak (*Quercus rubra* L.), white oak (*Q. alba* L.), and the evergreen rhododendron (*Rhododendron maximum* L.). The rhododendron understory provides

TABLE 1. Physical characteristics of the former treatment stream (FTS) and reference stream (RS).

	FTS	RS
Catchment		
Area (ha)	5.2	7.5
Elevation (m asl at flume)	820	810
Aspect	S	S
Channel		
Length (m)	145	170
Bankfull area (m^2)	327	373
Gradient (cm/m)	27	20
Mean annual discharge (L/s)		
1985	0.59	0.95
1986	0.33	0.50
1987	0.74	1.43
1988	0.42	0.69
1989	1.45	2.34
1990	1.56	2.48
Annual degree days (6-y avg.)	4535	4511

heavy shading of the streams even after the major leaf fall period (October to December).

Catchment 53 served as the former treatment stream (FTS), whereas Catchment 55 was the reference stream (RS). FTS received 4 seasonal pesticide treatments from its upstream spring seeps to a gauging flume during 1980 (Wallace et al. 1982). The pesticide, methoxychlor (1,1,1-trichloro-2,2-bis [p-methoxyphenyl]ethane; Chemical Abstracts Service (CAS) No. 72–43–5), was applied to the entire stream channel on each date for 5 h using 2 hand sprayers at a rate of 10 mg/L based on discharge at the flume. Although very low levels of methoxychlor can persist for years in stream sediments (Wallace et al. 1989), this residual pesticide appears to be tightly bound to sediments and inactive (see Murty 1986). Survivors and aerial adults were the primary mechanisms for macroinvertebrate recolonization of FTS (Wallace et al. 1991b) because the gauging flume prevented recolonization from downstream sources (Söderström 1987). Drift from upstream sources (Townsend and Hildrew 1976) was minimal because the stream was treated up to its source. Further details are available in Wallace et al. (1982, 1986) and Cuffney et al. (1984, 1990).

We initiated our study in 1985, 5 y after cessation of pesticide treatment. Annual precipitation over our 5-y study was 90.4% of the long-term average, yet the study period encompassed extremes in >60 y of record at Coweeta (US Department of Agriculture [USDA] Forest Service, Coweeta Hydrologic Laboratory, unpublished data). Drought conditions occurred from 1985 to 1988 (precipitation = 74.2% of average), including the lowest (1986 = 124.0 cm, 68.7% of average), and the 3rd-lowest (1988 = 126.7 cm, 70.2% of average) annual precipitations on record. In contrast, 1989–1990 were wet years (precipitation = 122.9% of average), with the highest annual precipitation on record in 1989 (234.1 cm, 129.8% of average), followed by an above-average year (1990 = 209.5 cm, 116.1% of average). As a result of this variation in precipitation, stream discharge varied considerably among years (Table 1, Fig. 1). In addition, the wetted area of stream channels ranged from 95 to 171 m^2 in FTS and from 206 to 266 m^2 in RS (Wallace et al. 1991a).

Stream discharge was measured by the USDA Forest Service during frost-free months (April through November) from 1985 to 1990 by using stage recorders attached to H flumes, which were installed at the base of FTS and RS. For winter months when the flumes could not be used, discharge was calculated using regressions of discharge in FTS and RS versus discharge in a nearby gauged catchment (C 2) with a V-notch weir (r^2 = 0.903 and 0.931 for C 2 versus FTS and RS, respectively).

Methods

Litter bag preparation

Red maple leaves from CHL were collected in mid-October of 1984, 1985, 1987, 1988, and 1989, and ca 15 g (air-dried weight) were placed into 20 × 35 cm plastic mesh bags (mesh size: ca 5 mm). In mid-December of each year, 60 litter bags were placed into mixed-substrate habitats of each stream. During baseflow, current velocity in these habitats is ca 10 cm/s (J. B. Wallace, unpublished data) and depth is <10 cm. Bags were secured to the stream bed with gutter nails in multiple reaches over the entire stream length.

Macroinvertebrate collection and processing

Each month from January to June of each year, and at 6-wk intervals during the last 1/2 of each

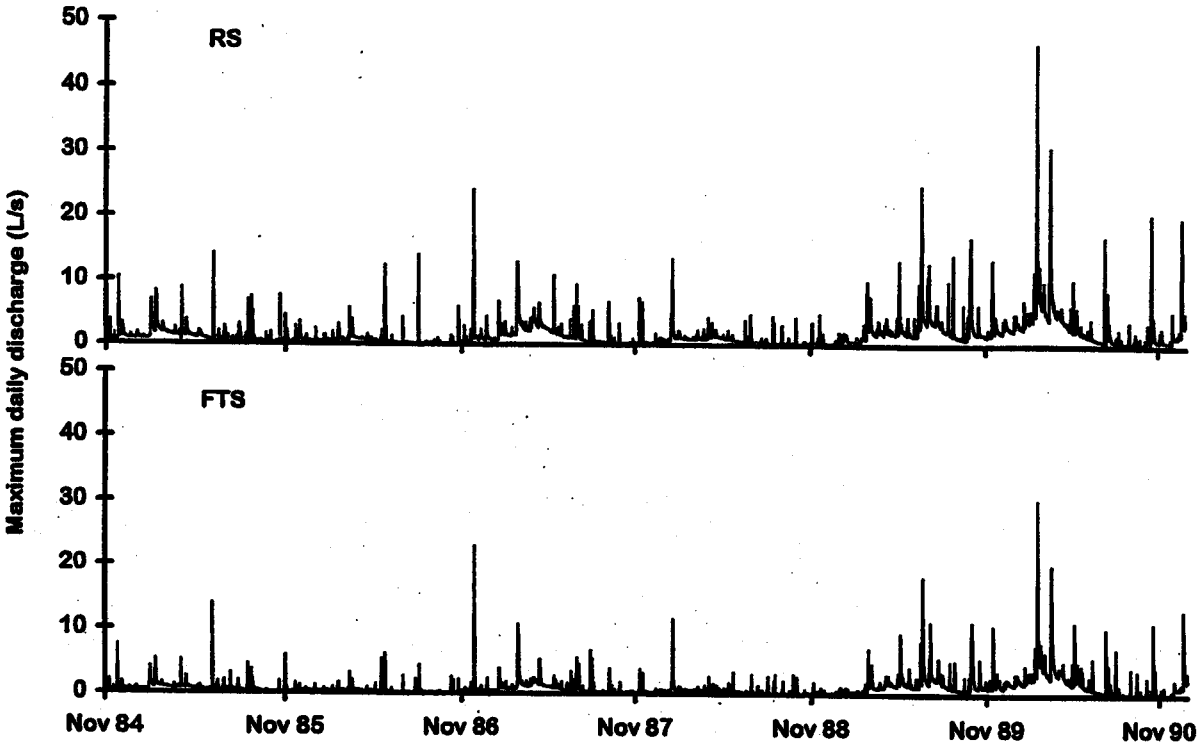

FIG. 1. Maximum daily discharge (L/s) in the reference stream (RS) and in the former treatment stream (FTS) during our study.

year, 5 litter bags were collected randomly from each stream. Sediment, detritus, and macroinvertebrates were washed from litter bags onto a 125-μm-mesh sieve, and preserved in a 6–8% formalin solution containing a small amount of Phloxine B dye to facilitate sorting macroinvertebrates from debris. Samples were processed through nested 1000- and 125-μm-mesh sieves. All macroinvertebrates retained on the 1000-μm sieve were removed and identified. The sample retained on the 125-μm sieve was subsampled (1/4 to 1/64 of the original sample) using a sample splitter (Waters 1969) before removing animals. Macroinvertebrates in subsamples were removed, identified, and measured to the nearest mm for conversion to ash-free dry mass (AFDM) using taxon-specific length–weight regressions (Huryn 1986, Huryn and Wallace 1987).

Taxonomic and FFG assignments followed that of Merritt and Cummins (1984) or other studies of the benthic fauna in CHL (Huryn and Wallace 1987, Lugthart 1991). We use the terms gatherers and filterers for collector-gatherers and collector-filterers, respectively, throughout the paper. Scrapers were not included in separate FFG analyses because they composed <1% of total abundance and biomass in litter bag assemblages.

Criteria for recovery and statistical analyses

We assessed macroinvertebrate recovery in FTS relative to RS using a variety of metrics or indicators, which included total abundance and biomass to examine the overall response to the pesticide treatment, and abundance and biomass of each FFG to evaluate recovery of trophic structure. Because estimates of absolute abundance can be extremely variable, we also included metrics based on the variability in means. These variation-based metrics improved our ability to evaluate recovery over time. Finally, we evaluated differences in taxonomic structure of macroinvertebrate assemblages in FTS and RS using ordination.

Total and FFG-specific abundance and biomass of macroinvertebrates were compared between streams, among years, and within years using a repeated measures analysis of variance. Abundance and biomass data were ln (x + 1) transformed to correct problems with heteroscedasticity. Analyses were conducted using the General Linear Model (GLM) of SAS (Release

6.03, SAS Institute Inc., Cary, North Carolina). This study, like most ecosystem-level manipulations, involved pseudoreplication. Therefore, differences between RS and FTS cannot be strictly attributed to treatment effects (Hurlbert 1984).

Variability in macroinvertebrate abundance and biomass between streams was compared using the coefficient of variation (CV) for total macroinvertebrates, for each FFG, and for the dominant shredder taxa. We chose CV as our metric because it is scaled to the mean, independent of sample size, and easily interpreted (Williamson 1984, Grossman et al. 1990, McArdle et al. 1990, Palmer et al. 1997). Within-year CVs were calculated using the means of litterbags collected on each sampling date within a given year, yielding 5 within-year CVs (1 for each year) for each group in each stream based on abundance or biomass. The means of replicate litterbags for each sampling date were used to calculate within-year CVs to remove the variability associated with sampling from temporal variability. Among-year CVs, in contrast, were calculated using the 5 annual means, yielding a single among-year CV for each group in each stream based on abundance or biomass.

We compared the within-year CVs for the abundance and biomass of total macroinvertebrates, of each FFG, and of the dominant shredder taxa between streams by comparing their 95% confidence intervals (CI) (Zar 1984). These within-year CVs were normally distributed and had equal variances. We could not statistically compare among-year CVs between streams because there was only 1 value per stream.

Life-history characteristics can affect temporal variability of macroinvertebrate abundance and biomass. Thus, we investigated whether there was a relationship between juvenile development time of individual taxa and their within-year CVs of abundance and biomass. Linear regressions were done between within-year CVs ($n = 5$) for each of 22 taxa and their respective cohort production intervals (CPI). CPI provides an estimate of development time measured as the mean length in days of the aquatic stage (Benke 1984). Separate regressions were done for FTS and RS. Within-year CVs of taxa were $\log_{10}$-transformed to correct problems with non-normality and heteroscedasticity. CPIs for most taxa in CHL streams have been reported by Lugthart and Wallace (1992), although some multivoltine taxa with unclear CPIs, i.e., Chironomidae and Copepoda, were conservatively estimated at 90 and 100 d, respectively (O'Doherty 1985, Huryn 1990). The 22 taxa used in this analysis represented 92–96% of total abundance and 89–94% of total biomass in both streams. These taxa included representatives from each FFG, except for scrapers. *Diplectrona metaqui* was excluded from the analyses for RS because it was not collected in 2 of 5 y.

Macroinvertebrate assemblage structure in litter bags was analyzed by ordinating the $\log_{10}(x + 1)$-transformed mean abundance and biomass of 11 common taxa in both streams on each collection date. Each of these 11 taxa composed at least 5% of total biomass in either stream in 2 or more years. Fewer taxa were used than the 22 above to reduce noise associated with rare taxa (Gauch 1982). We used detrended correspondence analysis (DCA, Hill and Gauch 1980) run with MVSP (Version 3.0, Kovach Computing Services, Anglesey, Wales, UK) to ordinate the data. DCA produces a similarity matrix based on chi-square distances.

Results

Discharge

Discharge was consistently higher in RS than in FTS (Table 1, Fig. 1), presumably because of the larger catchment of RS. However, the timing of discharge maxima was similar between streams (Fig. 1). Although drought conditions existed from 1985 through 1988, both streams remained perennial and experienced occasional small rainfall-induced increases in discharge (usually <10 L/s) during this period.

Within- and among-year analysis of macroinvertebrate abundance and biomass

Mean annual abundance of total macroinvertebrates and of each FFG, aside from filterers and shredders, did not differ significantly between streams (Table 2). Filterers were more abundant in RS than in FTS each year (Fig. 2), but only composed 0.1–0.4% of total abundance in any year. Although shredders were consistently more abundant in RS than in FTS (Fig. 2), this difference was heavily influenced by one stonefly, *Leuctra*. In fact, the other abundant shredders (i.e., *Lepidostoma*, *Tallaperla*, and *Pyc-*

TABLE 2. Results of each repeated measures analysis of variance comparing the ln (x + 1)-transformed abundance of total macroinvertebrates and functional feeding groups in the reference (RS) and former treatment (FTS) streams in each year and on each date. Stream = RS vs FTS, Year = among years (1985, 1986, 1988–1990), Date = collection dates within years, df = degrees of freedom, MS = mean square, $p < 0.05$ are in bold.

Variable		Stream	Year	Stream × Year	Error	Date	Date × Stream	Date × Year	Date × Stream × Year	Error (Date)
Total	df	1	4	3	32	8	8	32	24	256
	MS	0.112	13.916	1.898	0.390	3.197	1.469	0.993	0.421	0.372
	F	0.29	35.71	4.87		8.60	3.95	2.67	1.13	
	p	0.596	**<0.001**	**0.007**		**<0.001**	**<0.001**	**<0.001**	0.310	
Filterers	df	1	4	3	32	8	8	32	24	256
	MS	47.465	4.677	0.728	1.107	5.276	1.718	1.623	2.076	1.839
	F	42.87	4.22	0.66		2.87	0.93	0.88	1.13	
	p	**<0.001**	**0.007**	0.584		**0.005**	0.489	0.653	0.312	
Gatherers	df	1	4	3	32	8	8	32	24	256
	MS	0.300	16.358	2.190	0.436	3.796	1.421	1.122	0.449	0.423
	F	0.69	37.50	5.02		8.98	3.36	2.65	1.06	
	p	0.413	**<0.001**	**0.006**		**<0.001**	**0.001**	**<0.001**	0.390	
Predators	df	1	4	3	32	8	8	32	24	256
	MS	0.304	10.593	1.226	0.674	5.902	1.654	1.477	0.834	0.503
	F	0.45	15.72	1.82		11.74	3.29	2.94	1.66	
	p	0.507	**<0.001**	0.164		**<0.001**	**0.001**	**<0.001**	**0.030**	
Shredders	df	1	4	3	32	8	8	32	24	256
	MS	14.986	1.748	4.319	1.010	3.044	5.577	1.351	1.678	0.955
	F	14.84	1.73	4.28		3.19	5.84	1.41	1.76	
	p	**<0.001**	0.167	**0.012**		**0.002**	**<0.001**	0.076	**0.018**	

nopsyche) were usually more abundant in FTS than in RS. Macroinvertebrate assemblages in both streams were dominated by gatherers (86–92% of total abundance in FTS and 83–91% in RS), of which Copepoda and Chironomidae composed 90–95%. Thus, results for total annual mean abundance in both streams reflected the dynamics of these 2 groups.

Mean annual biomass of total macroinvertebrates and each FFG did not significantly differ between streams, except for filterers and gatherers (Table 3). Filterer biomass was higher in RS than in FTS, but again only composed a small proportion of total biomass (2–6%). Higher gatherer biomass in RS was attributed to a single mayfly, *Paraleptophlebia*. Conversely, other major gatherer taxa (i.e., *Amphinemura*, Chironomidae, Copepoda, and Oligochaeta) tended to be higher in FTS. The contribution of shredders, predators, and gatherers to total biomass was more evenly distributed than that observed for total abundance.

In most years and in both streams, mean abundance and biomass varied similarly among collection dates (Figs 3, 4). Within-year variation of mean abundance for shredders and filterers tended to differ more between streams than for other FFGs (Fig. 3), but this was not necessarily true of variation in mean biomass (Fig. 4).

Mean annual abundance of total macroinvertebrates and of each FFG, except for shredders, differed significantly among years (Table 2), primarily because mean annual abundance was lower in 1985 and 1986 than in 1988, 1989, and 1990 (Fig. 2). Significant Stream × Year interactions were also noted for most of these groups (Table 2) because abundance in FTS tended to be higher than in RS during 1985 and 1986, but lower than in RS during 1988 and 1990 (Fig. 2).

Significant differences in mean annual biomass among years were also noted for total macroinvertebrates and for each FFG (Table 3). As for abundance, biomass was usually lower in the first 2 y of the study compared to the last 3 y (Fig. 2).

The effect of the date of litter bag collection was always highly significant ($p \leq 0.005$) for the abundance and biomass of all macroinvertebrates and each FFG except for filterer biomass (Tables 2, 3). This result demonstrates that with-

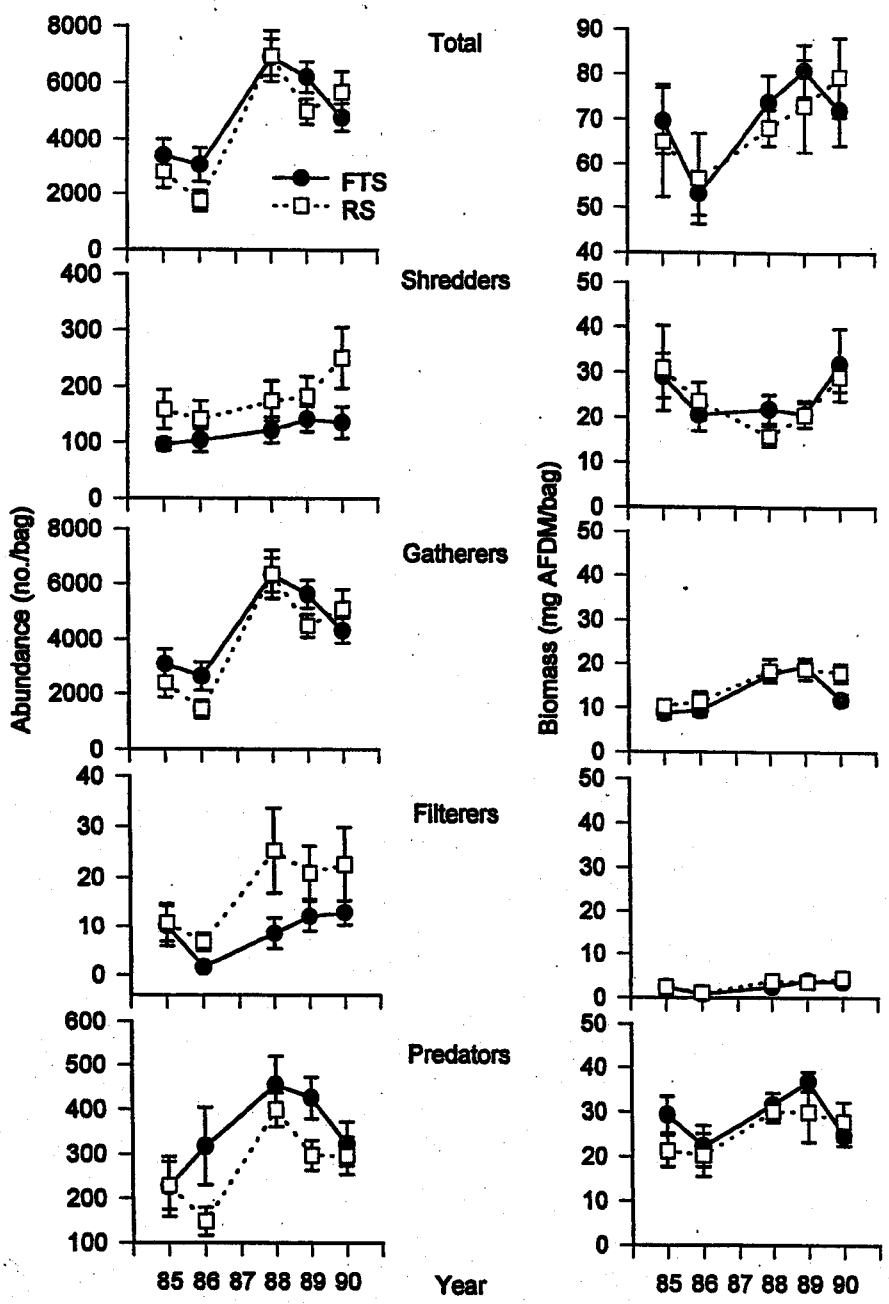

FIG. 2. Annual means (±1 SE) for abundance and biomass of each functional feeding group and total macroinvertebrates in the former treatment stream (FTS) and in the reference stream (RS) vs year. In some cases the error bars are hidden by symbols.

in-year changes in abundance and biomass were large sources of variation during the study.

Within- and among-year variance in macroinvertebrate abundance and biomass

Within- and among-year variability of macroinvertebrate abundance and biomass were similar between streams (Fig. 5), despite their different disturbance histories. There were no significant differences between streams in within-year CVs based on the abundance or biomass of total macroinvertebrates, of any FFG (95% CIs, Fig. 5), or shredder taxa except for the sericostomatid caddisfly, *Fattigia* (biomass only, Fig. 6).

Within-year CVs of abundance and biomass were usually higher than among-year CVs for total macroinvertebrates, each FFG, and individual shredder taxa (Figs 5, 6). These results dem-

TABLE 3. Results of each repeated measures analysis of variance comparing the ln (x + 1)-transformed biomass of total macroinvertebrates and functional feeding groups in the reference (RS) and former treatment (FTS) streams in each year and on each date. Stream = RS vs FTS, Year = among years (1985, 1986, 1988–1990), Date = collection dates within years, df = degrees of freedom, MS = mean square, $p < 0.05$ are in bold.

Variable		Stream	Year	Stream × Year	Error	Date	Date × Stream	Date × Year	Date × Stream × Year	Error (Date)
Total	df	1	4	3	32	8	8	32	24	256
	MS	0.251	1.028	0.697	0.301	1.324	0.517	0.597	0.349	0.261
	F	0.83	3.42	2.32		5.08	1.98	2.29	1.34	
	p	0.368	**0.020**	0.094		**<0.001**	**0.049**	**<0.001**	0.139	
Filterers	df	1	4	3	32	8	8	32	24	256
	MS	9.215	2.478	0.570	0.696	1.197	0.781	0.790	0.713	0.767
	F	13.25	3.56	0.82		1.56	1.02	1.03	0.93	
	p	**0.001**	**0.016**	0.493		0.137	0.423	0.428	0.563	
Gatherers	df	1	4	3	32	8	8	32	24	256
	MS	1.021	7.569	1.325	0.237	0.846	0.968	0.553	0.449	0.220
	F	4.30	31.89	5.58		3.85	4.40	2.51	2.04	
	p	**0.046**	**<0.001**	**0.003**		**<0.001**	**<0.001**	**<0.001**	**0.004**	
Predators	df	1	4	3	32	8	8	32	24	256
	MS	1.883	3.215	1.424	0.610	2.841	0.341	1.262	0.546	0.489
	F	3.09	5.27	2.34		5.81	0.70	2.58	1.12	
	p	0.088	**0.002**	0.092		**<0.001**	0.693	**<0.001**	0.325	
Shredders	df	1	4	3	32	8	8	32	24	256
	MS	0.207	2.466	0.942	0.523	4.413	1.814	1.074	0.577	0.568
	F	0.40	4.72	1.80		7.76	3.19	1.89	1.02	
	p	0.533	**0.004**	0.167		**<0.001**	**0.002**	**0.004**	0.446	

onstrate that changes in macroinvertebrate abundance and biomass were greater within years than among years.

Regression analyses of within-year CVs of abundance and biomass and CPIs for the 22 taxa (Fig. 7) indicated that within-year variability in both abundance (FTS: $p = 0.006$, $r^2 = 0.068$, $n = 110$; RS: $p = 0.012$, $r^2 = 0.059$, $n = 105$) and biomass (FTS: $p < 0.001$, $r^2 = 0.143$, $n = 110$; RS: $p < 0.001$, $r^2 = 0.146$, $n = 105$) increased with longer juvenile development times. Although these regressions explained relatively little of the variation seen in within-year CVs, they suggested that differences in life history influenced temporal variability, especially of biomass.

Comparisons of macroinvertebrate assemblage structure

Assemblage structure based on abundance and biomass was similar between streams and among years during the study because most of the ordination scores formed 1 large group in similar species space (Fig. 8). Initial collections in both streams during 2 drought years (1985 and 1986) clustered separately from the main group with lower scores on both axes, although this was not the case for the ordination of abundance in FTS. Most of the explained variation in each ordination (Axis 1) reflected different groups of taxa that colonized either relatively whole leaves soon after placement in the stream or more decomposed leaves later in the year. Axis 1 explained 34.2 and 33.4% of the variation in the abundance and biomass ordinations, respectively. The initial collections in January (denoted in Fig. 8 by a S next to its respective symbol) with most of the litter present had low Axis 1 scores, whereas later collections had higher scores. January assemblages were characterized by the shredders, *Pycnopsyche, Lepidostoma,* and *Tallaperla,* and a predator, *Beloneuria.* Later samples were dominated by small gatherers (Chironomidae, Oligochaeta, and Copepoda) and their predators (Ceratopogonidae and *Lanthus*), and 2 shredders, *Leuctra* and *Tipula.* Axis 2 only explained 15.7 and 16.1% of the variation in the

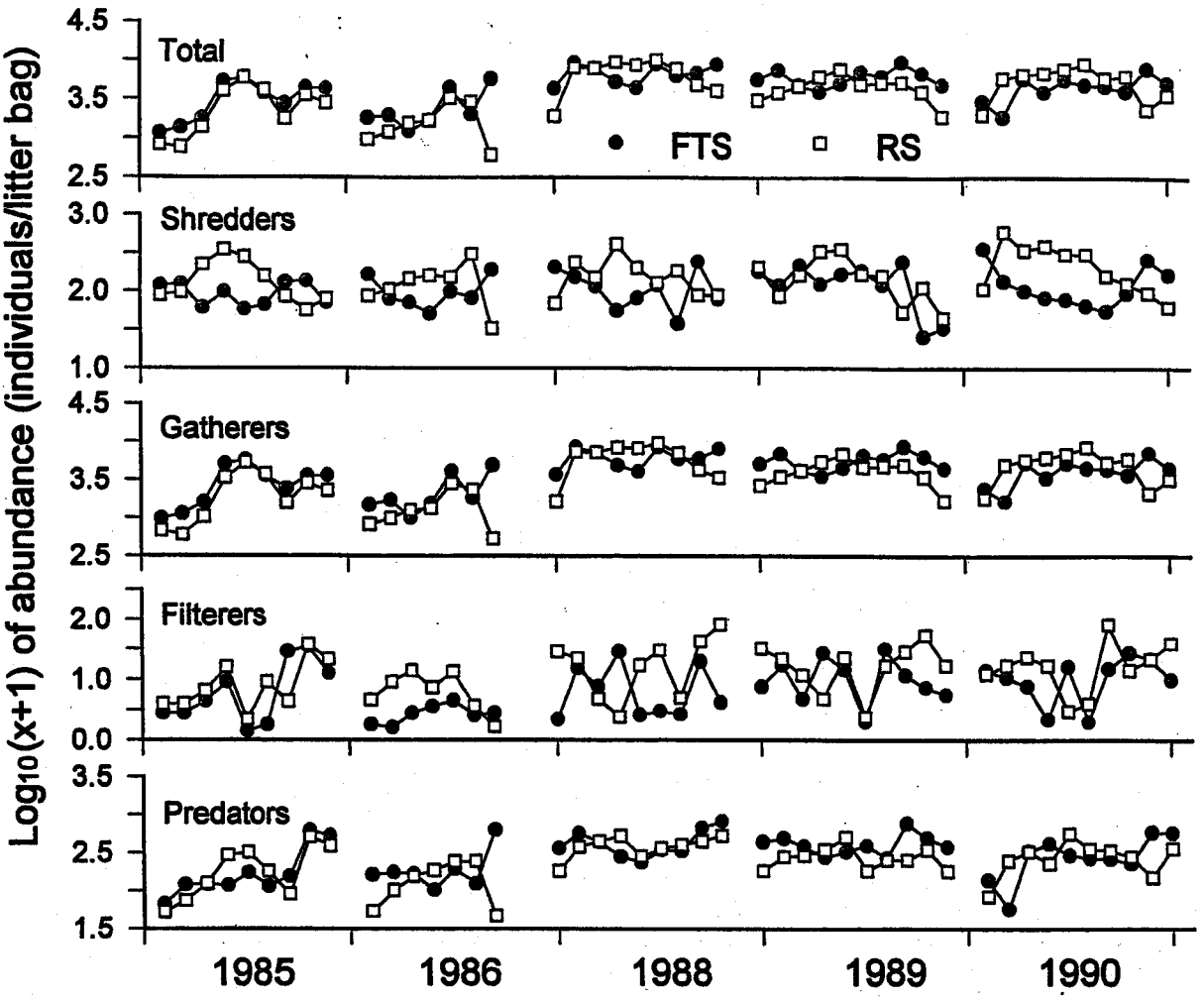

FIG. 3. Log_{10} (x + 1)-transformed mean abundance of total macroinvertebrates and each functional feeding group in the former treatment stream (FTS) and in the reference stream (RS) on each date of litter bag collection.

abundance and biomass ordinations, respectively. This axis was related to the dominance of either *Pycnopsyche* (high Axis 2 score) or *Tipula* (low Axis 2 score) in both abundance and biomass ordinations.

Discussion

Comparisons between streams

Following the initial pesticide treatment to FTS in 1980, total macroinvertebrate abundance recovered rapidly (117 d), but total biomass was only 1/3 that of the reference stream during the 1st year of recovery (Cuffney et al. 1984). The insect component of the macroinvertebrate assemblage suffered losses in abundance and biomass of >90% (Cuffney et al. 1984). After 2 y of recovery in FTS, mean annual abundance and biomass of total macroinvertebrates and FFGs did not differ between treated and reference streams (Wallace et al. 1986). During recovery years 5–10, mean annual abundance and biomass of total macroinvertebrates and most FFGs in FTS also did not differ from RS, and abundance and biomass typically had similar within-year dynamics. Recovery times of streams after direct application of pesticides are variable, but are often ≤1 y (Milner 1994). The somewhat longer time for recovery in FTS was a function of many factors, including 1) the lack of upstream sources of recolonization, and 2) the repeated seasonal applications of pesticide, which eliminated colonists that either hatched from surviving eggs or arrived from nearby streams between treatments (Wallace et al. 1986, Chung et al. 1993). The continued similarities in FFG abundance and biomass seen in our study indicated that there were no prolonged effects of residual pesticide in FTS sediments. Overall, our

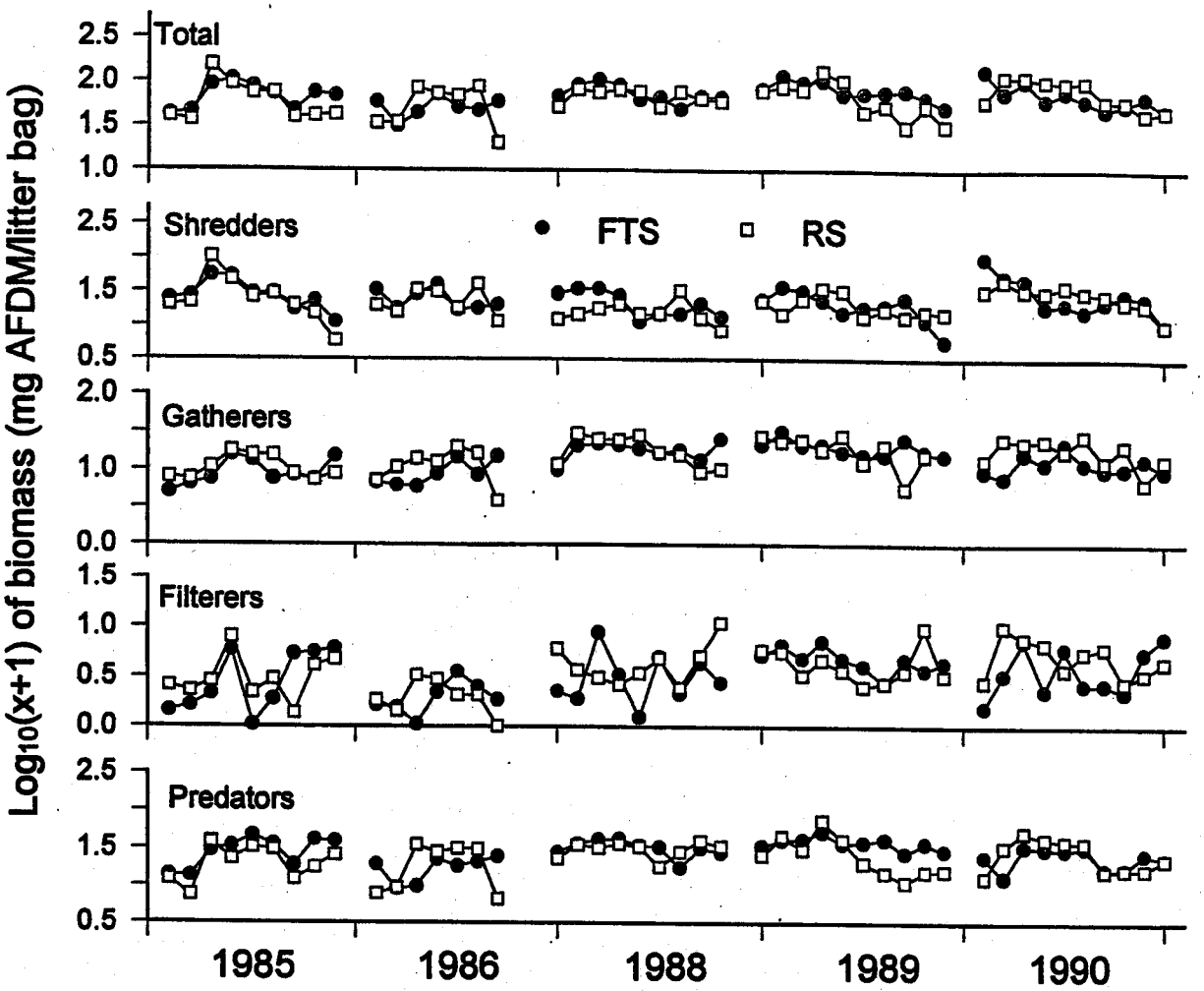

FIG. 4. Log_{10} (x + 1)-transformed mean biomass of total macroinvertebrates and each functional feeding group in the former treatment stream (FTS) and in the reference stream (RS) on each date of litter bag collection.

results agree with those expected from short-duration pulse disturbances because recovery was long term.

Some exceptions to the above patterns (shredder abundance and mean annual gatherer biomass) resulted from the dynamics of a single taxon in each group (*Leuctra* and *Paraleptophlebia*, respectively). *Leuctra* sometimes functions as a gatherer, especially in early instars (Hildrew et al. 1980, Dobson and Hildrew 1992), and the ordination scores for *Leuctra* were more similar to gatherer taxa than to shredder taxa. Thus, classifying *Leuctra* as a shredder may be questionable and merits further attention (also see Stewart and Stark 1993).

We used CVs to examine trends for absolute abundance and biomass, and to assess within- and among-year variability. We expected the mean abundance and biomass of macroinvertebrates to fluctuate more in FTS than in RS following the pesticide disturbance. Streams recovering from disturbance may harbor more invertebrate populations with short life cycles, rapid growth, and high fecundity compared to nearby, undisturbed streams (Wallace 1990). In addition, loss of a number of predatory taxa in FTS during the treatment year may have allowed various prey taxa to increase their survivorship and growth rates (Cuffney et al. 1984), which could also increase variability in FTS macroinvertebrates. However, the CVs showed no major differences in temporal variability between streams. Therefore, the results for variability around means agreed with those of means alone, and demonstrated that macroinvertebrate abundance and biomass in FTS had recovered from the pesticide disturbance. Detailed analysis of macroinvertebrate temporal dynamics provided by the CVs supported our contention that abundance and biomass had recovered in

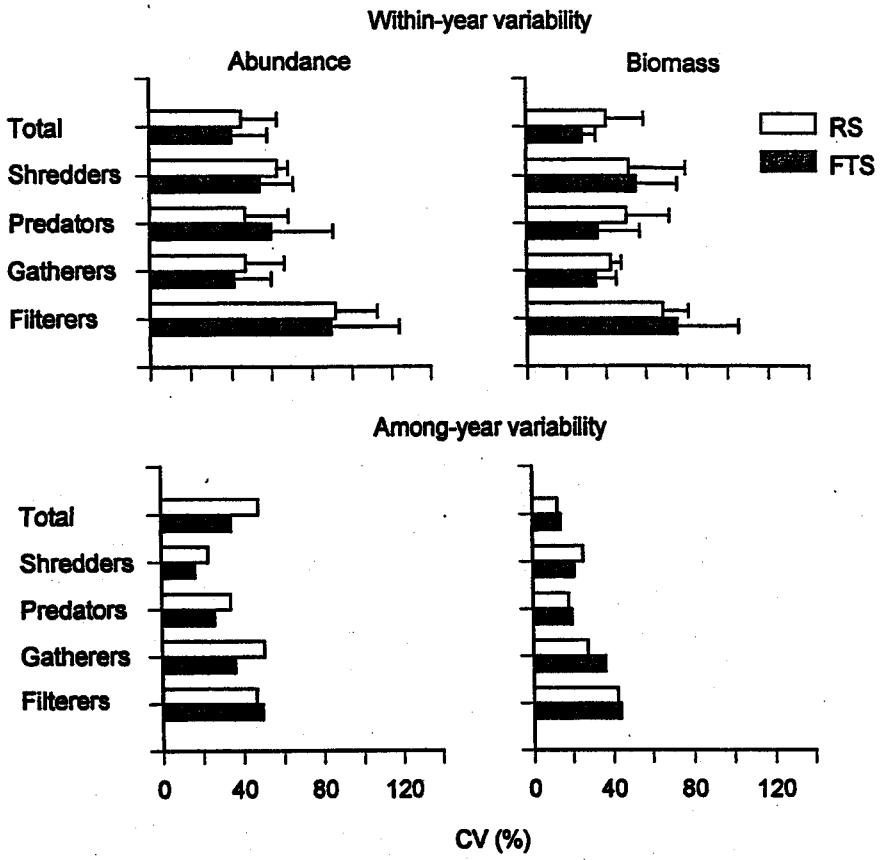

FIG. 5. Mean within- (top) and among-year (bottom) coefficients of variation (CV) for total macroinvertebrate and each functional feeding group abundance (left) and biomass (right) in the former treatment stream (FTS) and in the reference stream (RS). Error bars for within-year CVs represent +95% confidence intervals.

FTS relative to RS. The inclusion of end-points that are based on both mean responses and the variability of responses improved our ability to judge the completeness of recovery.

Macroinvertebrate assemblage structure in litter bags was similar between streams throughout this study as shown by the similar ordination scores between streams. Thus, as with macroinvertebrate density and biomass, assemblage structure had also recovered in FTS relative to RS during this study. Two years after pesticide treatment ended, Wallace et al. (1986) found major differences in taxonomic composition between these streams. The similarities seen in the present study (5–10 y after treatment) show that more time was required for recovery of assemblage structure compared to trophic structure (i.e., FFG abundance and biomass). The similarities in assemblage structure between RS and FTS partly resulted from their similar physical characteristics and close proximity (300 to 1000 m) to numerous headwater streams in the CHL basin, which served as sources of recolonists after pesticide treatment.

Comparisons among years

We found more differences in mean annual abundance and biomass among years than between streams. Studies that have examined multi-year trends (i.e., >2 y) in FFG or total macroinvertebrate abundance have also reported large among-year changes (McElravy et al. 1989, Boulton et al. 1992, Winterbourn 1997), but we are unaware of similar studies that have examined changes in biomass over many years.

The year-to-year differences we observed were primarily a result of lower macroinvertebrate abundance and biomass in the first 2 y of the study (especially in 1986, the driest year on record at CHL) than in the last 3 y. Stream macroinvertebrates often concentrate in the reduced wetted area during periods of drought, causing densities to increase (e.g., Larimore et al. 1959,

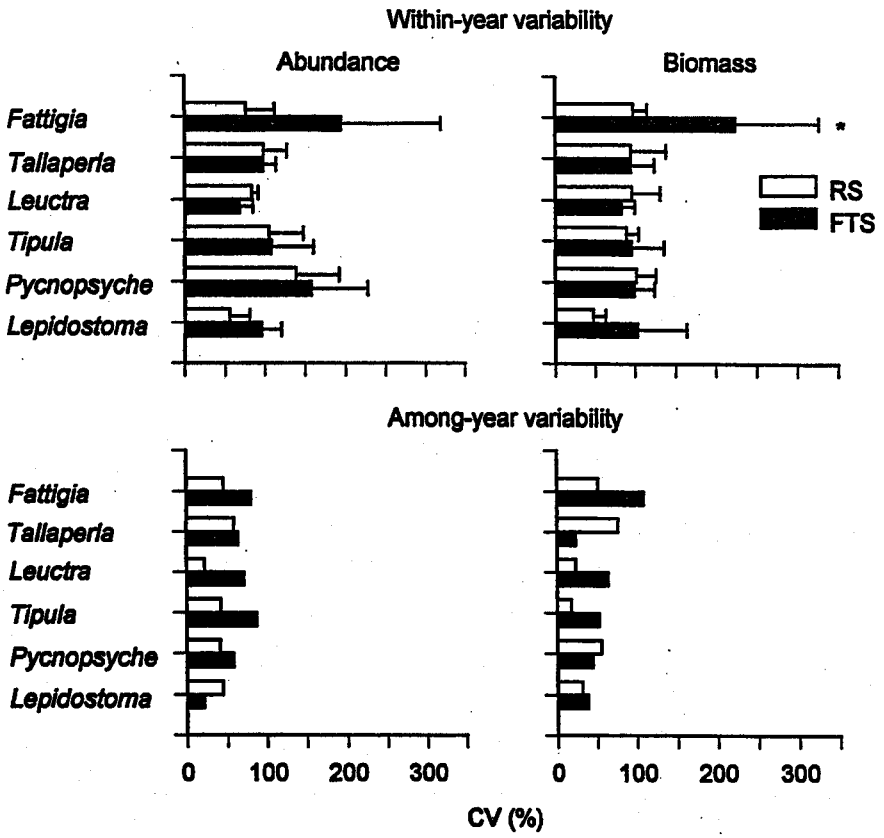

FIG. 6. Mean within- (top) and among-year (bottom) coefficients of variation (CV) for the dominant shredder taxa based on abundance (left) and biomass (right) in the former treatment stream (FTS) and in the reference stream (RS). Error bars for within-year CVs represent +95% confidence intervals. Asterisk indicates a significant difference between FTS and RS ($p < 0.05$).

Kamler and Riedel 1960, Stanley et al. 1994). However, other studies have reported both increases and decreases in annual abundance following droughts, depending on taxon-specific life-history characteristics (Boulton and Lake 1992, Boulton et al. 1992). We observed no consistent drought-induced pattern in macroinvertebrate assemblages, perhaps because mixed substrate habitats are less sensitive to drought effects than other habitats, such as bedrock outcrops (Lugthart and Wallace 1992). Finally, regional climate may be an important factor; larger and more consistent differences in abundance may be expected in regions with more pronounced differences in precipitation, e.g., the Sonoran Desert, USA (Boulton et al. 1992), northern California, USA (Mediterranean-type climate; McElravy et al. 1989, Power et al. 1996), and Australia (Boulton and Lake 1992) than the humid, temperate CHL. Even in the severe drought years of 1986 and 1988, RS and FTS continued to flow, although FTS decreased in wetted area by as much as 80% (Wallace et al. 1991a). In contrast, streams in some of the studies cited above became either intermittent or a series of disconnected pools.

Among-year CVs were usually lower than within-year CVs, especially when based on biomass, because macroinvertebrate abundance and biomass fluctuated more during a year than they did from year to year, which is not surprising when life-history patterns and colonization time are considered. Most taxa in CHL streams complete their life cycles within 1 y, meaning that sampling during a year encompasses the entire survivorship and growth curves. Also, availability of coarse particulate organic matter in these systems is strongly seasonal because of the large influx of autumn-shed leaves that subsequently break down. Thus, CHL stream macroinvertebrates naturally undergo changes in abundance and biomass during a year because of life-cycle events and variable resources. In contrast, much less is known about factors controlling natural inter-annual variation in the taxonomic composition and bio-

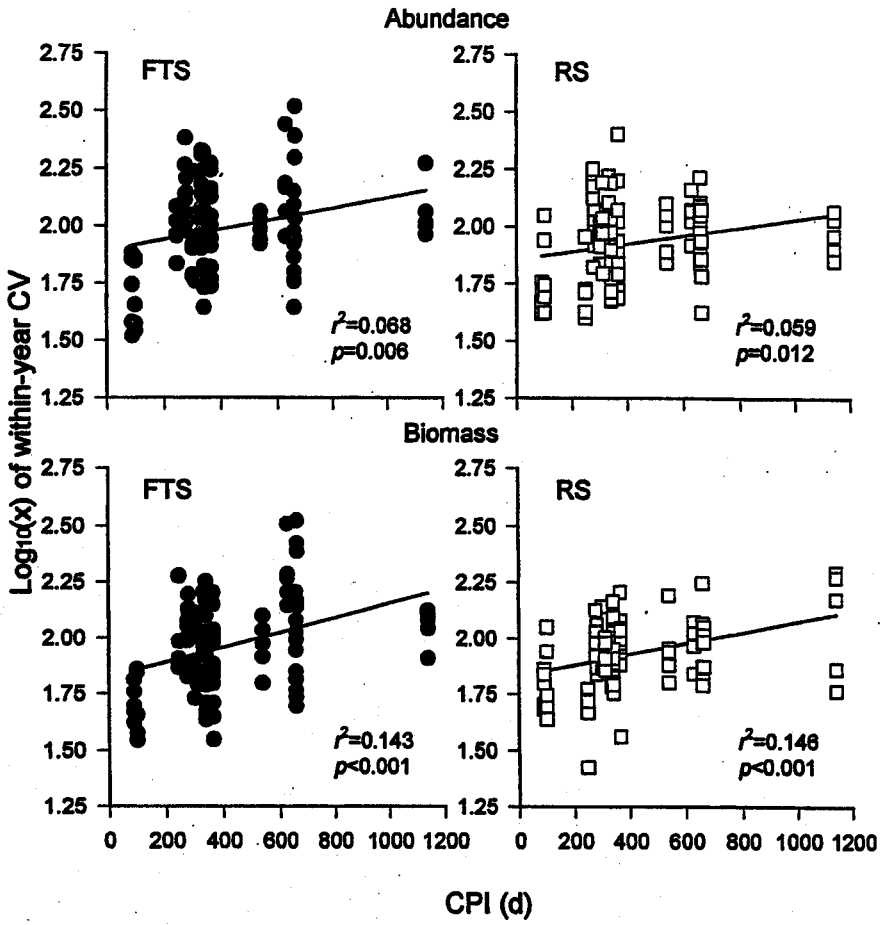

FIG. 7. Log_{10}-transformed within-year coefficients of variation (CV) for 22 taxa based on abundance (top) and biomass (bottom) vs their respective cohort production interval (CPI) in the former treatment stream (FTS) and in the reference stream (RS). The lines are fitted regressions.

mass of invertebrate assemblages in such streams. Using long-term organic matter budgets for the streams in this study, Wallace et al. (1997a) hypothesized that litter standing crops undergo multi-year cycles of accumulation and loss as a result of variable discharge. Decreased litter in some years could have detrimental effects on macroinvertebrates; experimental whole-stream reductions in litter reduced macroinvertebrate abundance, biomass, and secondary production (Wallace et al. 1997b). Different processes contributed to the variation observed at within-year versus among-year time scales.

Life-history characteristics of FTS and RS taxa also affected within-year variability in abundance and biomass. Those taxa with longer juvenile development times were more variable within years than those with shorter development times. This result was probably a function of sampling frequency relative to voltinism. Multivoltine taxa with overlapping cohorts, for example, would vary considerably in abundance and biomass between monthly sampling periods. In contrast, monthly sampling of univoltine taxa would detect changes in the number and size of individuals that are associated with normal life-cycle events because of the slower development of these taxa—abundance may range from 0 just before egg hatching to several thousand soon after hatching. Furthermore, for semivoltine and merovoltine taxa, 2–3 cohorts that greatly differ in abundance and mean individual size can co-occur, which would result in a highly variable within-year CV for both abundance and biomass. Nevertheless, the regressions of within-year CVs of abundance and biomass against CPIs left much of the variability unexplained, so that other factors (e.g., resources, biotic interactions, etc.) must also influence within-year changes in macroinvertebrate assemblages in these streams.

Macroinvertebrate assemblage structure was

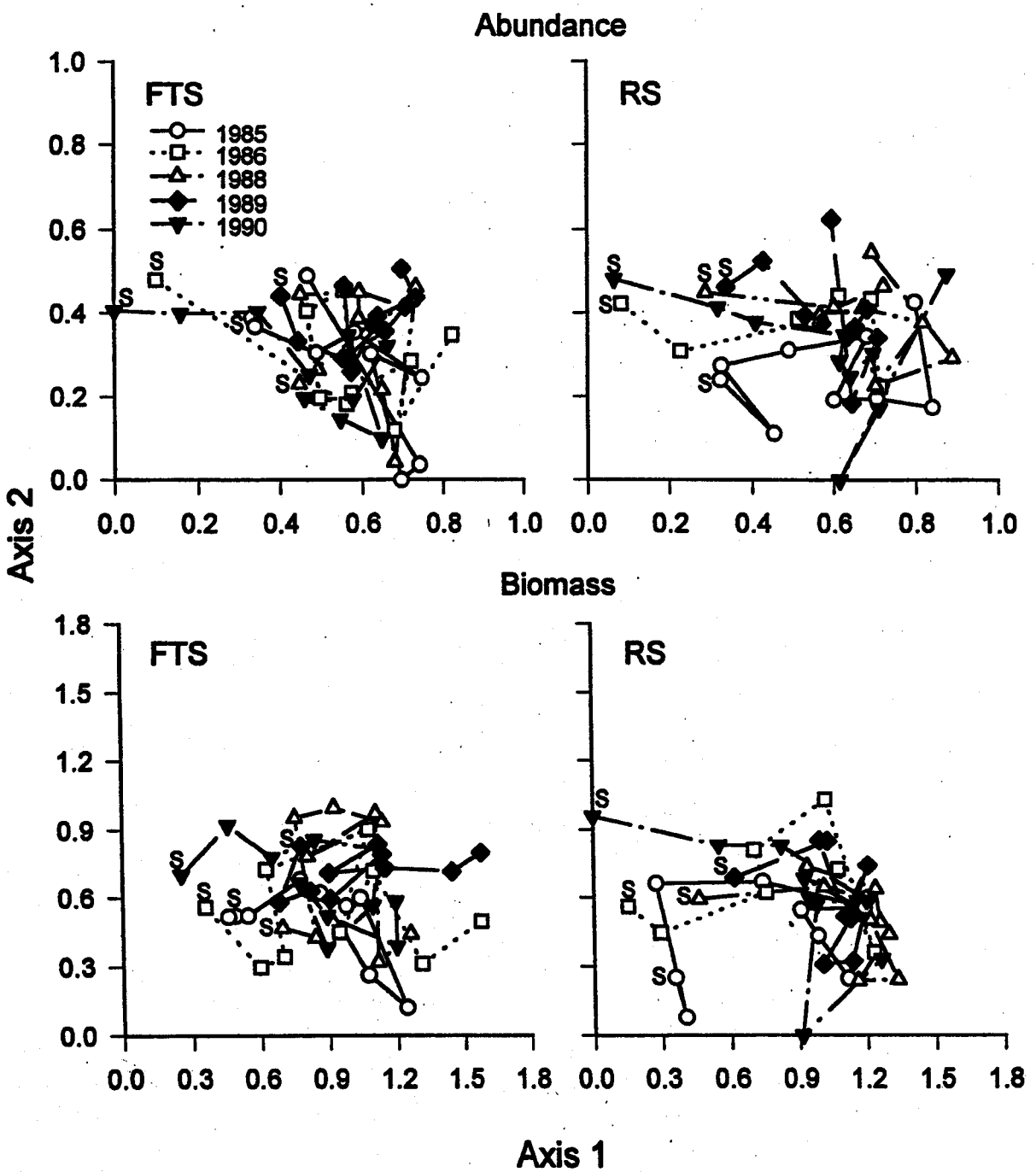

FIG. 8. Ordination plots of the first 2 axes from detrended correspondence analyses for the abundance (top) and biomass (bottom) of 11 macroinvertebrate taxa in the former treatment stream (FTS) and in the reference stream (RS) on each collection date. Open symbols represent drought years (1985, 1986, 1988) and closed symbols represent wet years (1989, 1990). The 1st collection date each year is denoted by S and subsequent collections are connected by the same line.

generally similar within either RS or FTS across years as shown by the ordination results, which agrees with some other multi-year studies of assemblage structure (but see exceptions below). McElravy et al. (1989) found that various community parameters for macroinvertebrates collected in late summer were similar among years, although some differences, related to discharge, were noted for late-spring samples. Richards and Minshall (1992) found similar relative abundance of common macroinvertebrates in 5 undisturbed streams in Idaho, USA, over 5

y. However, they also found that community structure in 5 streams disturbed by wildfire 1 y prior to the study varied more among years than the undisturbed streams because of decreased channel stability from large-scale loss of catchment and riparian vegetation in burned catchments. Other 4–5 y studies (Meffe and Minckley 1987, Weatherly and Ormerod 1990, Winterbourn 1997) also found that assemblage structure changed little in response to natural environmental fluctuations. These studies show that biotic parameters based on assemblage structure are robust to year-to-year changes associated with natural variability. However, this finding should be limited to regions with nearby, undisturbed populations available as sources for recolonization (Cushing and Gaines 1989). Interestingly, assemblage structure in some streams can be similar from year to year for reasons other than consistent proportions of taxa. For example, Boulton et al. (1992) found a consistent cycle of seasonal change in assemblage structure over 3 y in Sycamore Creek, USA, but this change was a result of variation in presence or absence of taxa rather than in their relative abundance. Similar results were obtained in 2 intermittent streams in Victoria, Australia (Boulton and Lake 1992). Still, including a parameter that measures assemblage structure in biomonitoring studies should be useful. In fact, an evaluation of various metrics used in the rapid bioassessment protocol of the US Environmental Protection Agency found low CVs in the Pinkham and Pearson community similarity index, a structure metric that incorporates abundance and compositional information, in unimpaired reference sites (Barbour et al. 1992).

Palmer and Poff (1997) examined how temporal and spatial heterogeneity influences patterns and processes in streams. These authors highlighted how variability within and across different spatial scales affects streams, but provided few examples illustrating effects of variability within and across different temporal scales. Our results demonstrate that examining temporal variability at different scales is useful for studying macroinvertebrate responses to anthropogenic disturbances and responses to a naturally changing environment. Future studies should examine what factors influence variation at different temporal scales, including macroinvertebrate life histories, resource variability, and biotic interactions.

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