Interactive Effects of Environmental Variability and Military Training on Stream Biota of Three Headwater Drainages in Western Louisiana

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Abstract.—We collected fishes and macroinvertebrates seasonally from eight headwater streams in three different drainage basins (the Red, Calcasieu, and Sabine rivers) crossing Peason Ridge Training Area in west-central Louisiana. Peason Ridge is part of the Fort Polk military training facility. We used multivariate analyses to test the effects of physical variables (i.e., current velocity, depth, and substrate), time (seasonal variability), drainage basin, and military training activities on assemblage structure. Tributaries of the Red River had the highest gradient and were predominated by shallow, swift-flowing runs with sandy substrates. Southern tributaries of the Calcasieu and Sabine rivers were of lower stream gradient and contained deep, sluggish runs and pools with large amounts of woody debris and silt. Fish assemblages were structured primarily by military training and drainage basin. Faunal differences among drainage basins probably reflect differences in stream gradient. Fish assemblages in tributaries of the Sabine River were less diverse and showed evidence of historical degradation. Macroinvertebrate assemblages also were structured primarily by military training but had a strong seasonal component related to their short life cycles and high seasonal turnover. In contrast to fishes, macroinvertebrate assemblages were similar among drainages. Because military training was most intense in the Red River basin, its significance in these models probably represents differences in stream gradient among the basins because we found no negative effect on stream biota resulting from current training activities. Rather, historical logging and the resultant siltation coupled with isolation of populations by reservoirs are probable explanations for the changes in fish assemblages in tributaries of the Sabine River.

The structure of stream fish and macroinvertebrate assemblages is influenced by a number of hierarchically ordered factors through space and time (Schlosser 1987; Tonn 1990). At large spatial and temporal scales, factors like climate, geomorphology, and zoogeographic history influence regional species pools (Vinson and Hawkins 1998; Ricklefs et al. 1999; Williams et al. 2002). Regional pools are, in turn, affected by biotic inter-

actions and abiotic factors at smaller spatial scales, producing local species assemblages. Abiotic factors have a strong influence on the structure of fish and macroinvertebrate assemblages (Gorman and Karr 1978; Grossman et al. 1982; Grimm and Fisher 1989). Temporal variability in discharge, for example, has a strong influence on assemblage structure, particularly in streams with dynamic hydrology (Capone and Kushlan 1991; Taylor and Warren 2001; Williams et al. 2003a). Until recently, however, many studies have focused on a single group of organisms over limited spatial and

temporal scales (Williams et al. 2002). Describing how different groups of organisms respond to stream habitat over various space and time scales is necessary for understanding the structure and function of lotic ecosystems.

Natural and anthropogenic disturbances also can have a strong influence on local species assemblages (Resh et al. 1988). Effects of disturbances, however, are variable and depend on stream morphology, hydrologic regime, and the spatial and temporal scale over which they occur (Wiens et al. 1986; Resh et al. 1988). Watersheds in the southeastern USA have been tremendously affected by a variety of anthropogenic disturbances during the 20th and 21st centuries (Warren et al. 2000). Physical alteration of habitat (e.g., channelization, sedimentation, and flow alteration) is probably the greatest threat to aquatic diversity in southern U.S. streams. Over the last 20 years, there has been a 125% increase in the number of endangered, threatened, and vulnerable fish species in the Southeast (Warren et al. 2000), and landscape perturbations have produced even more dramatic declines for many of the invertebrates in this region (Vaughn and Taylor 1999).

We sampled eight headwater streams from three different drainage basins (the Red, Calcasieu, and Sabine rivers) of Peason Ridge Training Area (PRTA), a 13,500-ha section of Fort Polk military training area in west-central Louisiana. The Sabine and Calcasieu drainages in the southern portion of PRTA share common physiography, geologic origin (lowland coastal plains), and fish species composition (Douglas 1974). The Red River drainage to the north, although differing in physiography and geology (upland drainage) from the other two drainages, has a similar fish species composition. Similarity in fish species composition between lowland coastal plain and upland drainages is explained by relatively recent connections in geologic time between the Red and Sabine river drainages and again between the Red and Calcasieu river drainages (Conner and Suttkus 1986).

We had three major objectives in this study: (1) to assess spatial and temporal trends in fish and macroinvertebrate assemblage structure within and among the drainages; (2) to determine which factors (physical and chemical variables, zoogeography, season, and anthropogenic modification) are important in maintaining the observed assemblage structure and how these factors differentially affect fish and macroinvertebrate assemblages; and (3) to determine what impacts, if any, military training activities have had on the fish and macroinverte-
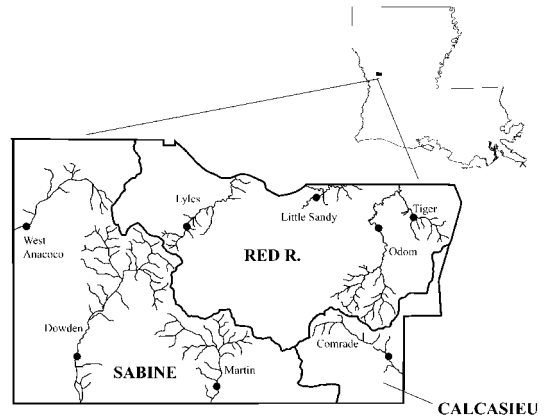

FIGURE 1.—Map of the Peason Ridge Training Area, which is part of the Fort Polk military training facility in west-central Louisiana, showing sampling locations (circles) of fish and macroinvertebrates and drainage basins for streams in the Red (Lyles, Little Sandy, Odom, and Tiger creeks), Calcasieu (Comrade Creek), and Sabine rivers (West Anacoco, Dowden, and Martin creeks).

brate assemblages. Our study is unique in that few studies have documented how both fish and macroinvertebrate assemblages are structured by different explanatory factors operating at various spatial and temporal scales (Jackson and Harvey 1993; Williams et al. 2002).

Study Area

Located in Vernon, Sabine, and Natchitoches parishes in west-central Louisiana, PRTA is part of the Hill Physiographic Unit (also known as the Kisatchie Wold), which is a portion of the Central Gulf Coastal Plain formed by erosions and depositions from fluctuating sea levels during periods of glaciation (Conner and Suttkus 1986). The headwaters of the Red, Sabine, and Calcasieu rivers, three independent drainages, originate within a 2-km^2 area of PRTA.

Streams of the Red River drainage (Tiger, Odom, Little Sandy, and Lyles creeks) capture overland runoff and seepage from the northern scarp of Peason Ridge and drain northeasterly into Kisatchie Bayou (Figure 1). Kisatchie Bayou drains into the Red River, which is a major tributary entering the Mississippi River in southeastern Louisiana. Watersheds of the Red River drainage are gently sloping to steep, have loamy to sandy soils (Martin et al. 1990), and contain mixtures of loblolly *Pinus taeda* and longleaf pines *P. palustris* on the upland areas and various hardwood trees (e.g., beech *Fagus grandifolia*, magnolia *Magnolia grandiflora*, white oak *Quercus alba*, wa-

ter oak *Quercus nigra*, and red maple *Acer rubrum*) along the lowland areas. From the southern scarp, tributaries of the Sabine River drainage (West Anacoco, Dowden, and Martin creeks) emerge and flow southerly into the Sabine River, whereas Comrade Creek emerges and flows southeasterly into the Calcasieu River. Both the Sabine and Calcasieu rivers drain directly into the Gulf of Mexico. Watersheds of the southern scarp are gently sloping to flat, have loamy to clay soils, and contain longleaf pine on the upland areas and various hardwood trees (e.g., baldcypress *Taxodium distichum*, white oak, water oak, and magnolia) along the lowlands.

The U.S. Army purchased the land occupied by PRTA in 1941. Before 1941, most of the area had been logged. After World War II, PRTA was partially used for training until 1950 through 1954, when it was fully opened during the Korean War. After 1955, it was used intermittently until its designation as an infantry-training center in 1962. During the 1960s, PRTA was heavily used for infantry training, serving as a ''little Vietnam.'' In 1968, PRTA was established with Fort Polk as a permanent base. Peason Ridge is located approximately 30 km north of the main base. From 1974–1992 it was the home of the 5th Mechanized Infantry Division. During this period, large numbers of tracked vehicles were used and heavy, mechanized training occurred on PRTA. In 1993, it became the Joint Readiness Training Center and was used for predominantly light infantry and small amounts of mechanized training during rotations. Currently, the military uses PRTA primarily for live-fire exercises and troop maneuvers; thus, portions of timber have been harvested from upper reaches of the watersheds to allow firing lanes and internal road systems, and numerous stream crossings have been constructed to handle troops and large equipment. Longleaf pine ecosystems, such as those found at Peason Ridge, are fire climax communities for which burning from lightning strikes have historically been an integral constituent (Bridges and Orzell 1989). Fort Polk maintains this area by incorporating prescribed burning on a 2–3-year cycle. Thus, this area contains mature longleaf pine trees and a very sparse understory (Figure 2) that supports several colonies of the red-cockaded woodpecker *Picoides borealis* (a federally endangered species). Efforts also have been made in recent years to regenerate longleaf pines on areas of the PRTA where logging in the early part of the 20th century had previously eliminated them (Figure 2).
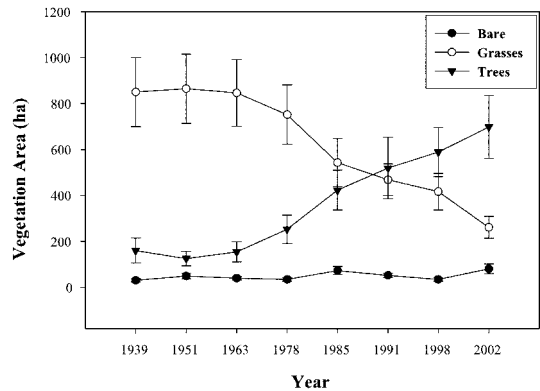

FIGURE 2.—Area (ha; mean ± SE) of trees, bare ground, and grasses over eight sampling periods from 1939 to 2002 for all eight subbasins sampled on the Peason Ridge Training Area. Area was determined from aerial photographs taken during the leaf-off period between November and March using Arcview Image Analyst software package.

Methods

Sampling methodology.—Biota were collected in each of the four seasons from June 2001 through August 2002 (summer was sampled in 2001 and 2002) in four northern scarp streams (Tiger, Odom, Little Sandy, and Lyles creeks) and four southern scarp streams (West Anacoco, Dowden, Martin, and Comrade creeks), except that macroinvertebrates were not collected from Lyles Creek in January 2002 nor were macroinvertebrates and fish collected from West Anacoco Creek in August 2002. For each stream, collection sites were located near the PRTA boundary to avoid intermittent flows, except for Lyles Creek, which was selected based on accessibility. Each site consisted of a minimum 100-m section of stream that contained mesohabitats (i.e., runs, pool, and riffles), substrate, and woody debris in similar proportions to those of the stream; thus, each site was considered representative of the conditions within each stream. Fish were sampled with a Smith-Root model-14 backpack electroshocker and seines (1.2 × 1.8 m with 6-mm mesh, 1.8 × 2.4 m with 9.5-mm mesh). Block nets were placed downstream of each stream section to prevent escape, and multiple passes were made with the electroshocker and seines to capture all fishes. Fish were identified to species, enumerated, and released, except for voucher specimens. We collected macroinvertebrates from each stream, along the same reaches sampled for fishes. D-frame kick-nets were used to sample all available microhabitats in the reach.

In addition, a 5-min Surber sample was taken at each locality in an effort to capture more benthic taxa that might have been missed with kick-nets. Because riffle habitats were a minor component of these streams, the 5-min Surber sample was adequate to cover this habitat type. Macroinvertebrate samples were preserved in the field with 95% ethanol and rose-bengal stain and transported to the laboratory for identification. Macroinvertebrates were identified to the family level (genus when possible), and families were used for all statistical analyses (Bowman and Bailey 1997).

Temperature, conductivity, pH, dissolved oxygen, and turbidity were recorded with a YSI Model 600 multiprobe meter at each site. Average width and visual estimates of percent substrate composition, woody debris (logs), detritus (leaf litter and sticks), and vegetation (Taylor and Lienesch 1996; Taylor and Warren 2001; Williams et al. 2003a) were recorded from at least three transects per stream reach. Mean current velocity (Marsh-McBirney Flowmate) and depth were obtained from three to four cross-sectional profiles per reach.

Statistical methods.—Physical and chemical variables by site were z-score-transformed (Krebs 1999) and assessed with principle components analyses (PCA) to detect temporal and spatial differences by site and drainage. Variables showing diel fluctuations (e.g., temperature and dissolved oxygen) were deleted from multivariate analyses.

Similarities of fish and macroinvertebrate assemblage structure by site and drainage were assessed with Renkonen similarity indices (RSI; Krebs 1999) and detrended correspondence analyses (DCA; Gauch 1982). For multivariate analyses, abundances were square-root-transformed, to dampen the effects of predominant taxa, and rare taxa were downweighted (McCune and Mefford 1999). In addition, taxa richness (S; species for fishes and families for macroinvertebrates), diversity (H), evenness, and turnover (RSI) were determined for each site across seasons. Diversity was calculated using the Shannon-Weiner index ($\log_e$ base), and evenness was represented by Buzas and Gibson's E ($E = e^H/S$; Hayek and Buzas 1997).

We used canonical correspondence analysis (CCA; ter Braak 1986) to examine the relationship between stream habitat and assemblage structure for fishes and macroinvertebrates. Canonical correspondence analysis is a direct gradient analysis where an ordination of one multivariate matrix is constrained by a multiple linear regression on variables in a second matrix (McCune and Grace 2002). We used a variance partitioning technique (Borcard et al. 1992; Magnan et al. 1994; Williams et al. 2002) to relate variation in assemblage structure to four explanatory variables: stream physical and chemical variables, season, drainage basin differences, and potential effects of military training. Military training intensity was represented by training days per hectare during the last 5 years, road density (m/ha), number of road crossings per hectare, hectares of thinned forest per hectare, hectares of clear-cut forest per hectare, and hectares burned $\times$ days burned per hectare (Table 1). Variance partitioning is accomplished by a series of partial CCAs, which are similar in function to partial regression techniques (Quinn and Keough 2002). For each of the four variables of interest, we used the other three factors as covariates in the analysis to assess the pure effect of each. For example, we examined the pure effect of military training (removing confounding effects of differences in physical and chemical variables, drainage basin, and seasonal variability). We computed the percent of variance in assemblage structure (for fishes and macroinvertebrates separately) that was explained by each independent variable set (i.e., habitat, season, basin, and training). Because of the potential for 2-way, 3-way, and 4-way interactions, we were unable to test for any shared variation (Quinn and Keough 2002; Williams et al. 2002) among the variables. For each partial CCA, we used Monte Carlo tests (1,000 permutations) to estimate the significance of each variable (ter Braak and Smilauer 2002).

Recent authors have used similar multivariate techniques (i.e., variance partitioning with CCA) to test hypotheses about species–environment relationships at different spatial and temporal scales (Wang et al. 2003; Williams et al. 2003b) or the effects of disturbances on aquatic assemblages (Jongman et al. 1995; ter Braak and Verdonschot 1995; Williams et al. 2002). For complex, large-scale questions in community ecology, standard parametric multivariate tools (e.g., MANOVA) often are inappropriate for testing hypotheses, and data rarely meet assumptions of these tests. Typical univariate analyses usually are inappropriate for these types of questions because intercorrelated response variables do not adequately express the complex relationships between dependent and independent variables (McCune and Grace 2002). Thus, multivariate analyses based on randomization procedures (e.g., Monte Carlo tests) usually are better at representing patterns affecting com-

Table 1.—Mean values for military training activities by creek (Cr.) and river (R.) in the Peason Ridge Training Area, Louisiana, as used in multivariate models to examine fish and macroinvertebrate assemblage structure.

Variable	Red R.			
	Lyles Cr.	Sandy Cr.	Odom Cr.	Tiger Cr.
Drainage area (ha)	978.85	705.43	1,377.58	224.24
Number training days	1,844	2,320	2,320	2,320
Training days/ha	1.88	3.29	1.68	10.35
Road density/ha	13.2	10.1	18	12.5
Number crossings/ha	0.0041	0.0028	0.0022	0.0045
Hectares thinned/ha	0.00	0.06	0.00	0.74
Hectares clearcut/ha	0.00	0.00	0.05	0.00
Hectares × days burned/ha	1.80	1.93	0.92	0.39

munity structure than are univariate methods (McCune and Grace 2002).

Results

Habitat Attributes

Width, conductivity, pH, turbidity, and percent aquatic vegetation of streams were similar across drainage and season (Table 2). Widths were less than 5 m for all streams and remained relatively constant across seasons. Conductivity and pH varied little across seasons, and low conductivity and nearly neutral pH were typical for streams in this area (Felley and Felley 1987). Turbidity increased immediately after intense rains, most notably in the Sabine drainage, but quickly dissipated via downstream transport and settling of suspended sediments. Percent aquatic vegetation was low (<10%) in all streams.

Differences were observed for substrate type, percent detritus and woody debris, depth, and current velocity among drainages and to a lesser extent among streams within a drainage. Using ordination, linear contrasts of these variables explained 47% of the observed variation among sites. The first PCA axis (29% of total variation) described a depth and current velocity gradient, and the second axis (18%) describing a substrate gradient. Sites in the Sabine and Calcasieu drainages were associated positively with axis 1, which described streams with greater depths, slower current velocity, and greater amounts of woody debris, detritus, and silt (Figure 3). In contrast, streams in the Red River drainage generally were shallower and swifter and had greater amounts of sand and cobble substrates. The second PCA axis generally segregated streams of the Red River drainage by percent substrate. Odom Creek and one collection on Lyles Creek were strongly associated with PCA axis 2, describing larger proportions of cobble substrate.

Taxa Abundance

Across seasons and streams, 4,461 fishes representing 11 families and 37 species were collected from the Red, Calcasieu, and Sabine drainages (Table A.1 in the Appendix). Cyprinidae represented 63% of the total assemblage, followed by Fundulidae (12%), Centrarchidae (8%), Percidae (5%), and Catostomidae (3%). Petromyzontidae, Ictaluridae, Esocidae, Aphredoderidae, and Atherinopsidae contributed less than 6% of the assemblage. By drainage, blackspotted topminnows *Fundulus olivaceus*, striped shiners, redfin shiners, Sabine shiners, and blackspot shiners represented 60% of the total fish assemblage for the Red River. Blackspotted topminnows, redfin shiners, and ribbon shiners contributed 64% of the fish assemblage for the Calcasieu River drainage; redfin shiners and ribbon shiners represented 75% of the Sabine River drainage assemblage. Species reported herein were similar to historical species accounts for Red River and Calcasieu River drainages (Douglas 1974) but differed for the Sabine River drainage. In the Sabine drainage, pallid shiners *Hybopsis amnis*, Sabine shiners, weed shiners *N. texanus*, striped shiners, scaly sand darters, cypress darters *Etheostoma proeliare*, and harlequin darters *Etheostoma histrio* were absent from recent collections, whereas ribbon shiners were absent from historical records yet composed 30% of the recent assemblage.

A total of 8,462 macroinvertebrates representing 16 orders and 70 families were collected from the three drainages and used for statistical analyses (Table A.2). The orders Oligochaeta, Achariformes, Anomopoda, Gastropoda, Hydroida, Hymenoptera, and Nematoda were excluded from quantitative analyses because they were extremely uncommon (only one or two individuals), or their capture was considered incidental in our sampling (e.g., Gastropoda). Chironomids were predomi-

TABLE 1.—Extended.

Variable	Calcasieu R. Comrade Cr.	Sabine R. Anacoco Cr.	Dowden Cr.	Martin Cr.
Drainage area (ha)	799.93	968.71	2,065.31	1,196.86
Number training days	2,212	2,180	1,971	1,955
Training days/ha	2.77	2.25	0.95	1.63
Road density/ha	20.9	16.3	15.9	10.6
Number crossings/ha	0.0050	0.0052	0.0039	0.0033
Hectares thinned/ha	0.23	0.00	0.00	0.00
Hectares clearcut/ha	0.00	0.00	0.00	0.00
Hectares × days burned/ha	0.51	0.65	0.44	0.92

nant in all drainages. The families Chironomidae (Diptera) and Caenidae (Ephemeroptera) were the only taxa that had relative abundances greater than 10% for any drainage. Unlike fishes, no comparative historical data exist for macroinvertebrates in PRTA streams.

Fish assemblage structure differed distinctly between the Red River drainage and the two southern drainages. The mean RSI was 0.49 (SE, 0.044) among streams of the Red River drainage and 0.50 (SE, 0.051) among streams of Calcasieu and Sabine drainages, but only 0.33 (SE, 0.034) when we compared streams of the Red River drainage with those of the Calcasieu and Sabine drainages (Table 3). That difference, however, was not apparent for macroinvertebrate assemblages. Mean RSI was 0.59 (SE, 0.047) among streams of the Red River and 0.61 (SE, 0.024) among streams of Calcasieu and Sabine drainages (Table 3). When we compared streams of the Red River drainage with those of Calcasieu and Sabine drainages, the RSI was

nearly the same as within drainage comparisons, 0.57 (SE, 0.03).

Detrended correspondence analysis of species and sites also reflected drainage differences between fish assemblages (Figure 4). Site scores of the first two DCA axes were plotted and enveloped by drainage to further illustrate fish assemblage distinctiveness between the Red River drainage (higher site scores on DCA axis 1) and the two southern drainages (lower site scores on DCA axis 1). Macroinvertebrate assemblages, however, were not distinct by drainage but were better described and enveloped by season. Summer samples tended to have higher site scores along DCA axis 1, and winter samples had the lowest scores (Figure 4).

Diversity and Evenness

Mean species richness, diversity, and evenness for fishes were generally highest and the least variable in the Red River drainage and lowest and most variable in the Sabine River drainage (Table 4). Lower

TABLE 2.—Mean habitat variables for each sampling site across collection dates, June 2001 through August 2002, for rivers (R.) and creeks (Cr.) in the Peason Ridge Training Area, Louisiana.

| Variable	Red R. Lyles Cr.	Little Sandy Cr.	Odom Cr.	Tiger Cr.	Calcasieu R. Comrade Cr.	Sabine R. West Anacoco Cr.	Dowden Cr.	Martin Cr.
Dissolved oxygen (mg/L)	8.3	8.7	8.7	9.0	7.4	7.2	8.2	7.0
Conductivity (µS/cm)	42.1	44.9	42.0	37.0	34.4	34.8	21.5	32.5
pH (range)	6.1–8.2	6.6–7.2	7.0–7.4	6.8–7.3	5.9–7.8	6.3–7.5	6.2–8.4	6.4–7.5
Turbidity[a]	44.3	36.1	18.0	26.7	23.7	38.0	21.7	19.3
Substrate type (%)								
Sand	75.7	97.0	97.2	96.8	88.7	94.2	82.8	89.0
Silt	4.3	2.3		3.2	11.3	5.8	17.2	5.8
Gravel	20.0		0.4					5.2
Cobble		0.3	2.4					
Detritus (%)	7.4	1.9	1.8	3.0	33.4	3.8	28.4	14.0
Cover (%)	3.5	8.2	5.7	15.3	25.0	4.7	16.9	26.7
Vegetation (%)	0.8	0.7	0.6	0	4.7	1.0	0	0.4
Mean width (m)	3.7	4.0	4.2	3.3	3.5	2.1	4.8	3.1
Mean depth (m)	0.29	0.21	0.18	0.25	0.31	0.22	0.57	0.39
Mean current velocity (m/s)	0.06	0.15	0.26	0.03	0.05	0.13	0.07	0.12

[a] Nephelometric turbidity units.
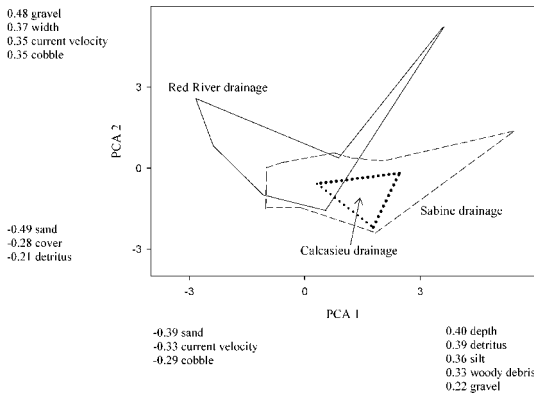
FIGURE 3.—The first two axes from a principal components analysis (PCA) of habitat data from subbasins sampled from June 2001 through August 2002 on the Peason Ridge Training Area. Individual drainage basins are enveloped in ordination space, and habitat variables loading high on PCA axes 1 or 2 are indicated in the margins.

diversity and evenness indices corresponded with redfin and ribbon shiners, composing 75% of the fish assemblage in the Sabine River drainage. Higher variability in these indices was related to lower mean RSI for fishes in the Sabine drainage, indicating greater species turnover through time (Freeman et al. 1988; Grossman et al. 1990).

Macroinvertebrate families showed the highest overall richness in the Red River drainage and the lowest in the Calcasieu River drainage (Table 4). On average, diversity and evenness were similar for all three drainages, albeit, slightly lower for the Sabine River drainage. Mean similarity within the Sabine River was highest among the three drainages; thus, evidence of low stability, as seen with fish assemblages in this system, was not evident for macroinvertebrates.

Canonical Correspondence Analysis

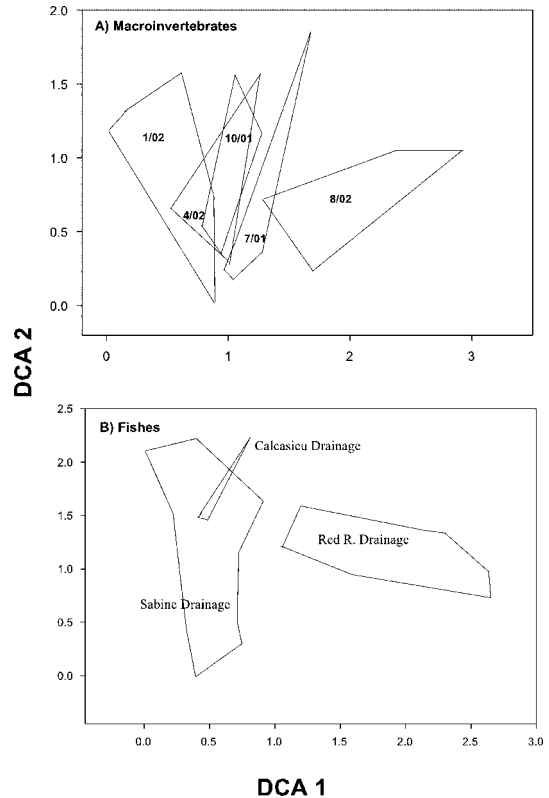Sixty-seven percent of the fish and 66% of the macroinvertebrate assemblage variability was ex-

FIGURE 4.—First two axes of detrended correspondence analysis (DCA) for (A) macroinvertebrates and (B) fishes from subbasins sampled from June 2001 through August 2002 on the Peason Ridge Training Area. Site scores corresponding to sampling dates for macroinvertebrates and drainages for fishes are enveloped.

plained by habitat variables, drainage basin, season, and training intensity (Table 5). Pure effects of habitat variables did not explain significant amounts of assemblage variability for fishes (25%; $P = 0.44$) or macroinvertebrates (20%; $P = 0.094$). Pure effects of drainage basin explained 9% ($P = 0.021$) of the variability in fish assemblages but

TABLE 3.—Renkonen similarity indices among streams of three drainages for fishes (upper right) and macroinvertebrates (lower left) collected from Peason Ridge Training Area, Louisiana, June 2001 through August 2002.

		Creek							
Drainage	Creek	Lyles	Sandy	Odom	Tiger	Comrade	Anacoco	Dowden	Martin
Red River	Lyles		0.65	0.32	0.51	0.52	0.61	0.26	0.30
	Sandy	0.77		0.45	0.53	0.43	0.33	0.17	0.21
	Odom	0.59	0.66		0.51	0.20	0.19	0.16	0.21
	Tiger	0.6	0.49	0.45		0.48	0.40	0.35	0.41
Calcasieu River	Comrade	0.66	0.53	0.46	0.61		0.59	0.55	0.54
Sabine River	Anacoco	0.56	0.57	0.53	0.3	0.52		0.35	0.34
	Dowden	0.64	0.64	0.58	0.45	0.59	0.63		0.64
	Martin	0.77	0.77	0.59	0.47	0.63	0.61	0.7	

TABLE 4.—Total species richness and the number of unique taxa (families for macroinvertebrates, species for fish) among three river drainages of Peason Ridge Training Area, Louisiana, June 2001 through August 2002. Within drainages, the means and standard errors for species richness, diversity, evenness, and the Renkonen similarity index (RSI; a measure of beta diversity) are presented by stream across sampling dates.

Drainage	Total species richness	Number unique	Creek	Species richness		Diversity		Evenness		RSI	
				Mean	SE	Mean	SE	Mean	SE	Mean	SE
Macroinvertebrates											
Red River	58	11	Lyles	15.0	3.11	1.93	0.290	0.32	0.116	0.437	0.143
			Sandy	18.4	3.41	2.41	0.534	0.38	0.107	0.538	0.122
			Odom	19.4	3.03	3.10	0.170	0.49	0.091	0.383	0.025
			Tiger	15.8	4.47	2.58	0.650	0.61	0.115	0.369	0.092
Calcasieu River	40	2	Comrade	18.0	2.51	2.87	0.140	0.44	0.059	0.529	0.055
Sabine River	56	8	Anacoco	11.0	3.40	2.12	0.373	0.50	0.090	0.536	0.026
			Dowden	20.6	2.25	2.64	0.258	0.31	0.027	0.586	0.081
			Martin	15.2	2.06	2.24	0.331	0.34	0.051	0.494	0.040
Fishes											
Red River	28	8	Lyles	13.8	0.86	2.15	0.081	0.63	0.033	0.572	0.023
			Sandy	13.2	0.73	2.04	0.097	0.60	0.055	0.566	0.039
			Odom	13.2	1.20	1.95	0.056	0.56	0.078	0.594	0.034
			Tiger	13.2	0.73	1.93	0.066	0.53	0.023	0.668	0.034
Calcasieu River	18	0	Comrade	10.6	1.29	1.85	0.098	0.63	0.038	0.573	0.094
Sabine River	30	6	Anacoco	8.0	1.21	1.55	0.215	0.63	0.042	0.277	0.090
			Dowden	10.0	1.30	1.32	0.310	0.43	0.112	0.299	0.170
			Martin	12.4	1.17	1.41	0.196	0.36	0.058	0.520	0.129

only 2% ($P = 0.214$) for macroinvertebrates. For fishes, variability explained by season was not significant (6%; $P = 0.43$), but season was important for macroinvertebrates, explaining 11% of their variability ($P = 0.001$). Training intensity, as measured in our analyses, explained 14% ($P = 0.034$) of the variability in fish and 13% in ($P = 0.001$) macroinvertebrate assemblages. Shared variation among variables that could not be partitioned (because of both 2-way and 3-way effects) represented 12% of the variation in fish assemblages and 21% for macroinvertebrates. Thus, observed fish and macroinvertebrate assemblages were associated with training intensity, followed by season for macroinvertebrates and by drainage for fishes. Habitat factors explained a relatively large portions (20–25%) of assemblage variations, yet were not statistically significant for fishes but, arguably, were marginally important for macroinvertebrates ($P = 0.094$). Lack of robust significance was attributed to substantial variation in habitat factors within each stream (compared with variation across streams) and the lack of strong habitat associations for a majority of the biota. However, some biota did exhibit strong associations among habitat factors.

Habitat factors with the highest positive centroids on the first environmental axis of CCA were current velocity (0.49) and sand substrate (0.43) for fishes and velocity (0.71) and silt substrate (0.15) for macroinvertebrates. Habitat factors with the highest negative centroids for fishes included detritus (−0.53), silt substrate (−0.43), and woody debris (−0.33) and for macroinvertebrates included depth (−0.74), percent detritus (−0.34), and woody debris (−0.33). Environmental axis 1 was highly correlated ($r^2 = 0.99$ for fishes and 0.87 for macroinvertebrates) to the first CCA taxonomic axis. Species (>1% of relative abundance by drainage) positively associated with axis 1, followed by biplot scaling score, which included Sabine shiners (1.3), southern brook lampreys (1.1), brown madtoms (0.9), striped shiners (0.8), red-

TABLE 5.—Percent of variance (derived from partial canonical correspondence analysis) in fish and macroinvertebrate assemblages in three watersheds sampled (June 2001 to August 2002) in the Peason Ridge Training Area, Louisiana, as explained by habitat variables, basin (3 levels), season (4 levels), and percent of watershed used for training. Statistical significance ($P < 0.05$) based on Monte Carlo randomization test is indicated by asterisks.

Factor	Variance explained (%)	
	Macroinvertebrates	Fishes
Habitat	20.4	25.0
Drainage basin	2.3	9.0*
Season	10.6*	6.1
Training	13.3*	14.1*
Full model	67.2*	66.1*

spot darters (0.7), creek chubs (0.7), blacktail shiners (0.6), blackspot shiners (0.3), creek chubsuckers (0.1), blackspotted topminnows (0.04), and dollar sunfish (0.01). Species negatively associated with axis 1 included banded pygmy sunfish (-1.2), slough darter (-1.2), warmouth (-1.2), bluegills (-1.1), redfin pickerel (-0.8), ribbon shiners (-0.7), pirate perch (-0.6), western mosquitofish (-0.6), redspotted sunfish (-0.5), bluntnose darters (-0.5), and redfin shiners (-0.4).

Abundant macroinvertebrate families positively related to axis 1 included Capniidae (1.5), Asellidae (1.4), Perlidae (1.3), Simuliidae (1.2), Gyrinidae (1.1), Cragonyctidae (1.0), Hydroptilidae (1.0), Baetidae (0.6), Leptophlebiidae (0.5), Chironomidae (0.3), Dytiscidae (0.3), Veliidae (0.3), Ceratopogonidae (0.2), and Ephemerellidae (0.2). These families presumably are more tolerant of silt and higher current velocity and may indicate some ability to withstand erosional effects. Abundant taxa related negatively along axis 1 included Hyalellidae (-3.6), Sialidae (-3.3), Leptoceridae (-3.3), Libellulidae (-3.0), Coenagrionidae (-2.7), Corixidae (-2.5), Gerridae (-1.3), Caenidae (-1.2), Elmidae (-0.7), Gomphidae (-0.7), and Corduliidae (-0.4). These taxa were associated with deeper pools containing abundant woody debris and detritus.

Military training intensity factors with positive centroids on the first environmental axis of CCA were hectares of clear-cut (0.64), hectares of burned land (0.34), number of training days (0.27), and hectares of thinned forest (0.16) for fishes and the number of crossings (0.11) and hectares of land burned $\times$ days of burning (0.10) for macroinvertebrates. Training intensity factors with negative centroids for fishes included number of road crossings (-0.65) and road density (-0.07) and for macroinvertebrates included hectares of clear-cut (-0.22), hectares of thinned forest (-0.17), road density (-0.12), and number of military training days (-0.09).

Discussion

Observed patterns for fish and macroinvertebrate assemblage structure in streams of PRTA varied through time and space and were primarily explained by military training and drainage for fishes and by military training and season for macroinvertebrates. Military activities (i.e., area clear-cut, area burned, area thinned, and training days) were greatest in the Red River drainage. However, the Red River drainage fish assemblage, compared to Sabine and Calcasieu drainages, was the most diverse and most similar in

composition to historical records; it was also persistent through time (e.g., lowest in species turnover), and composed of a larger number of species that prefer clear and shallow, swift moving currents such as striped shiners (Smith 1979; Trautman 1981), Sabine shiners (Moriarty and Winemiller 1997), southern brook lampreys, and creek chubs (Trautman 1981; Page and Burr 1991). In contrast, fish assemblages in Calcasieu and Sabine drainages were less diverse, less similar to historical composition, and composed of species that are more tolerant of turbid conditions and lentic habitats, such as redfin shiners and ribbon shiners (Snelson 1973; Smith 1979; Noltie 1989). Although macroinvertebrate assemblages were more similar across the three drainages than were fishes, more taxa were found in the Red River tributaries than the two southern drainages.

Because activities associated with military training were highest in the basin containing the most diverse and temporally stable assemblages (Red River tributaries), we can only assume that military training and silvicultural activities currently are not affecting biota in a negative way. More likely, training (and the significant drainage effect for fish) contrasts the Red River drainage from the Sabine and Calcasieu drainages, corresponding to differences in geological formation. Streams of the Red River drainage are higher in gradient (mean, 0.029; SD, 0.009) than the Sabine (mean, 0.017; SD, 0.001) and Calcasieu (0.0195 for Comrade Creek) drainages. Gradient differences among these streams were caused by depositions of sediment from fluctuating sea levels during periods of glaciation within the Sabine and Calcasieu drainages, whereas the Red River drainage escaped the sediment depositions and maintained a higher gradient (Conner and Suttkus 1986). Consequently, streams of the Red River drainage naturally have swifter flows, greater proportions of sand and cobble substrate, less detritus and woody debris, and less sedimentation, which combine to support different biota. The converse was found in the Sabine and Calcasieu drainages. Interestingly, physical attributes did not explain a significant portion of assemblage variation. We attributed this to high variability in physical variables within and among streams across the time of our collections and to the ubiquity of some fishes (20 of 38, 80% by relative abundance) in these habitats in both the Red River drainage and in at least one of the southern drainages.

Sources explaining apparent fish assemblage shifts in the Sabine drainage (loss of species and increase in turbidity-tolerant forms) are speculative

but most likely related to historical land-use change rather than current military training activities. Immediately south of PRTA, two reservoirs exist on the main stem of Anacoco Bayou, a tributary of the Sabine River that drains all the PRTA streams in that basin. Anacoco Lake (constructed in 1951; 1,053 ha) and Vernon Lake (constructed in 1963; 1,863 ha) isolate headwater streams in the Sabine River system. As a result of these reservoirs, fishes in headwater tributaries of the Sabine River originating in PRTA are essentially isolated from downstream reaches and have no recolonization potential if they become extirpated (Winston et al. 1991; Wilde and Ostrand 1999). Additionally, four fish that were not collected from PRTA streams of the Sabine drainage (Sabine shiners, striped shiners, scaly sand darters, and harlequin darters) are associated with swifter flows (Ross 2001). It is feasible that higher flows associated with clear-cuts in the early 1920s in the Sabine drainage provided habitat for these species, but recent revegetation efforts probably reduced flows and may have led to their extirpation. Once extirpated, reservoirs isolated the headwaters of the Sabine River drainage and prevented recolonization.

For macroinvertebrates, distinctiveness among drainages was less apparent because of species mobility and connectivity of habitat patches (streams within 2 km). Many of the insect larvae we collected have both a terrestrial and aquatic portion of their life cycle (Anderson and Wallace 1984); thus, they have the ability to migrate among the different drainage basins in search of appropriate habitat during certain times of year (Williams et al. 2002). Seasonal variation was important in structuring the macroinvertebrate assemblages, but these effects were not apparent for fishes. High site fidelity, degree of habitat specificity, and relatively short life cycles (compared with fishes) coupled with seasonal changes in habitat conditions (e.g., discharge) probably explain the strong seasonal component of the macroinvertebrate assemblages (Wade et al. 1989; Lammert and Allan 1999; Linke et al. 1999; Williams et al. 2002). Over the course of our sampling, several turnover events would have occurred in the macroinvertebrate assemblages, as produced primarily by the taxa that emerged from the aquatic environment for reproduction. After emergence, macroinvertebrates will then choose breeding sites based on their preferred habitat conditions and are free to cross over basin barriers to do so (Anderson and Wallace 1984; Williams et al. 2002). This turnover, followed by macroinvertebrate recolonization may

partially explain the strong seasonal aspect of their assemblage structure. Previous studies have shown that macroinvertebrates, more so than fishes, will respond to variability in local habitat conditions (Plafkin et al. 1989; Lammert and Allan 1999; Williams et al. 2002).

The lack of a significant effect of military training activities on fish and macroinvertebrate assemblages in our results differs from the findings of a recent study by Quist et al. (2003) that examined the effect of military training on stream habitat and fish assemblage structure at Fort Riley in northeast Kansas. Quist et al. (2003) found that military training was associated with increased silt and shifts in assemblages to more tolerant species and trophic generalists. There are numerous differences between streams in northeast Kansas and central Louisiana. The streams sampled by Quist et al. (2003) are located in the Flint Hills, an upland area associated with the Interior Highlands. These streams have a relatively steep gradient with limestone and shale substrate and significant groundwater flow. In contrast, streams in our study area have relatively low gradient and sand–silt substrate related to geological origin. As a result, fauna in central Louisiana streams must be resilient to abrupt changes in stream flow and seasonal influxes of silt and shifting sand. Because the natural disturbance regime in our streams is more ''harsh'' (Peckarsky 1983), we would expect anthropogenic disturbances to have less of an effect than in the more ''benign'' northeast Kansas streams (Williams et al. 2002). Streams in west-central Louisiana have a more severe natural disturbance regime because of the natural fires (and subsequent high silt loads following wildfire), unconsolidated underlying layers, and climatic events like hurricanes.

Examining the spatial and temporal patterns in assemblages described herein provides a regional model to monitor, detect, and predict future anthropogenic effects (military or otherwise) on stream biota in drainages with similar species compositions (i.e., west and central Louisiana and east Texas). In streams with higher gradients, sand substrate, and swifter currents, native invasive fishes (Scott and Helfman 2001) most likely to become abundant after anthropogenic disturbances that increase siltation and sedimentation include banded pygmy sunfish, slough darters, redfin pickerel, ribbon shiners, bluntnose darters, and redfin shiners. Correspondingly, fishes such as Sabine shiner, southern brook lamprey, brown madtoms, striped shiners, and redspot darters become less abundant.

Habitat modifications of low-gradient streams (i.e., channelization) also would invoke a predictable shift in species composition and abundance from low-gradient forms (e.g., ribbon shiners, redfin shiners, slough darters) to those species characteristic of higher-gradient streams. Regardless of direction (from low-gradient to high-gradient forms or high-gradient to low-gradient forms), species shifts because of habitat modifications will be most detrimental to those species endemic to only a few drainage basins (Meffe and Carroll 1997), such as Sabine shiners, brown madtoms, and redspot darters. Thus, the ability to detect assemblage shifts within the native biota will enable rapid quantification of anthropogenic effects on the stream biota. Which biota (fishes or macroinvertebrates) to use when quantifying effects of disturbance will depend on the question and issues of scale. From our study, fish assemblages seemed to be a better predictor of historical land-use change, and this is concordant with previous work suggesting that macroinvertebrates may respond more to local environmental conditions over shorter temporal scales than fishes (Lammert and Allan 1999; Williams et al. 2003b). Also, macroinvertebrates are more difficult to use for monitoring because their identification is labor intensive. However, to document short-term changes in assemblage structure related to land use, macroinvertebrates probably will be the most appropriate group to use for monitoring.

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Appendix: Fauna Relative Abundance

TABLE A.1.—Relative abundance (%) of fishes by drainage collected from Peason Ridge Training Area, Louisiana, June 2001 through August 2002.

Species	Red River drainage	Calcasieu River drainage	Sabine River drainage
Southern brook lamprey *Ichthyomyzon gagei*	1.7		
Blacktail shiner *Cyprinella venusta*	7.2		1.7
Striped shiner *Luxilus chrysocephalus*	15.6		
Redfin shiner *Lythrurus umbratilis*	11.3	21.3	45.0
Ribbon shiner *L. fumeus*	2.2	17.6	30.4
Golden shiner *Notemigonus crysoleucas*	0.5	0.4	0.1
Blackspot shiner *Notropis atrocaudalis*	8.1		1.3
Sabine shiner *N. sabinae*	8.2		
Mimic shiner *N. volucellus*			0.5
Pugnose minnow *Opsopoeodus emiliae*			0.1
Creek chub *Semotilus atromaculatus*	2.4		
Creek chubsucker *Erimyzon oblongus*	4.3	3.4	1.3
Spotted sucker *Minytrema melanops*			0.1
Blacktail redhorse *Moxostoma poecilurum*	0.04		0.1
Black bullhead *Ameiurus melas*	0.04		
Yellow bullhead *A. natalis*	0.2		
Tadpole madtom *Noturus gyrinus*		0.7	0.1
Brown madtom *N. phaeus*	3.3		
Redfin pickerel *Esox americanus*	0.3	3.4	0.1
Pirate perch *Aphredoderus sayanus*	1.7	5.2	2.2
Blackspotted topminnow *Fundulus olivaceus*	16.3	24.7	5.3
Western mosquitofish *Gambusia affinis*	3.6	0.7	1.9
Brook silverside *Labidesthes sicculus*			0.1
Banded pygmy sunfish *Elassoma zonatum*		2.2	0.8
Green sunfish *Lepomis cyanellus*	3.9	0.7	0.1
Warmouth *L. gulosus*		1.9	0.2
Bluegill *L. macrochirus*			1.5
Dollar sunfish *L. marginatus*	1.4	6.0	1.5
Longear sunfish *L. megalotis*	0.8	1.5	0.4
Redspotted sunfish *L. miniatus*	0.3	2.2	0.5
Other sunfishes *Lepomis* spp.	0.7	1.5	1.6
Spotted bass *Micropterus punctulatus*	0.2		0.1
Scaly sand darter *Ammocrypta vivax*	0.04		
Mud darter *Etheostoma asprigene*			0.1
Bluntnose darter *E. chlorosoma*	2.5	4.9	2.2
Slough darter *E. gracile*		1.5	0.5
Redspot darter *E. artesiae*	3.2		0.2
Dusky darter *Percina sciera*	0.2		0.1
Number of individual fish	2,542	267	1,652

TABLE A.2.—Relative abundance (%) of macroinvertebrate families collected from Peason Ridge Training Area, Louisiana, June 2001 through August 2002 by order and drainage.

Order	Family	Red River drainage	Calcasieu River drainage	Sabine River drainage
Collembola	Smirithuridae			0.03
Ephemeroptera	Baetidae	4.99	1.40	1.53
	Baetiscidae	0.17		0.03
	Caenidae	13.34	23.07	2.22
	Ephemerellidae	0.48	0.30	1.41
	Ephemeridae	0.15		0.27
	Heptageniidae	3.07	3.71	3.03
	Isonychiidae	0.05		
	Leptophlebiidae	0.27	0.90	3.12
	Tricorythidae	0.68		
Odonata	Aeshnidae	0.36	0.70	0.06
	Calopterygidae	0.34		0.06
	Coenagrionidae	0.73	6.22	3.72
	Cordulegastridae	0.15	0.10	0.03
	Corduliidae	0.58	2.11	0.99
	Gomphidae	2.54	0.50	0.87
	Libellulidae	0.05	2.11	1.02
Orthoptera	Gryllotalpidae	0.02		
Plecoptera	Capniidae	0.19		1.11
	Nemouridae	0.56	0.30	0.27
	Perlidae	1.55	0.10	0.72
	Perlodidae	0.12		0.03
	Taeniopterygidae			0.06
Hemiptera	Belostomatidae			0.06
	Corixidae	0.05	1.50	0.93
	Gerridae	2.81	1.20	1.14
	Hebridae	0.02	0.10	0.39
	Hydrometridae	0.02		0.06
	Mesoveliidae	0.02		
	Nepidae	0.02		
	Notonectidae	0.02		0.03
	Saldidae	0.10		
	Veliidae	1.09		0.09
Megaloptera	Corydalidae	0.56	0.20	0.06
	Sialidae	0.07	0.20	1.20
Trichoptera	Hydropsychidae	0.82	0.20	0.21
	Hydroptilidae	1.65	0.10	
	Leptoceridae	0.31	0.20	2.10
	Limnephilidae	0.15		0.60
	Molannidae			0.06
	Philopotamidae	0.07		0.06
	Phryganeidae	0.02		
	Polycentropodidae	0.12		0.30
	Psychomyiidae			0.03
Lepidoptera	Nepticulidae	0.05		
Coleoptera	Dryopidae		0.10	
	Dytiscidae	1.67	2.81	2.01
	Elmidae	1.53	0.10	1.74
	Gyrinidae	0.12	1.00	0.39
	Haliplidae		0.10	
	Hydrochidae	0.31	0.20	0.03
	Hydrophilidae		0.20	0.15
	Lampyridae			0.03
	Psphenidae	0.29		
	Scirtidae	0.05	0.40	0.09
Diptera	Ceratopogonidae	2.90	2.81	2.73
	Chaoboridae	0.65	0.80	0.09
	Chironomidae	49.16	28.59	47.06
	Culicidae	0.05	2.41	0.09
	Dixidae	0.10		
	Empididae	0.05		
	Simuliidae	1.48	0.60	2.40
	Tabanidae	0.22	0.40	0.18
	Tipulidae	0.44	0.10	0.42

TABLE A.2.—Continued.

Order	Family	Red River drainage	Calcasieu River drainage	Sabine River drainage
Amphipoda	Cragonyctidae	2.08	8.32	9.84
	Hyalellidae		1.30	0.06
Arachnida	Pisauridae	0.39	0.10	0.15
Decapoda	Palaemonidae			0.45
Isopoda	Asellidae	0.15	4.41	3.72
Mysidacea	Mysidae			0.48
Total	*N*	4,131	997	3,334