Effects of Riparian Forest Removal on Fish Assemblages in Southern Appalachian Streams

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Abstract: *Deforestation of riparian zones is known to influence the numbers and kinds of organisms that inhabit adjoining streams, but little quantitative information is available on how much deforestation must occur before the biota isaffected. We sampled fishes and stream habitats in 12 stream segments downstream from deforested but vegetated riparian patches 0–5.3 km long, all downslope from watersheds with at least 95% forest cover. We found an overall decrease in fish abundance with increasing length of nonforested riparian patch; sculpins, benthic minnows, and darters decreased, and sunfishes and water-column minnows increased in numbers. Introduced species were more common downstream from longer riparian patches. Habitat diversity decreased and riffles became filled with fine sediments as upstream patch length increased. Length of upstream nonforested patch and substrate particle size were much stronger predictors of fish occurrence than riparian patch width. Faunal characteristics and physical features of the stream changed in direct proportion to the gradient of riparian disturbance, but the abundance of several species underwent pronounced change at particular threshold patch lengths. These results suggest that riparian forest removal leads to shifts in the structure of stream fish assemblages due to (1) decreases in fish species that do not guard hidden eggs or that are dependent on swift, shallow water that flows over relatively sediment-free substrates, or (2) increases in fishes that guard their young in pebble or pit nests or that live in slower, deeper water. When watershed development is anticipated or planned, limited clearing of riparian trees may cause minor disturbance to the fish assemblage, but streams in even a heavily forested watershed with vegetated riparian buffers cannot tolerate disruption of riparian-zone trees over much more than 1 km in length. Riparian buffer length and area should be given stronger consideration in stream protection and restoration plans.*

Efectos de la Remoción del Bosque Ripario en Ensamblajes de Peces en Arroyos de los Apalaches del Sur

Resumen: *Es conocido que la deforestación de zonas riparias influencía el número y tipo de organismos que habita los arroyos adyacentes, sin embargo, existe poca información cuantitativa sobre cuanta deforestación puede ocurrir antes de que la biota sea afectada. Muestreamos peces y hábitats de arroyo en 12 segmentos de arroyo hacia abajo de parches riparios deforestados pero con vegetación de 0-5.3 km de longitud, todos pendiente abajo de cuencas con al menos 95% de cobertura forestal. Encontramos una disminución general en la abundancia de peces al incrementar la longitud del parche ripario no forestado; cótidos, ciprínidos bénticos, y pércidos disminuyeron, y los centrárquidos y ciprínidos de la columna de agua incrementaron en número. Las especies introducidas fueron mas comunes arroyo abajo de los parches riparios grandes. La diversidad del hábitat disminuyó y los rápidos estuvieron mas llenos de sedimento fino cuando la longitud del parche arroyo arriba incrementaba. La longitud de parches no arbolados arroyo arriba y el tamaño de la párticula del substrato fueron pronosticadores mucho mas fuertes de la ocurrencia de peces que la amplitud del parche ripario. Las características de la fauna y las características físicas del arroyo cam-*

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biaron en proporción directa al gradinete de perturbación riparia, pero la abundancia de varias especies sufrieron cambios pronunciados a particulares longitudes del parche. Estos resultados sugieren que la remoción de bosque ripario conduce a desplazamientos en la estructura de los ensamblajes de peces del arroyo debido a: (1) disminuciones en especies de peces que no custodian huevos escondidos o que dependen de aguas rápidas y someras que fluyen sobre substratos relativamente libres de sedimentos o (2) incrementos en peces que custodian sus crías en nidos de grava o roca o que viven en aguas mas lentas y profundas. Cuando se anticipa o se planea el desarrollo de cuencas, el clareo limitado de árboles riparios puede causar perturbaciones mínimas a los ensamblajes de peces, sin embargo, aún los arroyos que se encuentran en cuencas altamente deforestadas con zonas amortiguadoras riparias vegetadas no pueden tolerar perturbaciones en la zona de árboles riparios de mas de 1 km de longitud. La longitud y área de zonas riparias amortiguadoras deberán ser consideradas mucho mas en los planes de protección y restauración de arroyos.

Introduction

Throughout most of the Cenozoic, North America was a forested continent (Williams 1989). Even in relatively treeless areas, such as the arid desert Southwest or the Great Plains, streams were usually lined with a corridor of riparian trees. Consequently, North American stream fishes evolved in a forested landscape.

That landscape changed with the relatively recent intrusion of humans. Humans settled along water courses and typically cut down trees where they settled (e.g., Bartram 1794; Hudson 1976). As a result, stream fishes today live in a mosaic of forested and deforested habitats. Even in the southern Appalachians, where upland areas of most watersheds are presently covered in forests that have not been logged since the beginning of the twentieth century, riparian zones were long ago converted to agriculture (Bolstad et al. 1998). Such conversion causes numerous changes in stream habitats, including destabilization of stream banks, increased sedimentation from eroding fields, chemical changes from fertilizers and biocides, and alteration of light and thermal regimes and hydrologic flows. Such modifications to the stream and its surrounding landscape can be expected to affect stream fishes.

In the course of studying fish and invertebrate assemblages in forested and agricultural streams in the southern Appalachians, we found that a major correlate of faunal distribution was land use in the riparian buffer zone 1–2 km upstream of a sampling reach (Harding et al. 1998). Sites downstream from nonforested riparian patches differed in many characteristics from streams flowing through forested lands, regardless of land cover upland in the watershed (upland land cover was usually 85% or more forested). The importance of intact riparian vegetation to normal stream function is widely recognized (Waters 1995), but the literature on riparian buffer zones has emphasized riparian width, almost to the exclusion of consideration of how the length and area of the zone might affect downstream receiving systems (e.g., Castelle et al. 1994).

These observations led us to test for the possible causes of change in fish assemblage characteristics as a function of length of deforested riparian patches. We wanted to determine if alterations to the riparian zone were predictive of changes in the fish assemblage. We chose a series of sampling sites that were similar in upland land cover but that differed in degree of riparian deforestation. We sought a gradient of riparian clearing, from entirely forested to 5.6 km of deforested riparian corridor above the sampling site. We tested for relationships between this gradient of tree clearing and (1) the distribution and diversity of habitat types, (2) fine-sediment deposition, and (3) fish density, diversity, and assemblage structure.

Methods

Site Selection

Twelve sites in the Little Tennessee River drainage in Macon County, North Carolina, and Rabun County, Georgia, were chosen from maps produced by a geographic information system (GIS), using Arc/Info (Environmental Systems Research Institute 1997) (Table 1; Fig. 1). Land cover, interpreted from aerial photographs and satellite images from 1990 (Hermann 1996), was classified as forest or nonforest. Nonforested land cover varied among sites but was mostly a mixture of low-intensity cattle pasture and row-crop agriculture with occasional trees and shrubs; few of these sites were actively tilled to the point that soil was exposed. Land cover was roughly similar among sites and was typical for this region. Streams were digitized from U. S. Geological Survey topographic maps at 1:24,000 scale. Sites were chosen based on three criteria: (1) with the exception of two reference sites downstream from intact riparian zones, all sites had one continuous patch of nonforested land immediately upstream of the study site on both sides of the stream; (2) sites were distributed along a continuum of upstream riparian patch lengths; and (3)

Table 1. Study site characteristics, Little Tennessee River drainage.

Sites (lat/long)[a]	order[b]	Stream site area (m^2)	Stream site width (m)	Stream site gradient (m/km)	Stream site discharge (m^3/sec)	Upstream nonforested patch length (km)[c]	Upstream nonforested patch area (ha)	Upstream nonforested patch width (m)[d]	Watershed area (km^2)	Watershed nonforest (%)[e]
Short patch										
1. Tellico (35°17′31″N/83°29′40″W)	4	291	5.8	15.2	0.36	0	0	0	28.8	0.5
2. Lowery (35°06′56″/83°29′12″)	3	191	3.8	15.2	0.10	0	0	0	7.3	0
3. Poplar Cove (35°07′32″/83°29′36″)	3	228	4.6	15.2	0.15	0.78	13.9	242	8.5	0
4. Betty (34°58′20″/83°24′18″)	3	391	7.8	7.6	0.57	1.01	18.0	173	33.4	0.6
Medium patch										
5. Burningtown (35°13′50″/83°28′21″)	4	542	10.8	7.6	0.64	1.12	14.6	220	38.1	1.2
6. Cowee (35°16′24″/83°23′12″)	5	282	5.6	9.5	0.68	1.93	132.0	587	49.3	1.6
7. Watauga (35°13′54″/83°21′00″)	3	200	4.0	9.5	0.24	2.03	159.4	1628	16.2	1.4
8. Jones (35°05′56″/83°27′12″)	3	287	5.7	15.2	0.23	2.19	11.2	237	12.6	0
Long patch										
9. Allison (35°06′32″/83°28′12″)	3	277	5.5	15.2	0.26	2.86	15.7	260	14.1	4.5
10. Rabbit (35°12′48″/83°21′19″)	3	273	5.5	15.2	0.27	3.78	574.9	548	23.7	0
11. Up Little Tenn (34°56′10′′/83°24′22″)	4	357	7.1	1.9	0.53	4.26	601.8	1328	28.3	0
12. Iotla (35°14′13″/83°23′46″)	3	397	7.9	3.8	0.39	5.31	586.5	812	23.6	0

[a] *Sites are ordered by increasing straight-line length of the upstream nonforested patch. The first four locales were arbitrarily designated "short-patch" sites, the second four "medium-patch" sites, and the final four were "long-patch" sites, based on nonforested patch length. All stream segments were 50 m long. Site identification numbers correspond to locales on Fig. 1; sites are called "creeks" on most maps.*
[b] *Strabler method (Stanford 1996).*
[c] *Nonforested riparian patch length was correlated with patch area ($p = 0.02$) but with no other patch, stream, or watershed dimension ($p \gg 0.05$).*
[d] *Patch width was maximum width for patches of roughly uniform, rectangular shape. For irregularly shaped patches, the widest point and two to three other points were used to calculate an average width.*
[e] *Watershed nonforest refers to the region upland and upstream from the sampled patch, not including the sampled patch.*

sites drained moderate-sized watersheds that were forested except for the riparian patch. No sites were in the same stream. Most sites had nonforested patches and road crossings in close proximity downstream, which were logistically unavoidable but potentially complicating factors. Our level of resolution of cleared riparian patches was constrained by our imagery, mapping, and spatial analysis methods, making corridors narrower than 30 m wide unresolvable (Avery & Berlin 1992). Our nonforested patches also varied greatly in shape and were 175–1630 m wide (average width, 503 m; Table 1); all land contained in these continuous patches was considered part of the riparian zone. We sought streams that were as similar as possible in width, gradient, and discharge. Sites were selected on the basis of their accessibility and whether or not they fell along the continuum of nonforested upstream patch sizes. Nonforested patch size was not significantly correlated with any other site

selection characteristics (e.g., sampling reach area, stream order, water temperature, discharge, gradient, conductivity, elevation, or watershed area).

Fish Sampling

Fishes were sampled during August 1996 by means of backpack electroshockers, dipnets, and a 3 × 2 m seine. A 50-m section of stream (reach) was chosen at each site and was electroshocked and seined thoroughly during one upstream pass. Sampling required an average of 38 minutes (range 30–50 minutes), depending on reach area and complexity. Among reaches, we found no measures of fish abundance that were correlated with sample-site width or area, or with sampling effort. We chose representative stream reaches that contained two occurrences of major habitat types (i.e., two riffles, runs, and pools). We established 50 meters as an appropriate sam-
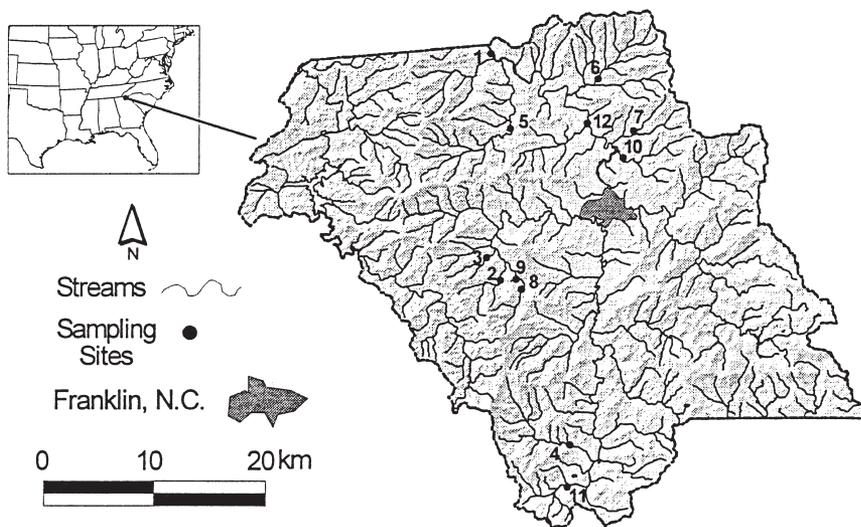
pling length after initially sampling 200-m sections at three sites. An asymptote in number of species captured was reached after about 50 m, indicating that a longer reach would not yield more than one or two additional species. All fishes were identified in the field and released at the capture site. Young-of-the-year were not included in the analysis.

Because fishes are particularly sensitive to alterations in breeding and spawning conditions (Muncy et al. 1979; Berkman & Rabeni 1987), for some analyses we placed fishes in one of six reproductive guilds, based on whether or not parental care was given and the substrates over which eggs were deposited (Appendix 1, guilds from Helfman et al. 1997 after Balon 1975). These guilds included fishes that (1) broadcast their eggs over the bottom and abandon them (open-substrate benthic spawners, e.g., blacknose and longnose dace, suckers, greenside and banded darters); (2) hide their eggs in un-modified bottom (brood-hiding benthic spawners, e.g., greenfin and gilt darters); (3) modify the bottom slightly prior to hiding eggs (brood-hiding benthic modifiers, e.g., lampreys, some minnows, trouts); (4) guard eggs spawned on rock undersurfaces (substrate choosers, e.g., sculpins, catfishes); (5) construct pebble piles and care for their eggs and the eggs of associate species that use the same pile (pebble-pile builders, e.g., river chub, warpaint shiner); and (6) construct pit nests in soft bottom areas (pit spawners, e.g., sunfishes).

Habitat Characterization

Instream habitat was quantified along the 50-m study reach at each site. Twenty-five cross-stream transects were set up at 2-m intervals in each study reach. Velocity and depth were measured at sampling points spaced at 0.5-m intervals along each transect. Velocity was measured with a digital velocity meter placed at 0.4 of the

water depth above the stream bottom (Gordon et al. 1992). To quantify percent fine sediment (particles <2 mm diameter), four transects were chosen at random, and a 0.5 × 0.5 m grid was placed on the substrate at three different locations (left, center, and right) along each transect. Two independent visual estimates of the percent coverage of fine sediments in the grid were made at each location; sandy and silty sediments were classified together (Gordon et al. 1992). To quantify coarse substrate, two people walked longitudinal transects the length of the study reach, randomly measuring the intermediate axis of 150 substrate particles; nine different particle-size categories were recognized, ranging from <2 mm to >256 mm (Gordon et al. 1992). We also recorded conductivity, water temperature, bank cross-section (triangulation of bankfull width minus wetted stream width), and we estimated bank stability based on occurrence of vegetative cover.

Eight different mesohabitat categories were erected based on depth and current speed, following Gorman and Karr (1978) and Aadland (1993). Each sampling point described above was assigned to one of the eight categories: shallow pool, moderate pool, deep pool, slow shallow riffle, moderate riffle, fast shallow riffle, raceway, torrent. The proportion of sampling points at a site in each mesohabitat category was used to characterize habitat distribution and diversity in each study reach; habitat diversity was calculated with a Shannon Index (Zar 1974).

Statistical Analysis

Fish assemblage and habitat data were analyzed by regression and correlation methods and analysis of variance (ANOVA). Regression methods were used to test for gradient effects; assemblage characteristics (density, frequency, Margalef's diversity index, number of spe-

cies) and habitat characteristics (percent fine sediment, diversity, and percent occurrence of mesohabitats) were regressed against patch length. For some analyses, nonforested patch length was arbitrarily grouped into three length classes (short, <1.1 km; medium, 1.1–2.2 km; long, 2.9–5.3 km), with four sites in each class, and the effects of grouped patch length were tested with ANOVA. Percentage data (i.e., representation of reproductive guilds and mesohabitats) were arcsine-square-root-transformed before analyses were run. Data reported are nontransformed values.

We also tested for the influence of environmental variables on assemblage characteristics, species densities within families, and species densities within reproductive guilds. Fifteen fish occurrence classes (five reproductive guilds, two assemblage-level characteristics measuring diversity and abundance, eight families) were compared with 37 environmental variables representing landscape-level traits (e.g., watershed area, nonforested patch length) and instream habitat variables (physicochemical measurements, stream order, habitat types, sediments) by means of Pearson correlation coefficients.

Results

Density Trends in Relation to Patch Length

Eight fish families, 29 species, and 2592 individuals were collected at the 12 study sites (Appendix 1). Overall fish density declined with increasing patch length ($r^2 = 0.458, p < 0.02$). No relationship was found between species diversity or richness and upstream patch length. The influence of patch length on density or frequency of species, families, and reproductive guilds differed among groups (Table 2). When divided into reproductive guilds, the density of nonguarding-benthic-modifying species and of species that do not clean silt from their nests decreased with increasing patch length, whereas the four pit-spawning sunfishes increased in density with increasing patch length. Relative frequencies showed related trends (Table 2). Nonguarding-benthic-modifying species and perhaps noncleaning species decreased in relative abundance, whereas nest-cleaning species (pebble-pile builders and pit spawners) increased in relative abundance with increasing patch length. No families and only four of 29 species showed definitive trends in density or frequency change. Creek chub, rock bass, and redbreast sunfish increased in density, whereas longnose dace decreased in density with increasing patch length (creek chub, $r^2 = 0.533, p < 0.01$; rock bass, $r^2 = 0.436, p < 0.05$; redbreast, $r^2 = 0.423, p < 0.05$; longnose dace, $r^2 = 0.36, p < 0.05$).

When densities are graphed relative to patch length, it appears that some species decreased or increased markedly at distinct points along the patch-length continuum (Fig. 2). The apparent threshold for declining density was shortest in rosyside dace, which was absent from five of the six sites downstream from patches longer than 1 km (Fig. 2a); 74% of 105 rosyside dace captured occurred below patches that were 1 km or less in length. Rosyside dace is the only species in our collections that appears on lists of sensitive fishes of the region (listed by North Carolina as "of special concern"). The four darter species and the two benthic-dwelling minnows (longnose dace and stoneroller minnows) showed apparent declines in density below patch lengths >2 km (Fig. 2b & 2c). Mottled sculpin and the two trout species dropped off markedly in density at a threshold patch length of about 3 km (Fig. 2d). Species that showed an apparent threshold response but that increased in numbers included the four sunfishes and a group of three water column–dwelling minnows (warpaint shiner, river chub, creek chub), which increased

Table 2.   Occurrence of reproductive guilds as a function of upstream riparian deforestation, Little Tennessee River drainage, North Carolina and Georgia.

	Regressions of density and frequency[b]	
Guild[a]	r^2 of density as function of patch length	r^2 of frequency as function of patch length
Nonguarders		
9 open-substrate brood hiders	0.181	0.175
2 benthic spawners	0.158	0.138
6 benthic modifiers	0.391,* negative	0.477,** negative
Guarders		
2 substrate choosers	0.268 ($p = 0.085$), negative	0.095
5 pebble-pile builders	0.158	0.461,* positive
4 pit spawners	0.587,** positive	0.688,** positive
Noncleaners (19 spp)[c]	0.530,** negative	0.318 ($p = 0.056$), negative
Nest cleaners (9 spp)[d]	0.230	0.545,** positive

[a] *Guilds are defined in Appendix 1.*
[b] *Direction of significant relationship is indicated as positive or negative (*p < 0.05; **p < 0.01).*
[c] *Noncleaners, all nonguarders + guarding substrate choosers.*
[d] *Cleaners, pebble-pile builders and associates and pit-nest spawners.*

in density below patches more than about 2 km long (Fig. 2e). All 21 individuals of the three *Lepomis* sunfishes and 9 of 11 rock bass individuals occurred only below longer patches. Five of the 29 species collected are introduced to this region (yellowfin shiner, flat bullhead, rainbow and brown trout, and redbreast sunfish; Menhinick 1991). With the exception of the two trout species, which were rare everywhere and essentially absent downstream from longer patches, 54 of the 57 individuals of the other three introduced species occurred only downstream from patches longer than 3 km.

Habitat Diversity and Sediment Distribution

Overall, habitat diversity (H') decreased with increasing riparian patch length, but the regression was marginally nonsignificant ($r^2 = 0.301$, $p = 0.065$, $n = 12$). However, one of the completely forested sites, Lowery Creek, had the third lowest habitat diversity value. Lowery was the smallest, narrowest stream in our samples, and its small size may also have affected habitat diversity. When Lowery Creek was removed from the analysis, the inverse relationship between habitat diversity and patch length became highly significant, despite the reduced sample size ($r^2 = 0.493$, $p = 0.016$, $n = 11$).

Sediment distribution varied as a function of riparian patch length and also among stream habitat types. Fine-sediment coverage increased with increasing upstream patch length in both pools and riffles (pools, $r^2 = 0.476$, $p = 0.01$; riffles, $r^2 = 0.361$, $p = 0.04$; $n = 12$ in both comparisons). When stream sites were grouped as downstream from short (<1.1 km), medium (1.1–2.2
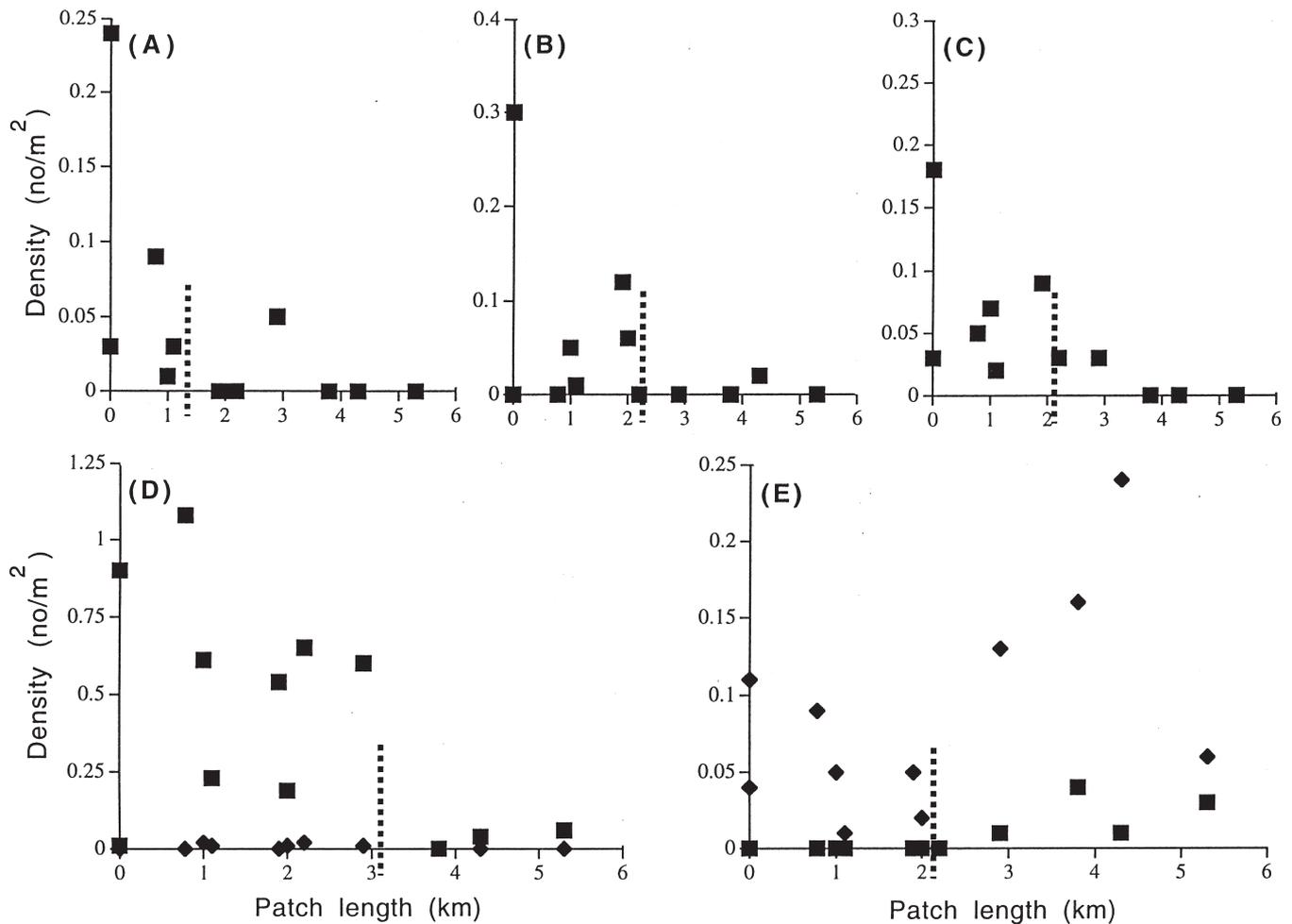

Figure 2. Possible threshold effects of deforested patch length on fish abundance. Densities of some species and ecological groups fell or rose noticeably at different thresholds of nonforested patch lengths. Data shown are densities at each site. Dashed vertical line indicates possible threshold patch length at which density showed a marked fall or rise: (a) rosyside dace; (b) four darters; (c) two benthic minnows; (d) mottled sculpin (squares) and two trout species (diamonds); (e) four sunfishes (squares) and three water-column–dwelling minnows (diamonds).

km), and long (2.9–5.3 km) patches and analyzed by ANOVA, fine sediments in pools did not differ as a function of grouped patch length, but riffles downstream from long patches contained significantly more fine sediments than did riffles below medium and short patches (Fig. 3). Riffles below long patches contained as much sediment as pools, whereas riffles below short and medium patches contained less sediment than pools.

Effects of Patch Dimensions, Instream Habitat, and Upland Forest Cover

Factors at both the landscape level (nonforested patch measures, elevation) and instream habitat level (sediment abundance and size, conductivity) influenced fish occurrence (Table 3). Patch length, width, and area differed in their apparent influence on assemblage characteristics. Patch length (measured as a straight-line distance) was significantly correlated with 4 of our 15 fish occurrence measures. It was positively correlated with abundance of sunfishes and of pebble-pile builders and was negatively correlated with total fish density and density of nonguarding benthic modifiers. Patch width
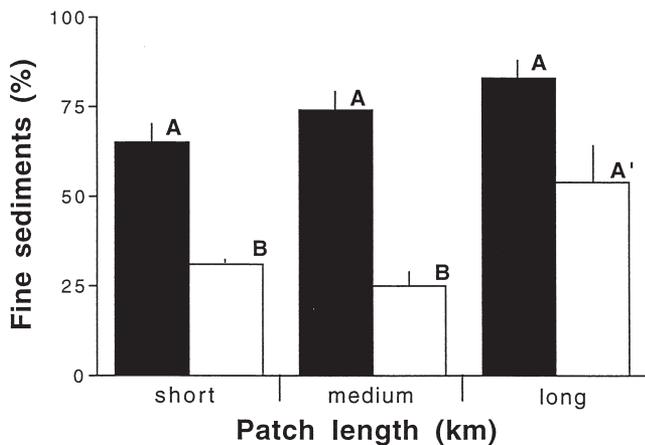

Figure 3. Distribution of fine sediments (<2 mm) in pools and riffles as a function of length of upstream nonforested patch. Solid bars are pools; open bars are riffles. Bars with the same letter are not significantly different. Below short and medium patches, riffles contained less fine sediment than corresponding pools (A vs. B, paired t tests, p < 0.001), whereas riffles and pools below long patches were not different with respect to sediment load (A vs. A'). Riffles downstream from long nonforested patches contained significantly more fine sediments than riffles downstream from short and medium patches (B vs. A', analysis of variance, p < 0.01; Tukey HSD, p < 0.01). Samples sizes for pools below short, medium, and long patches were 12, 13, and 15; for riffles, 38, 22, and 16. Values presented are means; vertical lines are standard errors.

showed a significant correlation with only two measures, one of which (minnow density) was not significantly correlated with patch length. Area was actually the best patch measure correlate (six correlations), adding sculpin and minnow density and rock undersurface spawners (of which sculpins are a major constituent) to the list of significantly correlated measures. Total percentage of the watershed not in forest accounted for seven significant correlations, but when the upstream and upland patch data were removed from this category, all correlations became nonsignificant. This result indicates that the statistical effect of the nonforest category was actually caused by what was happening in the nonforested riparian zone and by the few nonforested areas upstream and upland from the riparian patch (basically, the effects of riparian patch area and of total percent nonforest were identical).

We also found six significant correlations when patch length was measured along the streams' contours rather than linearly; this measure included the banks of tributary streams within the riparian patch (Table 3). In addition to the fish occurrence groups accounted for by straight-line patch length, minnows and suckers were positively correlated and sculpins were negatively correlated with this complex curvilinear measurement of patch length.

The strongest instream habitat predictors of fish abundance were percent fine sediments in riffles and abundance of small rocks 64–128 mm in diameter. These two variables were complementary in that fish groups and categories that were positively associated with abundant fine sediments (minnows, suckers, sunfishes, and pebble-pile nesters) were negatively associated with small rocks. Particles in other size groups were also strong predictors of fish abundance, with many taxonomic groups showing particle size complementarity (i.e., positive correlations with smaller particles and negative correlations with larger particles, or negative correlations with smaller particles and positive correlations with larger particles).

Discussion

Numerous studies have shown a sensitivity of stream communities and fish assemblages to riparian deforestation, attesting to the importance of intact riparian borders along streams (Detenbeck et al. 1990; Armour et al. 1991; Lowrance et al. 1991; Schlosser 1991; Waters 1995; Burkhead et al. 1997). We found that longer deforested patches were associated with decreased abundance of benthic-dependent species, which were replaced by sediment-tolerant and sometimes invasive species. Our findings indicate some of the possible processes and mechanisms by which fragmentation of the riparian zone leads to changes in the abundance and

Table 3.   Correlations of landscape and instream habitat variables with total fish density and density within families and reproductive guilds[a].

Faunal measure[b]	Conductivity (mMhos)	Elevation	Patch length (km)[c] straight	Patch length (km)[c] curved	Patch area	Total nonforest (%)[d]	fines in riffle (%)	Substrate particles[e] abundance as function of size (mm) <2	32–64	64–128	128–256
Density (number/m^2)			−0.64*	−0.67*	−0.64*	−0.61*		−0.68*	0.89**		
Petromyzontidae							0.61*				
Cyprinidae		−0.58*		0.67*	0.78**	0.79**	0.68*			−0.79**	−0.67*
Catostomidae	0.66*			0.61*		0.59*	0.62*			−0.59*	
Ictaluridae	0.82**						0.60*				
Salmonidae		0.60*									0.71**
Cottidae		0.70*		−0.58*	−0.68*	−0.69*				0.65*	
Centrarchidae[f]	0.75**		0.69*	0.79**	0.78**	0.82**	0.65*	0.96**	−0.68*	−0.73**	−0.58*
Nonguarders											
open-substrate								0.77**			
benthic modifiers			−0.67*								
Guarders											
substrate choosers	0.70*			−0.67*	−0.68*				0.64*		
pebble-pile builders		0.64*	0.72**	0.83**	0.80**	0.83**			−0.66*	−0.76**	

[a] Pearson correlation coefficients are given for habitat variables that accounted for three or more significant values; 25 variables that produced less than three significant correlations were not tabulated (*p < 0.05; **p < 0.01). Variables tested that showed only one significant correlation: temperature, study reach area, percent deep pools, percent fast shallow riffles, percent moderate riffles, habitat evenness, percent fines in pools, width:depth, number of 16–32 mm particles, >256 mm particles. Variables showing two significant correlations: patch width, percent torrents, habitat diversity, cross-sectional area, number of 2–4 mm particles, 4–8 mm particles. Variables showing no significant correlations: watershed area, stream order, gradient, discharge, percent shallow pools, percent moderate pools, percent slow shallow riffles, percent raceways, 8–16 mm particles. No correlations were found between habitat variables and number of species, or diversity (Margalef's), or density of darters, brood hiders, or nonguarding benthic spawners.

[b] See Appendix 1 for reproductive guild descriptions and species list.

[c] Patch length, straight-line distance between upper and lower edges of patch (straight), or riverbank and embedded tributary length (curved; see text).

[d] Total nonforest (%) represents all nonforested areas above and including the upstream patch. When the upstream nonforested patch was subtracted from all nonforested coverage, no significant correlations were found.

[e] Substrate size represents the number of particles of that size sampled at a site.

[f] All centrarchids were pit spawners, so the two categories are autocorrelated; "pit spawners" were dropped from the analysis.

ecological composition of fish assemblages in streams. Our findings also suggest that length and area as well as width of riparian buffer zones should be emphasized in mitigation and management applications.

Deforestation as Disturbance

Our results support the general observation that removing trees from the area adjoining a stream has direct and indirect effects on fishes, mediated perhaps through instream habitat alteration. Of the 37 habitat variables we measured, one of the strongest predictors of differences in the fish assemblage was length of the nonforested riparian patch upstream of a sample site: patch length was directly associated with decreased fish abundance. Although numerous factors that could affect fishes are associated with clearing of the riparian zone (Waters 1995), one consequence of riparian clearing is increased sediment inputs into streams (e.g., Castelle et al. 1994). Among the strongest predictors of faunal differences in our study were various measures of sediment load, with higher quantities of fine particles associated with reduc-

tions in overall fish abundance as well as with changes in assemblage composition.

Changes in instream habitat characteristics were also associated with increasing riparian disturbance. Overall habitat diversity declined with increasing patch length, and riffles became filled with sediments. Although fish abundance decreased with increasing patch length, assemblage diversity did not differ significantly across the gradient of riparian deforestation. These patterns indicate a general deterioration of appropriate habitat for many fishes as a result of riparian disturbance. However, numerical losses in some species were apparently offset by increases in others. Similar responses of stream fishes and habitats to disturbance, particularly to increased sediment loads, have been found in other fish assemblages (Gorman & Karr 1978; Berkman & Rabeni 1987; Weaver & Garman 1994; Wood & Armitage 1997).

Changes in fish abundance were most obvious when species were grouped into guilds according to reproductive behavior (Table 2). The groups that appeared to be affected negatively by increasing deforested patch length were those that nest on the bottom and do not

clean silt from their nests. Common species in this group include stoneroller minnows, longnose dace, rosyside dace, the two species of trout, mottled sculpin, and all darters. Fishes that increased in both absolute and relative abundance were those that keep their nests free of silt, such as the four species of sunfishes and the mound-building river chub and its nest associates. Mound-building and mound-using minnows appear to be relatively tolerant to disturbance because they occur less frequently in lists of imperiled species than do minnows that use other reproductive modes (Berkman & Rabeni 1987; Johnston 1999). Regardless, the factor most strongly implicated in shifts in fish abundance was silt concentration, which increased with increasing patch length. Hence, the function that riparian vegetation serves in slowing the accumulation of fine sediments in streams may interact directly with riparian patch length and reproductive behavior to affect species composition and assemblage structure in these small Appalachian streams.

Other patterns in our data implicate forest clearing and related agricultural practices as serious disturbances to the system. Several features characterize degraded as compared with less disturbed aquatic systems, including a reduction in rare and sensitive species and a higher proportion of introduced species (Hughes & Noss 1992; Moyle & Leidy 1992; Weaver & Garman 1994; Moyle & Light 1996). Notably, rosyside dace, the only native species that we encountered that is considered potentially imperiled, was absent from most sites downstream from patches longer than 1 km. In addition, most introduced nonsalmonids at our sites (95% of the 60 individuals of three introduced species) occurred downstream of patches longer than about 3 km. A decrease in a sensitive species and increases in introduced species with increasing patch length indicate that deforestation of the riparian zone disrupts fish assemblages, and that the scale of effect increases with increasing alteration of the riparian zone.

The abundance of several species and guilds reflected a response to the gradient of riparian disturbance (Fig. 2). Some species also underwent apparent numerical shifts at breaks along the patch-length continuum, suggesting that some species are more tolerant than others of the effects of deforestation and that the response of many fishes may be to a threshold of disturbance (see also Roth et al. 1996). Biological systems often show resistance to perturbation, followed by collapse or sudden change at some critical value of an influential variable (e.g., Redfearn & Pimm 1987). The most sensitive species, those with the lowest apparent threshold to disturbance, were the rosyside dace and some of the darters (Fig. 2a & 2b). The potentially imperiled rosyside dace is a benthic brood hider that does not provide parental care after spawning. Darters are classic riffle dwellers and spawners and make up a substantial fraction of the

fishes listed as imperiled throughout the southeast (e.g., Etnier 1994; Warren & Burr 1994; Burkhead et al. 1997).

In sum, our results suggest that loss of riparian forests leads to a decrease in species that are dependent on rapidly flowing, shallow water in relatively sediment-free stream reaches, or that hide but do not guard their eggs. An absence of riparian trees may be less harmful or even relatively beneficial to fishes that live in slower, deeper water or that protect their young from sediments, but deforested riparian zones along low-order streams in the southern Appalachians are unquestionably a disturbed condition. Slow, deep habitats and extensive nest guarding also characterize nonsalmonid exotic species at our sites. The presumed interactions among, and ecological results of, habitat loss and alteration, breeding biology, and population change underscore the necessity of protecting all adult habitats. (Comparatively little is known about nursery habitats of southeastern stream fishes.)

Riparian Conservation and Management

How can our results be applied to strategies of watershed planning and development? If riparian deforestation drives the changes in assemblage structure that we observed, what measures of riparian clearing are most useful in making decisions about stream management? How much clearing can a riparian zone sustain before the assemblage changes. How does riparian vegetation interact with vegetation higher in a watershed to influence stream fishes?

Patch width receives the most attention in assessments of riparian function. Our findings suggest that patch length and area could also be important predictors of fish abundance. Patch area was actually the best predictor in our study, but area is difficult to interpret because it incorporates both length and width. Our findings indicate that, of the two axes of a patch that are likely to be measured, length contributes more strongly, perhaps because erosion of stream banks along a stream's length contributes more sediment than run-off from the wider riparian border (e.g., Lyons & Courtney 1990; Waters 1995). We focused on deforested but otherwise vegetated riparian zones in otherwise forested landscapes. Whether our observations apply to forested riparian buffers in relatively deforested areas, or to riparian zones narrower than the 175–1600 m zones we analyzed, requires additional study. Regardless of the mechanisms affecting fish occurrence, our findings suggest that riparian length and area deserve increased consideration in decisions about riparian disruption and stream buffer zones.

Our curvilinear measure of patch length, which included small tributaries within an upstream patch, was an even stronger predictor of fish occurrence. Correlations with this variable were similar to those associated with patch area, which is logical given that tributary

streams were embedded within the patch. Total curvilinear stream length is probably a better measure of actual stream length within an area, but it is logistically complicated by the resolution capabilities of most mapping programs. A measure of total curvilinear stream length within a riparian patch has considerable potential where reasonably exact determinations of total stream density and distance can be made; such determinations should become easier as mapping resolution and geographic information system technology improve.

Our results also indicate that the riparian zone and its fauna can sustain some disturbance, but regardless of degree of upland forest cover, removal of trees in the riparian zone can have substantial effects on the habitats and fishes immediately downstream. Our findings suggest that continuous disturbance of riparian forests restricted to a kilometer or less may constitute a relatively minor disturbance to some fish assemblages, assuming that the watershed upstream and upslope is still largely forested and that the riparian zone is still vegetated. Although the threshold level of deforestation differed among species, it was in all cases between 1 and 3 linear km of tree clearing. If an ecologically sensitive family such as the darters is taken as an indicator group, our findings indicate that land planners should strongly discourage the clearing of trees from riparian strips longer than 1 km. Clearing in excess of 1–3 km will have substantial effects on fish assemblages. The literature on recovery of streams from logging disturbance suggests that forested riparian areas upstream of a locale can serve as refugia or sources for recolonization (Niemi et al. 1990). Our findings indicate that thresholds exist beyond which recovery will be much less likely: upslope trees can mitigate against riparian disturbance, but only to a point.

Our study was designed to establish the degree of riparian disturbance that would cause a change in the fishes living there, assuming an otherwise intact watershed. Unanswered are questions of mitigation and extent. For example, are streams flowing through alternating patches of forest and pasture substantially different from streams such as ours that are downstream from relatively isolated nonforested patches? How much riparian forest must be restored upstream of a deforested strip to allow the stream to return to a more natural state? Does 2 km of riparian clearing require at least 2 km of riparian reforestation upstream?

Finally, how is the balance struck between riparian function and upland deforestation? Stream and forest management practices call for riparian protection and restoration to mitigate against the effects of disturbance higher in a watershed. Our findings suggest that, even in watersheds that are over 95% forested, riparian disturbance alone can affect the stream biota. Wang et al. (1997) found that Wisconsin watersheds that had been extensively (>50%) converted to agriculture contained significantly altered streams regardless of riparian tree cover. Analogously, Roth et al. (1996), also working in a largely deforested (<25% forest cover) midwestern agricultural watershed, found that extent of vegetated cover in riparian zones was a poorer predictor of fish occurrence than were land-use measures at the catchment level. Roth et al. (1996: 153) suggested that "Upstream processes may overwhelm the ability of local, isolated patches of riparian vegetation to support stable instream habitat." Where, between our extensively forested upland situation and the extensively deforested upland situation studied by Wang et al. and Roth et al., does riparian function collapse? At what point can riparian trees no longer counter the effects of upstream agriculture? Alternatively, how much deforestation can be allowed in a watershed before irreversible changes will occur in the receiving lotic systems, regardless of riparian condition? At what level of disturbance are stream fishes, with their evolutionary histories tied to forested watersheds, no longer able to tolerate the cumulative effects of cutting of the terrestrial landscape through which their habitats flow?

Our investigation was an initial attempt at understanding interactions between upstream nonforested patches and stream fishes; many aspects of our design and sampling were far from ideal. A more definitive treatment of this issue would involve a greater number and range of upstream patch sizes, including replication; better control of patch shape (i.e., symmetrical on both sides of the stream); better control of possible downstream influences such as downstream nonforested patches and road crossings; measurement of additional landscape variables such as soil type; better accounting of actual land-use practices (vegetation type and density, farming practices, building density, site history); sampling over a longer reach than 50 m to include multiple occurrence of representative habitat types; and sampling downstream from narrower riparian patches, because our patches were much wider than the narrow corridors that are the focus of most management-oriented investigations. Ultimately, sampling downstream from forested riparian patches embedded in a deforested watershed and comparative testing in different regions would determine the general applicability of our conclusions.

Acknowledgments

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Appendix 1

Reproductive guilds[a] and species of fishes sampled, Little Tennessee River basin.

Nonguarding species
    Open substrate spawners:
        Benthic spawners (egg-broadcasters on substrate, eggs not hidden, no parental care)—mirror shiner (*Notropis spectrunculus*); blacknose dace (*Rhinichthys atratulus*); longnose dace (*R. cataractae*); white sucker (*Catostomus commersoni*); northern hog sucker (*Hypentelium nigricans*); black redhorse (*Moxostoma duquesnei*); golden redhorse (*M. erythrurum*); greenside darter (*Etheostoma blennioides*); banded darter (*E. zonale*).
    Brood hiders
        Benthic spawners (choose places to hide eggs in benthos): greenfin darter (*Etheostoma chlorobranchium*); gilt darter (*Percina evides*).
        Benthic modifiers (modify substrate to hide eggs but no care given): mountain brook lamprey (*Ichthyomyzon greeleyi*); central stoneroller (*Campostoma anomalum*); rosyside dace (*Clinostomus funduloides*); whitetail shiner (*Cyprinella galactura*); rainbow trout (*Oncorhynchus mykiss*);[b] brown trout (*Salmo trutta*).[b]
Guarders
    Substrate choosers:
        Rock undersurface spawners (place eggs on undersurface of rocks, guard eggs): mottled sculpin (*Cottus bairdi*); flat bullhead (*Ameiurus platycephalus*).[b]
    Nest spawners
        Pebble pile builders (build piles or use piles built and guarded by other species as "nest associates"): warpaint shiner (*Luxilus coccogenis*); river chub (*Nocomis micropogon*); Tennessee shiner (*Notropis leuciodus*); yellowfin shiner (*N. lutipinnis*)[b] creek chub (*Semotilus atromaculatus*).
        Pit spawners (excavate depression on soft bottom): rock bass (*Ambloplites rupestris*); redbreast sunfish (*Lepomis auritus*);[b] green sunfish (*L. cyanellus*); bluegill sunfish (*L. macrochirus*).
Undetermined
Fatlips minnow (*Phenacobius crassilabrum*).

[a] *Reproductive guilds from Helfman et al. (1997) after Balon (1975).*
[b] *Introduced species according to Menhinick (1991).*