

Fish Habitat and Fish Populations in a Southern Appalachian Watershed before and after Hurricane Hugo

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Abstract.—Habitat features and relative abundance of all fish species were estimated in 8.4 km of a small mountain stream system before and 11 months after Hurricane Hugo crossed the southern Appalachians in September 1989. There was no change in the total amount (area) of each habitat type but the total number of habitat units decreased and average size and depth of habitat units increased. Transport and sorting of streambed sediments was evident from the increased proportion of habitat units in which cobbles and small boulders were the most common constituents. Large woody debris more than doubled from 228 to 559 pieces/km of stream channel. At the watershed scale, there were only minor changes in the fish community 11 months after the hurricane. Eleven species were found both before and after the storm, and most species were uncommon. Among common species, densities increased in riffles for darters *Etheostoma* spp., increased in pools for blacknose dace *Rhinichthys atratulus*, and were largely unaffected for rainbow trout *Oncorhynchus mykiss*. The results of this case study suggest that the effects of catastrophic disturbances on fish habitat and populations depend on the predisturbance condition of instream and riparian habitat, timing of the disturbance, and life histories of individual species.

In many streams and rivers, floods are a common type of disturbance (Gerking 1950; Ross and Baker 1983). Floods scour streambed sediments and transport habitat-forming elements (e.g., large rocks, debris; Hack and Goodlet 1960), and they may displace or destroy fish, macroinvertebrates, and other taxa (Yount and Niemi 1990). The persistence or stability of fish communities that are subject to regular (seasonal) floods, however, is highly variable. Rather than a destructive disturbance, predictable floods are an essential feature of many lotic ecosystems (Reice et al. 1990). The impact of a particular flood on fish communities depends on the composition of the community (Meffe 1984; Matthews 1986), the condition of habitats before the event, the availability of refugia (Sedell et al. 1990), and the timing and magnitude of the flood (Elwood and Waters 1969; Erman et al. 1988; Yount and Niemi 1990).

In contrast to regular seasonal floods, infrequent and unpredictable floods, such as those brought on by hurricanes, can be destructive, at least in

the short term (Reice et al. 1990). During a hurricane, high winds topple streamside trees into stream channels, where they obstruct and redirect flow, altering habitat structure and patterns of sediment scour and fill (Bisson et al. 1987). Heavy precipitation greatly increases the erosive power of streams, and sediments scoured from channels are transported and redeposited downstream or on floodplains (Gregory et al. 1991). The possibility of change in habitat structure and fish communities increases greatly during such events. The effects of major disturbances such as hurricanes are poorly documented, however, because investigators usually lack information on predisturbance conditions or are unable to address change in conditions over appropriate spatial and temporal scales (Sousa 1984; Lamberti et al. 1991).

In this paper, we document changes in the type, amount, and characteristics of stream habitat and in the species composition and relative abundance of fish in an Appalachian Mountain watershed affected by Hurricane Hugo in 1989. A basinwide habitat and fish population survey had been completed 6 weeks before Hugo, which provided an opportunity to document the effects of a major storm on a small southeastern montane stream

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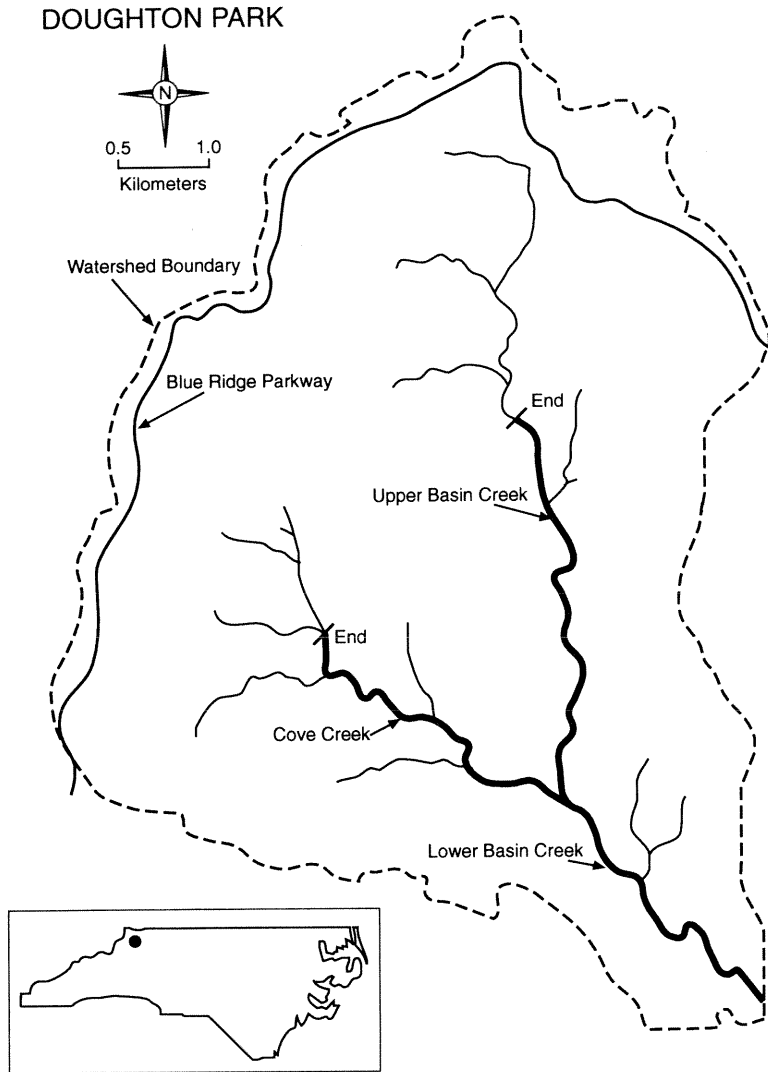


FIGURE 1.—Basin Cove watershed, Doughton Park Ranger District, Blue Ridge Parkway, North Carolina, showing the reaches (bold) of Lower Basin, Upper Basin, and Cove Creeks along which surveys of fish habitat and fish population were conducted before and after Hurricane Hugo.

system. We revisited the watershed approximately 1 year after the hurricane.

Study Area

Basin Cove watershed occupies about 2,428 ha in the Doughton Park Ranger District of the Blue Ridge Parkway (Figure 1). Basin Cove is typical of small, high-elevation watersheds in the southern Appalachians; most of the drainage was cleared for timber and subsistence agriculture by early settlers and has reverted to mostly forest in the last 30–80 years. Habitats in the entire 2,400-m reach

of Lower Basin Creek from a concrete dam near the lower Park boundary to the confluence of Basin and Cove Creeks, in about 3,270 m of Upper Basin Creek, and in 2,740 m of Cove Creek were inventoried during June 1989 (before the hurricane) and April 1990. Fish were sampled in the same reaches during June–July 1989 and August 1990. The upper boundary of the sampled reach of Upper Basin Creek was delimited by a cascade and falls and that of Cove Creek by a road crossing. These arbitrary upper boundaries did not include all habitat occupied by fish, because young-

of-the-year (age-0) rainbow trout *Oncorhynchus mykiss* were observed above the ends of the surveyed reaches. We estimate that at least 0.5 km of usable stream habitat in both Upper Basin and Cove Creeks were excluded from the inventories.

In September 1989, Hurricane Hugo swept northward across western North Carolina and into the Appalachian Mountains. A category 4 hurricane at landfall near Charleston, South Carolina, Hugo was one of the most destructive storms in U.S. history (M. Lawrence, National Weather Service, unpublished 1989 report). Forest ecosystems were hit especially hard; over 1.8 million hectares of timberland were damaged over a 27-county area of South Carolina. The destruction continued into North Carolina, where Hugo damaged nearly 0.65 million hectares of timberland even after it was reclassified as a tropical depression (Sheffield and Thompson 1992). Although high winds caused the most visible damage, more than 15 cm of rain fell at several locations along Hugo's track and caused local flooding. Daily mean discharge (m^3/s) during the storm at the U.S. Geological Survey stream gage on Roaring River, about 27 km downstream from Basin Cove, was one of the highest on record.

Methods

Habitat surveys.—We inventoried habitat in the Basin Creek watershed using the visual estimation methods outlined by Hankin and Reeves (1988). All habitat units in each of the three study reaches were classified as one of three distinct habitat types: pool, riffle (Platts et al. 1983), or cascade. Cascades were found in the very steep (typically the most upstream) portions of the stream profile. The streambed of cascades ranged from relatively straight bedrock slides to large rocks, boulders, or woody debris that formed series of small stepped pools. We separated cascades from steep riffles primarily on the basis of gradient; gradients of riffles were less than 12% and those of cascades 12% or greater.

Although other researchers have defined additional habitat types (Platts et al. 1983) and have divided major types into subcategories (Bisson et al. 1982; Hawkins et al. 1993), the above three types are the least likely to be misclassified. Additional categories were identified only as subcategories of one of the three basic types. This hierarchical classification ensured that all subcategories of habitat could ultimately be assigned to one of the three primary types for analysis.

The same individual was responsible for designating habitat units and estimating all stream

features both before (June 1989) and after (April 1990) the hurricane. Starting at the downstream end of the first habitat unit, this person walked upstream, identified each habitat unit by type (pool, riffle, etc.), and estimated its surface area. The surface areas of 20% of the pools and 10% of the riffles and cascades were measured with a meter tape to calibrate visual estimates. Maximum depth (± 5 cm) in each habitat unit was estimated with a wading staff marked at 10-cm intervals.

We also estimated the dominant substrate and amount of large woody debris in each habitat unit. Substrate categories were based on a modification of the Wentworth scale and included fine organic material, silt, sand (particles up to 2 mm diameter), small gravel (2–10 mm), large gravel (11–100 mm), cobble (101–300 mm), boulder (> 300 mm), and bedrock. The dominant substrate type (covering the greatest percentage of the stream bottom) was classified in each habitat unit by another crew member. Large woody debris included all pieces of wood that were at least 1 m long and 5 cm in diameter, and each piece in a habitat unit was assigned to one of seven size categories (Table 1) and tallied.

Habitat structure is directly influenced by the amount of water flowing in the stream channel (discharge). Comparisons of habitat variables such as surface area and depth therefore should be based on estimates made at similar discharge or stage. We are confident that although Basin Cove does not have a stream discharge gage, stage during the two habitat surveys was similar. We either delayed or discontinued sampling whenever stage appeared to be elevated by rainfall. In addition, daily mean discharge at the nearby Roaring River stream gage during the first habitat survey (mean, $5.5 \text{ m}^3/\text{s}$; SE, 0.56; $N = 8$) was not significantly different from discharge during the second survey (mean, $7.3 \text{ m}^3/\text{s}$; SE, 0.73; $N = 6$; Student's $t = -2.001$, $P > 0.05$).

Fish population surveys.—We censused fish populations during 1 week in late June–early July 1989, before Hurricane Hugo, and again during mid-August 1990, about 11 months after Hugo. Fish in about 20% of all pools and 10% of all riffles and cascades were counted by a diver equipped with face mask, snorkel, and writing slate. Upon arrival at the downstream end of a designated habitat unit, the diver carefully entered the water and observed the species and numbers of all fish and the relative sizes of rainbow trout. About 10% of the pools, riffles, and cascades sampled by the diver also were sampled by electrofishing. Block nets

TABLE 1.—Classification of large woody debris in the Basin Cove watershed.

Length (m)	Diameter (cm)			Rootwad
	5–10	11–50	Over 50	
1–5	Class 1	Class 2	Class 3	Class 7
Over 5	Class 4	Class 5	Class 6	

were used only when habitat units were not sufficiently isolated by natural features, such as an abrupt shallow-water transition between a pool and riffle. Although populations in the sampled habitat units in lower reaches were estimated by multiple-pass removal (Zippin 1958), many habitat units in the upstream reaches were small enough to allow removal of all individuals by intensive electrofishing, yielding a total fish count.

Species identifications were confirmed by examining specimens captured by electrofishing. All fish were identified, measured (± 1.0 mm total length), and weighed (± 0.1 g) before they were returned to the location of capture. Rainbow trout were grouped into two age-classes by their length frequencies.

Data analysis.—The equations of Hankin and Reeves (1988) and Dolloff et al. (1993) were used to estimate the surface area of habitat and the size of fish populations in each habitat type within each reach. For the most common species, population estimates derived from multiple-pass removal electrofishing were computed with Microfish (Van Deventer and Platts 1989), a computer program

based on the maximum-likelihood model. These population estimates and total fish counts by electrofishing were used to calibrate diver counts across all sampled habitat units (Dolloff et al. 1993). The calibrated diver counts were then averaged for each habitat type and used to estimate density (number/100 m²) by habitat type in each sampled reach and for all habitat types and reaches combined.

In Lower Basin Creek, we estimated density for two darter species combined, two dace species and shiners combined, and age-0 and adult rainbow trout. We treated Upper Basin and Cove Creeks similarly, except that densities of blacknose dace *Rhinichthys atratulus* were separately estimated.

Results

Habitat Surveys

The total number of habitat units in the three reaches decreased by 20% after Hugo (Table 2). The greatest change occurred in Lower Basin Creek, where the number of pools decreased by about 56%. The number of habitat units decreased least in Upper Basin Creek, where the breakup of cascades resulted in the formation of new riffles and pools. Heterogeneity also decreased greatly after Hugo, because numerous small, complex habitat units (e.g., pocket pools within riffles) coalesced into larger, more uniform habitat units (Figure 2).

Reflecting this coalescence, the average area of habitat units increased by 16%, from 42.8 to 49.8 m². Average pool and riffle area increased by 32% and 22%, respectively, whereas average cascade

TABLE 2.—Numbers of habitat units, estimated average areas of habitat, and average maximum depths in sampled sections of Basin Cove before and after Hurricane Hugo.

Section	Pools		Riffles		Cascades		Total	
	Before	After	Before	After	Before	After	Before	After
Number of habitat units								
Lower Basin	139	61	53	41	0	0	192	102
Upper Basin	353	355	85	97	70	40	508	492
Cove	286	204	119	90	39	30	444	324
Total	778	620	257	228	109	70	1,144	918
Area (m²)								
Lower Basin	56.6	130.8	161.9	225.1	0	0	85.7	168.7
Upper Basin	31.5	31.4	49.1	43.2	47.6	31.0	36.6	33.7
Cove	19.3	32.6	38.5	59.7	30.2	25.0	25.4	39.4
Total	31.5	41.6	67.6	82.4	41.4	28.4	42.8	49.8
Depth (cm)								
Lower Basin	54.6	82.5	35.2	43.7	0	0	49.1	66.9
Upper Basin	54.9	59.6	27.2	31.1	47.4	44.3	49.2	52.7
Cove	44.6	56.3	25.5	32.4	33.9	55.7	38.5	49.6
Total	51.1	60.8	28.1	33.9	42.6	49.2	45.1	53.2

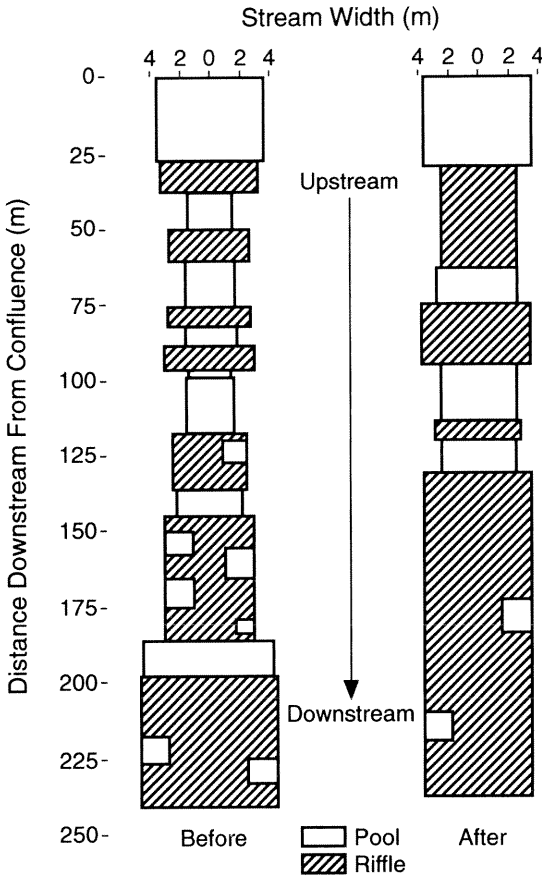


FIGURE 2.—Schematic maps of major habitat types in about 240 m of Lower Basin Creek from the confluence of Upper Basin and Cove Creeks downstream (top to bottom) based on basinwide habitat survey data recorded before and after Hurricane Hugo. Pools within riffles are shown as small open rectangles. Widths (m) are approximate averages for individual habitat units.

area decreased by about 31%. Maximum depth increased by an average of about 18% across all habitat types.

With the exceptions of total pool area in Cove Creek and total cascade area in Upper Basin Creek, total area of each habitat type in each section did not change significantly after Hurricane Hugo (Figure 3). The pool:riffle ratio was essentially unchanged in all sections (Table 3).

Larger or scoured substrates dominated streambeds after Hugo, when cobbles, boulders, or exposed bedrock were most common in more than half of all habitat units (Figure 4). Before Hugo, large gravel and sand were the dominant streambed substrates in about 75% of all habitat units.

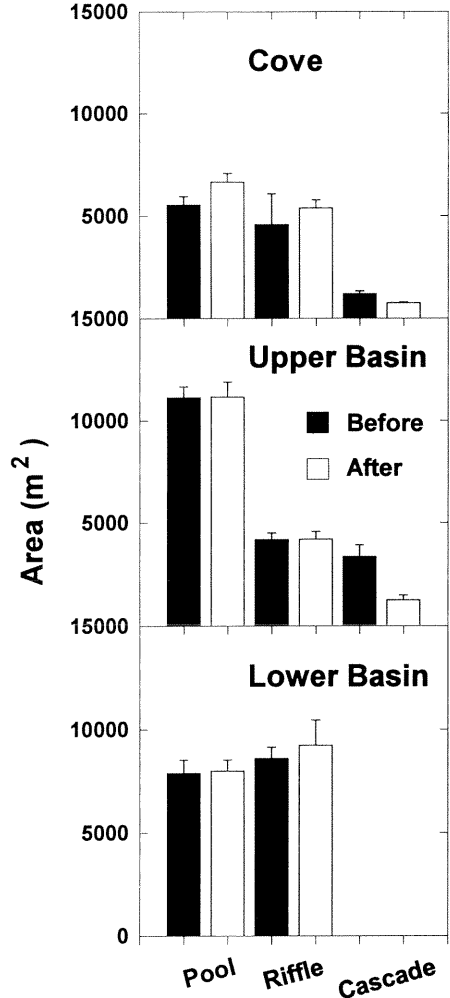


FIGURE 3.—Total areas (and upper 95% confidence limits) of habitats in sampled reaches of the Basin Cove watershed, before and after Hurricane Hugo.

After Hugo, the abundance of large woody debris more than doubled from 228 to 559 pieces/km of stream channel (Figure 5). Both before and after Hugo, such debris was dominated by small trees, branches, and broken tree fragments (classes 1 and 2). Very few larger-diameter pieces (classes 3 and 6) or rootwads were found either before or after the storm. Abundance of sapling and larger trees (classes 4 and 5) decreased in Upper Basin Creek after Hugo but increased in Lower Basin Creek. Although saplings virtually disappeared from Cove Creek, the number of larger trees per kilometer doubled after Hugo.

TABLE 3.—Pool : riffle ratios in sampled sections of the Basin Cove watershed before and after Hurricane Hugo.

Section	Before	After
Lower Basin	0.92	0.86
Upper Basin	2.66	2.66
Cove	1.21	1.24
Total	1.41	1.37

Fish Population Surveys

The species composition and distribution of fish were very similar before and after the storm. Lower Basin Creek contained rainbow trout, blacknose dace, rosieside dace *Clinostomus funduloides*, fantail darters *Etheostoma flabellare*, tessellated darters *Etheostoma olmstedii*, redlip shiners *Notropis chiliticus*, creek chubs *Semotilus atromaculatus*, bluehead chubs *Nocomis leptocephalus*, highback chubs *Notropis hypsinotus*, white suckers *Catostomus commersoni*, and margined madtoms *Naturus insignis*.

In Upper Basin and Cove Creeks, only two species, rainbow trout and blacknose dace, were consistently found in habitat units throughout the sampled reaches. Three additional species (bluehead chub, redlip shiner, and fantail darter) also were found before and after the storm in the lower 1,100 m of Upper Basin Creek but were infrequently sampled. Species composition and distribution before and after the storm were similar in Cove Creek, where bluehead chubs, redlip shiners, and fantail darters were uncommon but present in the lower 1,000 m.

We could not estimate the densities of white suckers, margined madtoms, and the individual species of darters, daces, and chubs in Lower Basin Creek. White suckers and margined madtoms were rarely seen or captured, and divers did not consistently distinguish the individual species of darters, daces, and chubs. Although fish (primarily rainbow trout) were seen in cascades both before and after Hugo, their frequency of occurrence was generally too low to permit calculation of population density.

The population responses to the Hugo-induced habitat changes varied among the fish groups. After Hugo, darter densities were either unaffected or lower in pools but higher in riffles (Figure 6). Blacknose dace densities more than doubled in Upper Basin and Cove Creeks, but densities of various cyprinid species in Lower Basin Creek were essentially unaffected by the habitat changes. Densities of age-0 rainbow trout decreased in the low-

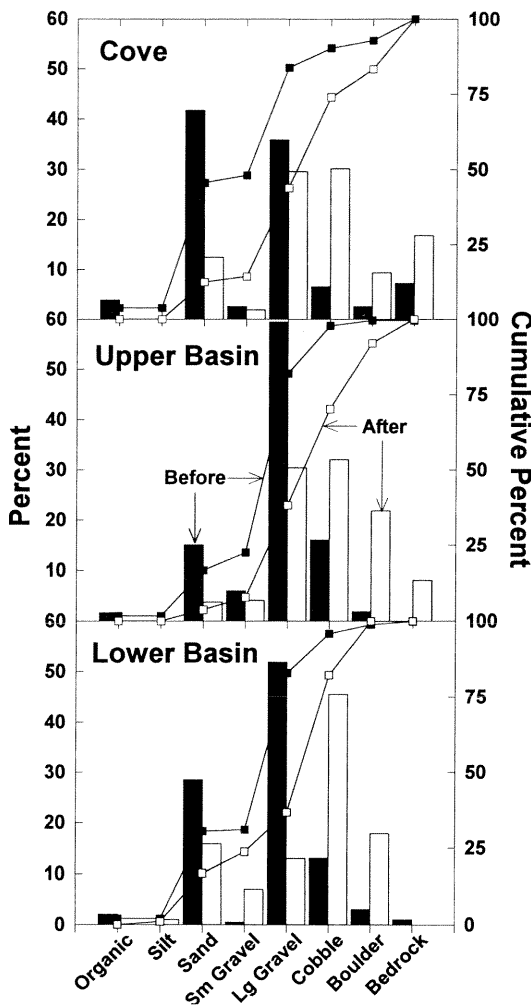


FIGURE 4.—Percentages (bars) and cumulative percentages (lines) of occurrence of dominant substrates in three reaches of the Basin Cove watershed before and after Hurricane Hugo (Sm is small; Lg is large).

est stream reach, increased in Upper Basin Creek, and increased in pools but decreased in riffles in Cove Creek. Densities of older rainbow trout increased in pools and decreased slightly in riffles after the storm. For the whole study area, densities of blacknose dace, darters, and rainbow trout were not significantly different from prestorm densities approximately 1 year after the storm (Table 4).

Over the whole study area, mean lengths and weights of blacknose dace were significantly greater (Mann-Whitney test, $P < 0.05$), but darters and rainbow trout were not significantly larger, approximately 1 year after the storm (Table 4).

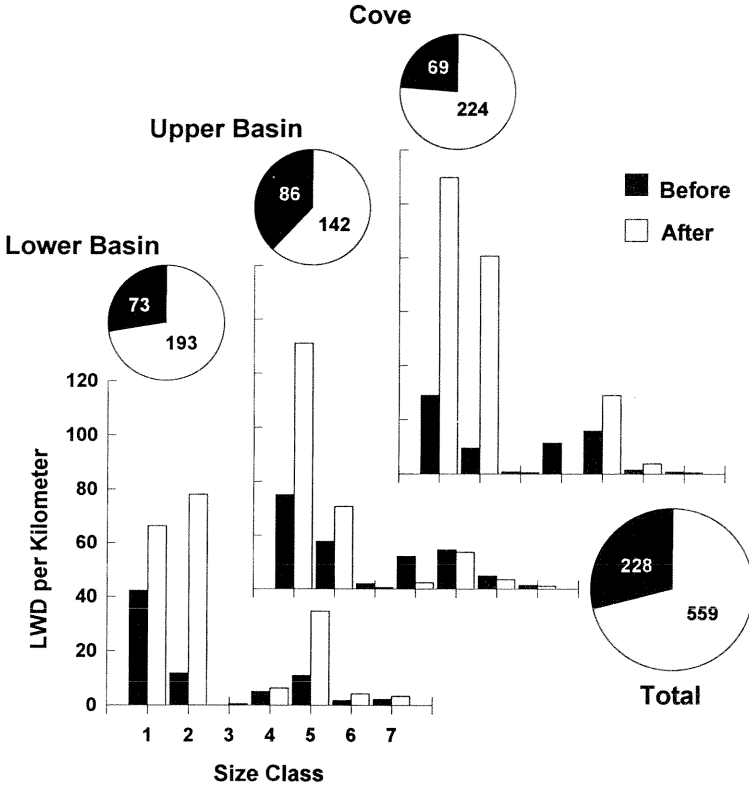


FIGURE 5.—Abundances of large woody debris (LWD) per stream kilometer (pie charts; dark = before, open = after) and distributions of sizes of LWD per stream kilometer (bar charts) in three sampled sections of the Basin Cove watershed before and after Hurricane Hugo. Refer to Table 1 for key to LWD size-classes.

Discussion

Habitats

The winds and high flows associated with Hurricane Hugo caused significant habitat changes in the streams of Basin Cove. After Hugo, there were fewer but larger and deeper pools and riffles. Complex habitat configurations were reordered into simple linear sequences. Substrate dominance shifted to the larger size-classes, and loading of large woody debris (LWD) more than doubled. The total surface area of habitat and the proportion of each habitat type, however, did not change.

Basin geomorphology and past land use influence the intensity of floods (Swanson et al. 1987). Streamflow in the moderate- to high-gradient channels in Basin Cove is confined by steep banks and narrow floodplains. Lateral movement of water is limited during floods, when greater water depth and velocity in stream channels greatly magnify erosive power. Under these conditions, fine sediments were readily scoured by the Hugo

flood, and underlying cobbles, and boulders were exposed.

Past land use in Basin Cove influenced habitat before Hugo in part by its magnification of previous disturbances. The steep mountainsides of Basin Cove were cleared for home sites and subsistence agriculture during the mid-1800s (Ross 1983). Since that time, there have been at least two recorded floods equal to or exceeding the magnitude of the 1989 flood. In July 1916, three days of nearly continuous rain generated a series of landslides and debris flows that swept down the cleared slopes to Basin Creek. Once in the creek, the resulting debris torrents destroyed many of the more than 50 homes in the basin and killed three inhabitants (Lord 1974). In the words of an eyewitness: "Whole half-acres just started sliding with timber until they hit the hollow. The water would dam up for a spell and then bust through. It made a roaring noise just like thunder." Although floods alone can be destructive, debris torrents can wipe out entire faunas, at least temporarily (Lamberti

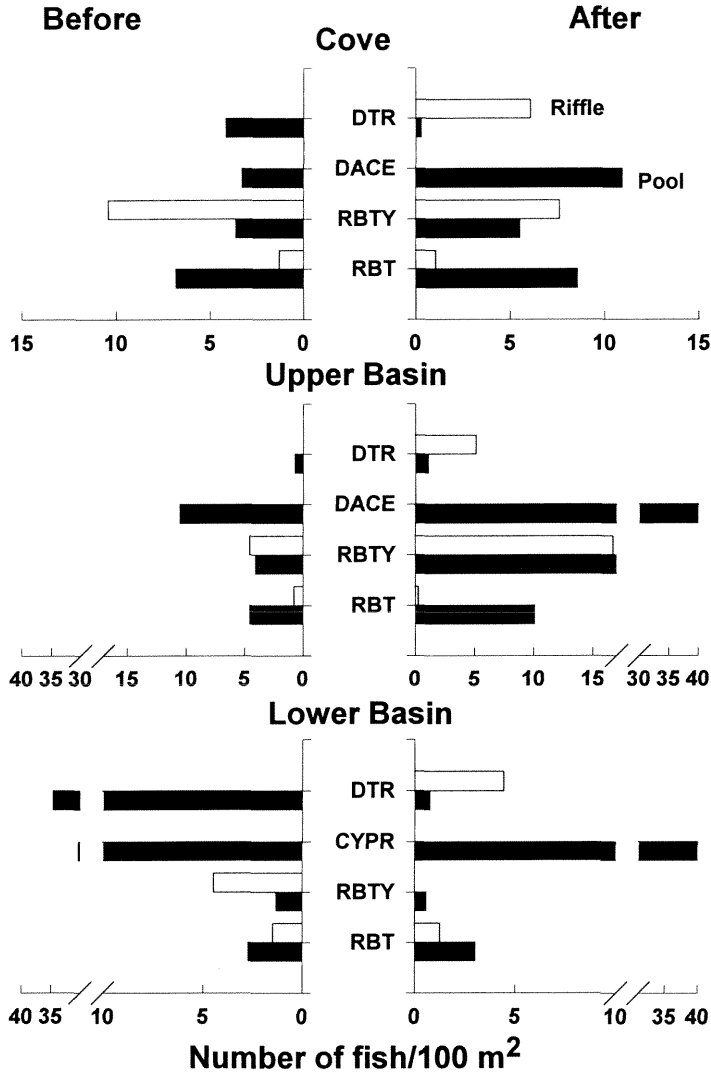


FIGURE 6.—Densities of fish groups in riffles (white bars) and pools (black bars) of three sampled reaches of the Basin Cove watershed before and after Hurricane Hugo: DTR = fantail and tessellated darters; DACE = blacknose dace; CYPR = blacknose dace, roside dace, and redlip shiners; RBTY = young (age-0) rainbow trout; RBT = adult rainbow trout.

et al. 1991). Another large flood occurred in 1940 but was less well described, because most residents had moved out of the watershed after the flood and debris torrents of 1916.

In contrast to the observed basinwide increase in LWD, the abundance of saplings and short, large-diameter fragments in the upper watershed decreased after Hugo. These small pieces were more readily floated and transported downstream or onto the floodplain. During the resurvey, we observed numerous trees and clumps of debris

high up on the banks, well away from the active channel. Because the stability and instream persistence of LWD is a function of piece size, small LWD has less direct influence on habitat except where clumped into debris dams or jams (Bilby and Likens 1980; Bisson et al. 1987).

The size, amount, and distribution of LWD reflected the development of riparian forest canopy during the 70–75 years after residents abandoned Basin Cove and the slopes began to revegetate. Contributions of larger sizes of LWD from sec-

TABLE 4.—Numbers of fish captured (n), mean (SE) lengths and weights, and population estimates ($\hat{N}/100 \text{ m}^2$) with 95% confidence intervals (CI, in parentheses) for blacknose dace, darters (fantail and tessellated combined), and rainbow trout in Basin Cove before and after Hurricane Hugo. Asterisks denote significant differences between pre- and posthurricane values (Mann–Whitney test, $P < 0.05$ for length and weight).

Species and time	n	Mean length (mm)	Mean weight (g)	\hat{N} (CI)
Blacknose dace ^a				
Before	39	61.69 (2.62)	2.83 (0.31)	6.43 (3.70–9.16)
After	71	*68.95 (0.90)	*3.77 (0.16)	14.26 (3.98–24.54)
Darters				
Before	40	54.90 (1.53)	1.51 (0.15)	8.39 (5.41–11.37)
After	23	56.00 (2.67)	1.76 (0.20)	2.47 (0.0–7.32)
Rainbow trout				
Before	62	113.95 (6.09)	20.56 (2.51)	3.22 (1.02–5.42)
After	143	104.46 (4.17) ^b	22.78 (2.53) ^b	4.73 (2.99–6.47)
Age-0 trout				
Before				4.34 (3.10–5.58)
After				7.21 (3.25–11.17)

^a Based on data from Upper Basin and Cove Creeks only.

^b Adult trout.

ond-growth riparian stands that are less than 100 years old are limited because the trees have not grown and matured to the point at which they can be recruited to stream channels (Harmon et al. 1985). In unmanaged, second-growth riparian forests typical of the southern Appalachians, trees must grow longer than 73 years (in this instance from 1916 to 1989) before they are able to contribute large amounts of LWD (Hedman 1992). Andrus and others (1988) determined that only 14% of the total LWD load (pieces at least 10 cm in diameter and 1 m long) in a small Oregon Coast Range watershed was derived from second-growth riparian forest 50 years after logging.

Fish Populations

Because fish assemblages are adapted to their prevailing flood regime, major changes in species composition are not expected following periods of “normal” flooding (Welcomme 1979), particularly when refuges are present (Hill and Grossman 1987; Sedell et al. 1990). Whether or not Hurricane Hugo could be considered normal is debatable; however, the major changes in habitat features suggest that it was an extreme if not totally catastrophic event. Despite these apparently dramatic changes in the physical environment, there were few detectable changes in the composition of the fish community. The distribution of the 11 species found before the hurricane was the same during the resurvey, 11 months later. Variation in density, although large in some cases, was within the probable natural range for stream fish in the southern Appalachians (Grossman et al. 1990).

Although we did not sample immediately after

the hurricane, we are confident that all fish present 11 months later were either survivors or the offspring of survivors within the study area. A 3-m-high concrete dam at the lower end of Lower Basin Creek prevented any possible recruitment from downstream areas. Recolonization from upstream habitats was unlikely, because few fish of any species were seen above the study area before Hugo.

Resistance of fish assemblages to the effects of a catastrophic disturbance is in part a function of the timing of the disturbance and the associated life history stages of the fish (Seegrist and Gard 1972; Detenbeck et al. 1992). Hurricane Hugo occurred in early fall, when most species may have been able to resist displacement. The fish species found in Basin Cove typically finish spawning by midsummer (Lee et al. 1980), which would have allowed ample time for incubation and dispersal of young-of-the-year fish into suitable microhabitats or potential refuges. Harvey (1987) suggested that small differences in the timing of reproduction and floods can have major impacts on young-of-the-year survival. In both natural and artificial streams, he observed that various cyprinids and centrarchids that had grown larger than 10 mm were less likely to be displaced during floods.

The response of the only exotic species in the watershed, rainbow trout, might be expected to differ from that of the native fish fauna. The only salmonid native to the southern Appalachians, brook trout *Salvelinus fontinalis*, spawns in the fall and young emerge from gravel in early spring. In contrast, rainbow trout are spring spawners whose young emerge later in the spring or early summer. Young salmonids are most vulnerable to

displacement after their yolk sacs have been absorbed but before the fish have "settled in" to a suitable microhabitat (Ottaway and Clarke 1981). Many of the 1989 year-class of rainbow trout survived the hurricane, and recruitment in 1990 was at least as successful as in 1989.

The type and availability of refuges may also have influenced the response of fish during the storm. Although we documented major changes in habitat, many potential refuges remained intact. Refuges exist at multiple spatial scales (Sedell et al. 1990), ranging from individual particles (e.g., boulders, LWD, rootwads; Shirvell 1990) to hydraulically complex reaches (Pearsons et al. 1992) or subbasins. In Basin Cove, after Hugo, decreases in the number of potential refuges at the habitat unit scale (i.e., fewer units) probably were offset by increases at the particle scale (e.g., greater depth, exposure of large sediments, more abundant LWD).

Changes in the type and availability of potential refuges may influence the response of fish during future floods. Fish that hide in streambed interstices or are closely associated with LWD cover should better resist displacement during subsequent high flows. For example, darter densities increased in riffle habitats, which had larger sediments and greater depths (+20.6%) after Hugo.

Despite major changes in habitat structure, we could not detect major changes in the composition or distribution of the fish community 11 months after Hurricane Hugo. Our results suggest that the effects of large disturbances on fish habitat and populations depend on the predisturbance condition of instream and riparian habitats, on the timing of the events, and on the life histories of the affected species.

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