

Response of a Brook Trout Population and Instream Habitat to a Catastrophic Flood and Debris Flow

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Abstract.—In June 1995, a massive flood and debris flow impacted fish and habitat along the lower 1.9 km of the Staunton River, a headwater stream located in Shenandoah National Park, Virginia. In the area affected by debris flow, the stream bed was scoured and new substrate materials were deposited, trees were removed from a 30-m-wide band in the riparian area, and all fish were eliminated. In the area that was unaffected by debris flow, habitat was moderately altered by the flood and fish populations persisted at decreased densities. Basinwide fish population and habitat surveys provided data to compare (1) the pre- and postevent population densities of brook trout *Salvelinus fontinalis* and instream habitat conditions and (2) postevent population density, brook trout growth, and instream habitat in the debris-flow-affected and unaffected areas. By June 1998, brook trout had recolonized the entire debris-flow-affected area, and population density exceeded preevent levels. Brook trout growth was significantly greater in the debris-flow-affected area than in the unaffected area through fall 1998, but it was not significantly greater in 1999. Population density appeared to have a negative influence on fish growth. A 1995 postevent habitat survey revealed increases in the number of pools and riffles and substrate size and decreases in pool and riffle surface area and depth. By 1999, the total number, surface area, and depth of pools and riffles had returned to near preevent levels and substrate size had decreased. Between 1995 and 1999, the amount of large woody debris increased in the debris-flow-unaffected area, where riparian trees had remained intact, and decreased in the affected area, where riparian trees had been eliminated. A number of factors, including a relatively intact watershed and nearby source populations, allowed the Staunton River to quickly respond to this dramatic natural event. Given the proper conditions for recovery, such events are less catastrophic than activities that lead to chronic stream degradation.

Streams occupied by salmonid populations are subject to natural disturbances that lead to changes in instream habitat and fluctuations in population abundance. These disturbances range from moderate and predictable events over seasonal or annual intervals, to more extreme, so-called catastrophic events, with return intervals measured in decades or centuries. Both moderate and extreme

events play important roles in shaping lotic ecosystems (Sousa 1984; Reice et al. 1990).

In the Appalachian Mountains, extreme flooding can alter both instream habitat and fish populations and produce more localized reaches of mass wasting where the stream channel and riparian areas may be drastically altered (Hack and Goodlet 1960). While changes brought about by mass wasting events can appear devastating, lack of preevent data often hampers the ability of investigators to quantify changes in fish populations or habitat (Lamberti et al. 1991; Dolloff et al. 1994).

A handful of studies with pre- and postevent data have indicated that salmonid populations can be quite resilient to “catastrophic” disturbances. Typically, disturbed populations returned to preevent densities within 3 years (Lamberti et al. 1991;

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Propst and Stefferud 1997; Swanson et al. 1998) unless the event created unsuitable habitat conditions (Elwood and Waters 1969). When the habitat after a catastrophic event is suitable, abundance and density can actually rebound beyond preevent levels (Lamberti et al. 1991; Thorpe 1994).

Although limited in their ability to detect changes, studies without preevent data can still provide valuable insight into how fish populations and instream habitat respond to conditions created by episodic events. For example, several researchers have observed greater growth rates by fish that recolonized areas affected by mass wasting than in areas of the same stream that were not affected by mass wasting (Lennon 1961; Elwood and Waters 1969; Lamberti et al. 1991; Letcher and Terriker 1998; Swanson et al. 1998).

Debris flows, one of the more spectacular types of mass wasting events, occur in high-gradient watersheds that also commonly support salmonid populations. Debris flows occur when landslides combine with floodwaters to produce a mobile slurry of rocks, soil, water, and trees moving downstream at up to 10 m/s, tearing trees from the stream banks, scouring stream channels, depositing new materials, and eliminating entire instream faunas (Hack and Goodlet 1960; Gecy and Wilson 1990; Swanson et al. 1998). These events are rare on any given stream, with recurrence times of more than 50 years in the Pacific Northwest (Swanson et al. 1987) and more than 100 years in the Central Appalachian region (Hack and Goodlet 1960).

The unpredictable and infrequent nature of such events, coupled with a lack of knowledge of preevent conditions, has led to a poor understanding of how episodic events influence habitat and populations, as well as to the perception that such events are catastrophic. Studying the response of stream habitat and fish populations following extreme events provides the information needed to make and defend decisions that promote and preserve natural response mechanisms.

Over a 5-d period in June 1995, soils in the Shenandoah National Park (SNP), Virginia, became saturated by nearly continuous rainfall, culminating with more than 20 cm of rain over the final 24 h of the period (Karish et al. 1997). The result on SNP's Staunton River was a streamwide flood, coupled with landslides and a massive debris flow along the lower 1.9 km of the stream to its confluence with the Rapidan River (Eaton 1999; Figure 1).

Changes caused by the debris flow were dra-

matic and included the scouring of the stream channel and deposition of new substrates, the elimination of trees from a 30-m-wide band in the riparian area, the piling of large woody debris (LWD) in massive stacks on the stream banks, and the complete extirpation of fish from the debris-flow-affected area (U.S. Forest Service, Center for Aquatic Technology Transfer [USFS-CATT], unpublished data). Fish populations remained intact, although at decreased densities, in the debris-flow-unaaffected area of the stream. The existence of preevent data (Newman 1996) provided a rare opportunity to examine how the brook trout *Salvelinus fontinalis* population and instream habitat were changed by and responded to the flood and debris flow.

Study Site

The Staunton River is a second-order stream that flows east from an elevation of 975 m through the central district of SNP to its confluence with the Rapidan River (Figure 1). The stream is approximately 6.3 km long with an average width of 3.5 m. The channel consists of pools separated by step pool cascades, small (<2 m) waterfalls, and bedrock slides. The Staunton River contains mainly two species of fish: brook trout and blacknose dace *Rhinichthys atratulus*. American eels *Anguilla rostrata* are found throughout the stream at very low densities, and a warmwater fish assemblage occupies the Staunton from its confluence with the Rapidan River to the base of a steep bedrock cascade approximately 150 m upstream of the confluence. Postevent fish assemblage and species distributions (Table 1) were similar to those observed before the event (authors' observation).

On June 22, 1995, moderate rain began falling in SNP and culminated in heavy rains on June 27 and June 28. Measured rainfall amounts in some areas of SNP exceeded 20 cm on June 27 alone. Graves Mill, a small community just southeast of the Staunton River, may have received as much as 60 cm of rain during the 5-d event. More than 800 people in the vicinity were displaced from their homes, eight deaths were attributed to flooding, and 2,000 homes were damaged. An account of the storm and its immediate effects on SNP can be found in Karish et al. (1997).

Methods

Population density.—Brook trout population density was estimated by dividing estimated population abundance by estimated stream area. Population abundance was estimated using basinwide

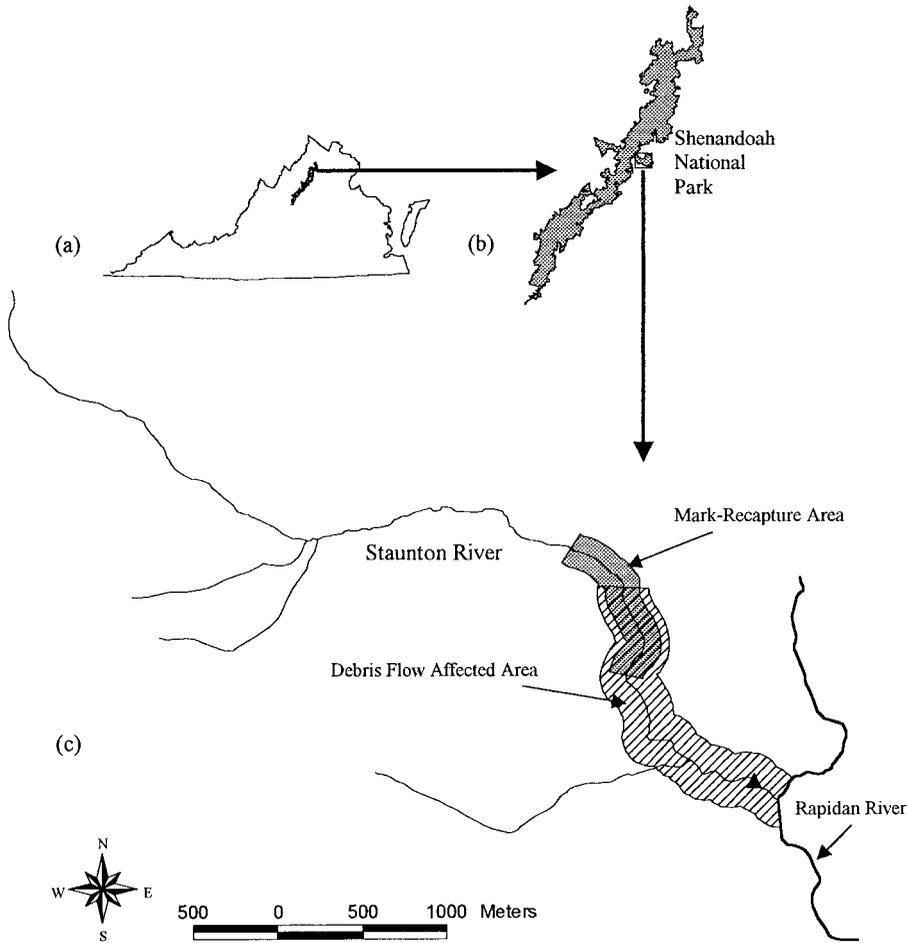


FIGURE 1.—Maps showing the locations of (a) Shenandoah National Park (SNP) in Virginia, (b) the study site within SNP, and (c) the Staunton River with the debris-flow-affected area, mark-recapture study section, and stream gauge (closed triangle) shown.

visual estimation technique (BVET) fish surveys (Dolloff et al. 1993), which were performed in the spring and fall of each year from 1993 to 1999. Stream area was estimated using BVET habitat surveys (Dolloff et al. 1993) performed in June 1993, October 1995, and June 1999.

Population densities by habitat type for June 1993–May 1995 were calculated using the June 1993 habitat survey. The October 1995 habitat survey was used to calculate postdebris-flow densities for October 1995 and May 1996. Densities between October 1996 and November 1999 were calculated using the 1999 habitat survey, as a flood in September 1996 may have caused changes in the stream area following the October 1995 habitat survey. Density estimates were made for the debris-flow-affected and unaffected areas of the

stream in addition to the total stream for all surveys following the June 1995 debris flow.

BVET fish surveys were performed using a combination of diver counts and electrofishing methods. During the fish surveys divers counted fish in every 5th pool and every 10th riffle from the confluence to the upper limits of habitability by fish (stream meter: 6,300) and recorded the number of age-0 and adult fish in each habitat unit. Population size structure prevented us from dividing fish older than age 0 into more than one size-class (Figure 2), thus throughout this paper “adult” refers to all fish older than age 0. Electrofishing was used to calibrate a subsample of the units (typically 10 pools and 10 riffles) that were sampled by divers. Three passes were made through each subsample unit using a backpack electrofishing unit. The

TABLE 1.—Furthest upstream observation of species sighted by divers or captured by electrofishing in the Staunton River from 1995 (after debris flow) to 1999. Distance is meters upstream from the confluence with the Rapidan River.

Species	Furthest upstream observation
Common shiner <i>Luxilus cornutus</i>	150
Northern hog sucker <i>Hypentelium nigricans</i>	150
Rosyside dace <i>Clinostomus funduloides</i>	150
Sculpin <i>Cottus</i> spp.	150
Fallfish <i>Semotilus corporalis</i>	150
Longnose dace <i>Rhinichthys cataractae</i>	150
Smallmouth bass <i>Micropterus dolomieu</i>	150
White sucker <i>Catostomus commersoni</i>	150
Bluehead chub <i>Nocomis leptocephalus</i>	175
Torrent sucker <i>Moxostoma rhothoecum</i>	450
Blacknose dace <i>Rhinichthys atratulus</i>	3,000
American eel <i>Anguilla rostrata</i>	3,500
Brook trout <i>Salvelinus fontinalis</i>	6,000

number of age-0 and adult fish captured in each pass was recorded. The estimated number of fish in each unit was calculated using methods presented in Kwak (1992). Total abundance of YOY and adult fish in pools and riffles were calculated using methods described in Dolloff et al. (1993).

Fish growth.—Average length—at age and in-

dividual fish growth were examined using data from a post-debris-flow mark-recapture study. The mark-recapture area spanned a continuous 965-m reach of the Staunton River, with 575 m in the debris-flow-affected area and 390 m in the unaffected area of the stream (Figure 1). Trout were first marked for the study in October 1996. Before electrofishing, the mark-recapture reach was divided into riffle-pool complexes. Each complex was a continuous 10–40-m reach of stream typically encompassing several pools and riffles and terminating at potential low-flow barriers to fish passage (e.g., boulder cascades or waterfalls). Trout were captured by single-pass electrofishing through each habitat complex. Length (mm), weight (g), and the location of capture were recorded for each fish. Brook trout greater than 100 mm in length were given a passive integrated transponder (PIT) tag, allowing us to individually identify them upon recapture. Fish were returned to the riffle-pool complex from which they were captured. We collected length and weight data, marked additional fish, and recaptured PIT tagged individuals by repeating this procedure in May 1997, October 1997, June 1998, October 1998, June 1999, and October 1999.

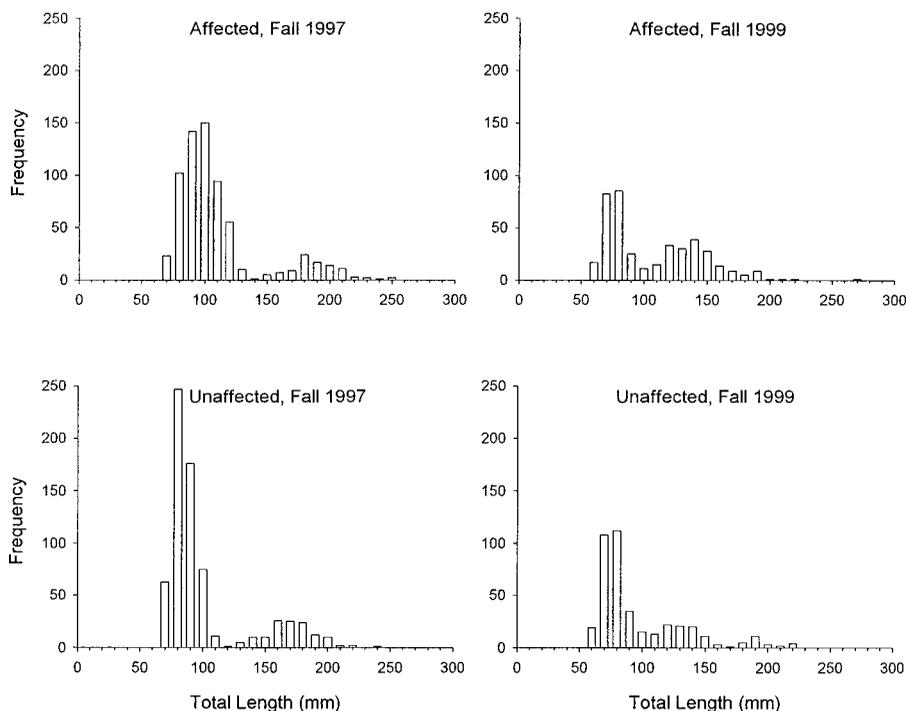


FIGURE 2.—Length-frequency histograms for Staunton River brook trout captured during the mark-recapture study in the debris-flow-affected and unaffected areas during fall 1997 and fall 1999.

Data from all fish captured on each date were used to test for significant differences in average length at age between age-0 and adult fish, sections (affected and unaffected), and dates of capture. The length data were log transformed to minimize the effects of unequal variance and a generalized linear model was applied to the data.

Data obtained from individually marked (PIT-tagged) fish that were recaptured the first date after which they were marked were used to test for differences in change in length and weight between affected versus unaffected sections of the stream and between periods (see Figure 7 for periods). Fish that moved between sections (less than five per period) were excluded from the analysis. Generalized linear models were applied to the data to test for significant interaction among variables (date, section, and age). Following these tests, the data were divided into ten groups representing the affected and unaffected sections during each time period. Two-sample *t*-tests were used to examine significant differences between affected and unaffected sections within each period.

The relationships between change in length or weight and density were investigated by plotting the change in length and the change in weight from time t_1 to time t_2 (as calculated from mark-recapture data) versus density at time t_1 (as calculated from BVET data). A line was then fitted to the data.

Instream habitat.—The habitat in the Staunton River was inventoried using the BVET habitat survey described in the population density portion of the Methods section. In addition to calculating the total area of the Staunton River, we estimated pool and riffle surface area, maximum depth, LWD loading, and the dominant substrate in each pool and riffle from the confluence with the Rapidan River to the upper limits of habitability by fish (approximately stream meter 6,300).

Habitat surveys were performed by two-person crews, with one individual responsible for estimating habitat and features and the other responsible for measuring cumulative distance and recording data. The crew began at the downstream end of the first habitat unit and progressed upstream. The surface areas of 20% of the pools and 10% of the riffles were measured with a meter tape to calibrate visual estimates. The maximum depth of each unit was measured with a wading staff marked at 5-cm intervals.

Dominant substrate (the substrate covering the greatest percentage of the stream bottom) and large woody debris (LWD) loading were also estimated

TABLE 2.—Classification of large woody debris in the Staunton River.

Length (m)	Diameter (cm)		
	5 to 10	11 to 50	>50
1–5	Class 1	Class 2	Class 3
>5	Class 4	Class 5	Class 6

for each habitat unit. Substrates were divided into seven classes: organic debris, small-diameter substrate (<2 mm), gravel (3 mm–10 mm), pebble (11 mm–100 mm), cobble (101 mm–300 mm), boulder (>300 mm), and bedrock. LWD included all pieces greater than 1 m in length and 5 cm in diameter. LWD was assigned to one of six size-classes based on length and diameter (Table 2).

Differences in discharge can affect estimates of habitat features (Herger et al. 1996; Hilderbrand et al. 1999). During the 1993 and 1999 habitat surveys, discharge on the Staunton River was monitored with a stream gauge (Department of Environmental Sciences at the University of Virginia, Charlottesville) located 140 m upstream from the confluence with the Rapidan River (Figure 1). Discharge during the 1995 survey was calculated by correlation from data collected at nearby gauging stations, as the 1995 debris flow had destroyed the Staunton River gauge.

Results

Population Density

Density estimates varied widely for both age-0 and adult brook trout before and after the June 1995 debris flow (Figure 3). The most precise estimates (smallest confidence intervals) were obtained for age-0 and adult fish in pools. Because most brook trout in the Staunton River occupy pools (Roghair 2000) and the most precise estimates were obtained for pools, these data were used to test for trends in density. In the stream as a whole, the highest density estimates for age-0 and adult brook trout were observed within 2–3 years of the debris flow (Figure 3). Since distances were not recorded during the fish surveys, we could not split preevent fish population density data between affected and unaffected sections.

Fish Growth

When a generalized linear model was applied to the length-at-age data, significant interactions between date and section and date and age were found ($P < 0.001$). The model was split by date, allowing comparison among sections and among

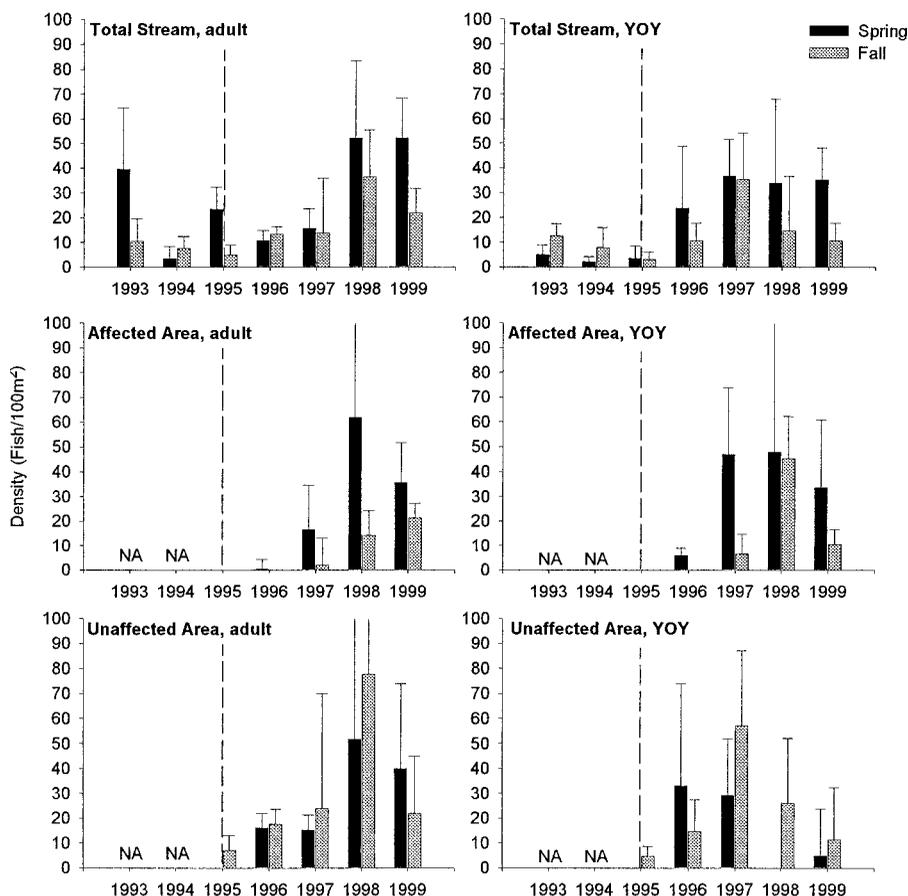


FIGURE 3.—Density of adult and age-0 (YOY) brook trout in Staunton River pools estimated using basinwide visual estimation techniques from 1993 to 1999. Estimates are by season for the total stream, the debris-flow-affected area, and the debris-flow-unaffected area. Dashed line indicates date of debris flow. Bars represent 95% confidence intervals.

ages within each date but preventing statistical comparisons across dates. The split model revealed significant interaction between age and section for the October 1996 data, precluding any further analysis for that date. No significant interactions were found for any other dates, allowing us to interpret the split model results for those dates.

The split model revealed significant differences in average length at age between the affected and unaffected areas of the stream from June 1997 to October 1998 for age-0 and adult brook trout (Figure 4). Over the period from June 1997–October 1998, the average lengths of fish in the affected area were consistently higher than those in the unaffected area. Although differences between years could not be compared statistically (because of significant interaction between date, section,

and age discussed above), there was a decreasing trend in average lengths from 1996 to 1999 for age-0 fish in fall, adults in spring, and adults in fall (Figure 4).

When generalized linear models were applied to the individual fish growth data, significant interactions between date and section and date and age were found ($P < 0.001$) so that differences across periods could not be examined. The data were divided into ten groups representing the affected and unaffected sections of the stream during each period. A Levene's test rejected the notion that the variances between the groups were the same ($P = 0.003$); thus a Welch's analysis of variance (ANOVA) was employed to examine for significant differences between groups (SAS Institute 1996). The ANOVA results revealed significant differences among the ten groups ($P = 0.0001$), and

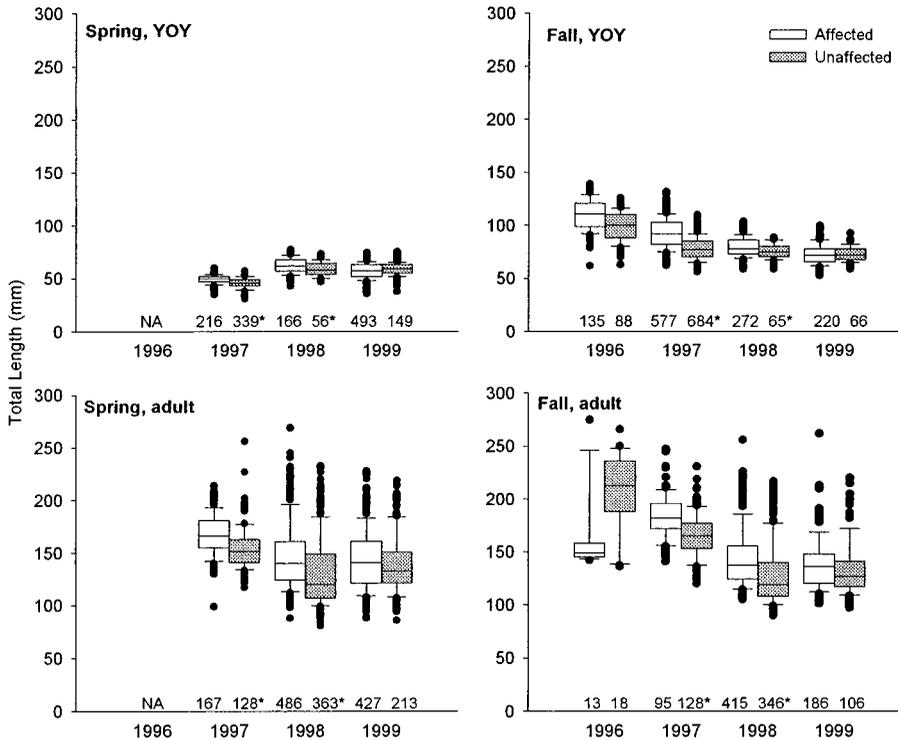


FIGURE 4.—Length-at-age of adult and age-0 brook trout in the Staunton River in spring and fall from mark-recapture data. Box plots represent the 25th and 75th percentiles and median values. Bars represent the 10th and 90th percentiles. Closed circles represent the entire range of data. Numbers below box plots are sample sizes. Asterisks indicate a significant difference between affected and unaffected areas (generalized linear model: $P < 0.001$).

two-sample *t*-tests were used to examine for significant differences between affected and unaffected sections within each period.

Significant differences ($\alpha = 0.05$) in change in length and weight between affected and unaffected sections were found during period 1 (June 1997–October 1997) and period 2 (October 1997–June 1998; Figure 5). Changes in length and weight were greater for the affected area than for the unaffected area during these periods. Although differences among periods could not be statistically compared (because of the significant interaction between date, section, and age discussed above), there was a decreasing trend in change in length and weight from period 1 (June 1997–October 1997) to period 5 (June 1999–October 1999).

The linear regressions for median change in length ($P < 0.0001$) and weight ($P < 0.0001$) versus density were significant. As density increased both change in length ($r^2 = 0.48$) and change in weight ($r^2 = 0.45$) decreased (Figure 6).

Instream Habitat

Discharges during the 1993 (0.14 m³/s) and 1995 (0.16 m³/s) habitat surveys did not differ significantly ($P > 0.30$); however, the 1993 and 1995 surveys were significantly different from the 1999 survey ($P < 0.001$), when drought conditions resulted in an average discharge of 0.03 m³/s. In past studies, decreased discharge has led to an increased number of habitat units, decreased average surface area, and decreased total stream area (Heger et al. 1996; Hilderbrand et al. 1999). In the present study the opposite effect was observed between 1995 and 1999, indicating that any effect the decreased flow may have had on estimates was overridden by large changes in channel morphology.

The total number of habitat units increased by more than 50% in 1995, immediately following the flood and debris flow (Table 3). The increased number of units was reflected in a 50% decrease in average surface area for both pools and riffles

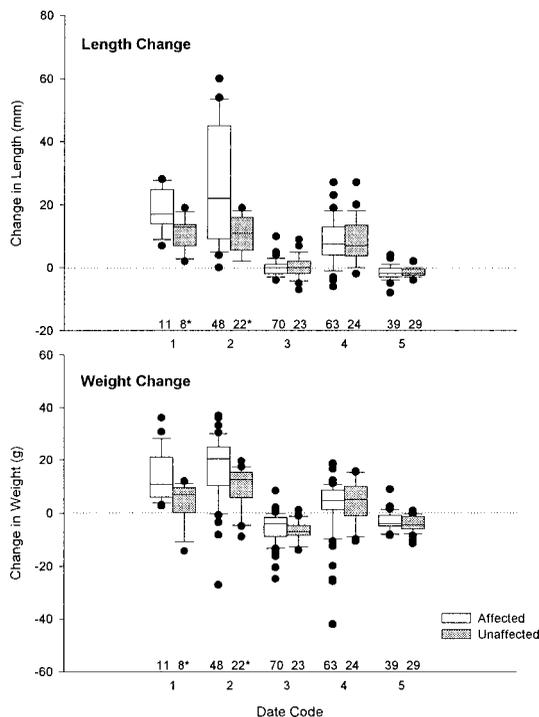


FIGURE 5.—Change in length and weight of adult brook trout marked with PIT tags and later recaptured in the Staunton River during the mark–recapture study. Box plots represent the 25th and 75th percentiles and median values. Bars represent the 10th and 90th percentiles. Closed circles represent the entire range of data. Date codes: 1 = June to October 1997; 2 = October 1997 to June 1998; 3 = June to October 1998; 4 = October 1998 to June 1999; 5 = June to October 1999. The numbers below the box plots are sample sizes. Asterisks indicate a significant difference between affected and unaffected areas ($\alpha = 0.05$, two-sample *t*-test).

in debris-flow-affected and unaffected areas of the stream. The maximum depth of habitat units also decreased following the debris flow, most obviously in the debris-flow-affected area, where they decreased by more than 25%. The total number of habitat units, average surface area, and maximum depth had all returned to near preevent levels by 1999.

Confidence intervals for riffle area and total stream area did not overlap when the 1995 survey was compared with both the 1993 and 1999 surveys, suggesting significant changes in the habitat immediately following the flood and debris flow. However, confidence intervals for stream area and the area in pools and riffles did overlap when the 1993 and 1999 habitat surveys were compared, suggesting that pre- and postevent stream area were not significantly different by 1999 (Figure

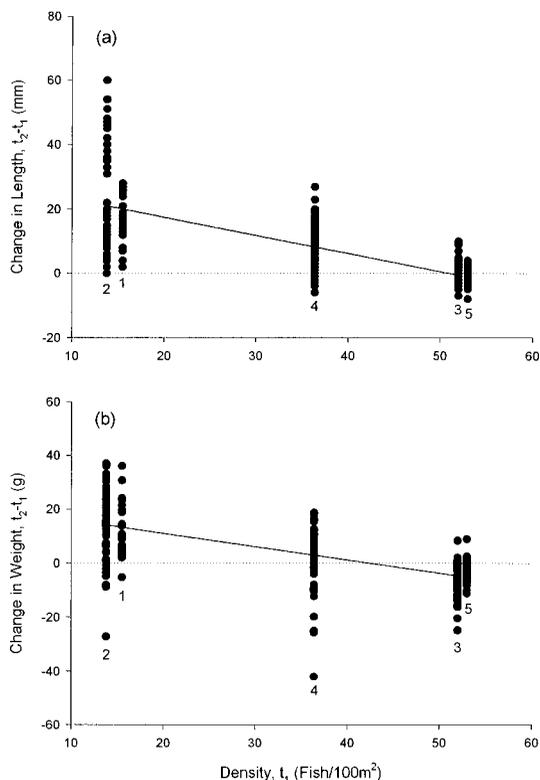


FIGURE 6.—Change in (a) individual fish length ($r^2 = 0.48$) and (b) individual fish weight ($r^2 = 0.45$) versus total stream population density for adult brook trout marked with PIT tags in the Staunton River. Numbers indicate the time periods during which data were recorded: 1 = June to October 1997; 2 = October 1997 to June 1998; 3 = June to October 1998; 4 = October 1998 to June 1999; 5 = June to October 1999.

7). The total pool area did not differ between any of the surveys.

More than 25% of preevent habitat units had substrates dominated by small-diameter substrate particles, with other size-classes evenly distributed throughout the remainder of the habitat units. Large size-class cobbles and boulders dominated postevent substrates (Figure 8). Substrate composition in the debris-flow-affected and unaffected areas were nearly identical during all three surveys. In 1999, the percentage of habitat units with a dominant substrate of cobble decreased substantially as the percentage with gravel substrate increased more than threefold and returned to preevent levels.

Overall, the amount of LWD per kilometer increased in both the debris-flow-affected and unaffected areas of the stream in 1995 (Figure 9). Small-diameter LWD (sizes 1 and 4) showed

TABLE 3.—Number of habitat units, estimated average surface area of individual pools and riffles, and average maximum depth in the Staunton River before and after the June 1995 debris flow. The affected section in 1993 represents the lower 1.9 km of the stream. Total is affected and unaffected areas combined.

Section	Pools			Riffles		
	1993	1995	1999	1993	1995	1999
Number of habitat units						
Affected	107	176	105	86	121	76
Unaffected	211	328	190	178	259	166
Total stream	318	504	295	264	380	242
Average surface area of individual habitat units (m²)						
Affected	43.0	22.0	38.6	75.9	36.9	55.7
Unaffected	21.8	18.0	23.7	53.7	25.8	60.0
Total stream	29.0	19.4	29.0	60.9	29.4	58.7
Average maximum depth (cm)						
Affected	71	52	58	34	25	36
Unaffected	65	57	58	24	27	31
Total stream	67	55	58	27	26	32

marked increases in both sections, as did large-diameter LWD (sizes 3 and 6), with the exception of size 6 in the unaffected area. The amount of medium-diameter (sizes 2 and 5) LWD per kilometer did not increase in 1995.

In 1999, the amount of LWD per kilometer continued to increase in the debris-flow-unaffected area, but decreased in the debris-flow-affected area (Figure 9). Small- (sizes 1 and 4) and large-diameter (sizes 3 and 6) LWD decreased substantially in the debris-flow-affected area, whereas medium-diameter LWD increased. The amount of LWD per kilometer increased for size-classes 1, 2, and 5, and remained approximately the same for size-classes 4 and 6, but decreased for short, large-diameter LWD (size 3) in the debris-flow-unaffected area.

Discussion

Population Density

The brook trout population of the Staunton River responded vigorously following the June 1995 debris flow. In the stream as a whole, age-0 density exceeded pre-debris-flow levels within 1 year, and adult density exceeded pre-debris-flow levels within 2.5 years. Both remained above preevent levels for the remainder of the observation periods. Further study is currently underway to determine if population density will remain at its currently high level (USFS-CATT, unpublished data).

Future fluctuations in density are likely since brook trout are known to have highly variable rates of survival due to the unstable nature of the streams they occupy (Elwood and Waters 1969;

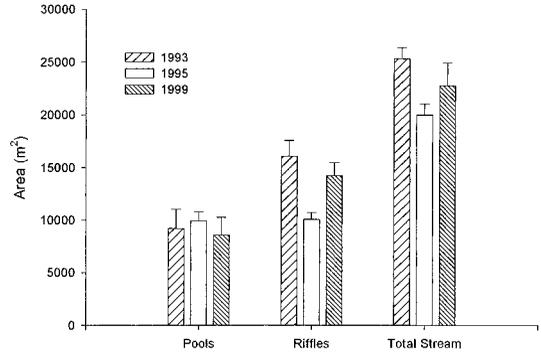


FIGURE 7.—Total areas and 95% confidence intervals of habitats before (1993), immediately following (1995), and 4 years after (1999) a flood and debris flow on the Staunton River.

Hunt 1974; Reice et al. 1990; Marschall and Crowder 1996). The unstable nature of stream environments has led to the assertion that stream fish populations may essentially be in a constant state of recovery from disturbance (Reice et al. 1990). Given that brook trout evolved in such systems, the rapid response of the population following the debris flow was not surprising.

Stocking or transplanting of fish was not necessary to facilitate rapid recolonization of the debris-flow-affected area or a rapid increase in population density. A number of necessary components—including an intact, nearby source population, suitable habitat conditions, and a lack of barriers to recolonization—were in place following the flood and debris flow that allowed a rapid population recovery (Detenbeck et al. 1992). Even if the entire brook trout population of the Staunton River had been eliminated, it still would likely

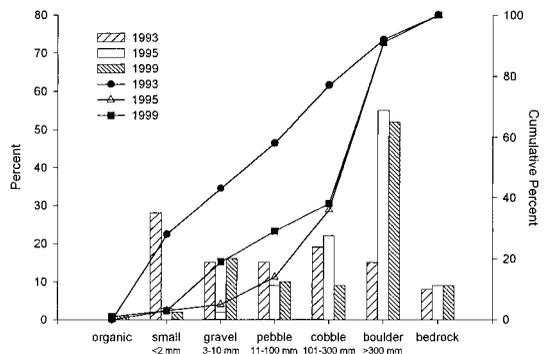


FIGURE 8.—Percentages (bars; left scale) and cumulative percentages (lines; right scale) of the occurrence of dominant substrates in the Staunton River before (1993), immediately following (1995), and 4 years after (1999) the June 1995 flood and debris flow.

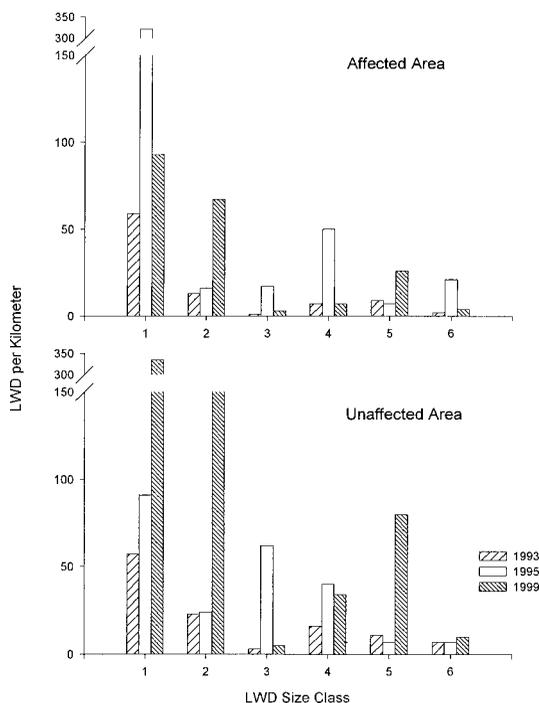


FIGURE 9.—Large woody debris (LWD) per kilometer in debris-flow-affected and unaffected areas of the Staunton River before (1993), immediately following (1995), and 4 years after (1999) the June 1995 flood. The affected area in 1993 represents the lower 1.9 km of the stream.

have been repopulated by brook trout from the nearby Rapidan River. The luxury of a source population, however, is not shared by all streams within SNP.

Streams that support brook trout populations originate within SNP and flow outside of the Park, where deforestation, development, and agriculture often create unsuitable habitat conditions for trout. The brook trout populations in many of these streams may be isolated for decades from other populations because of the habitat conditions outside of the Park. Should a debris flow or other catastrophic event eliminate the brook trout population from such a stream, it is unlikely that it would be quickly, if ever, repopulated. If this scenario were encountered, transplanting fish from other streams may become an option. Because populations within different areas of SNP have been shown to differ genetically and the extent of this variation is not yet fully known (Poompson et al. 1997), this would not be a desirable situation. Maintaining and restoring habitat links between salmonid populations should be considered a pri-

ority if populations are expected to persist in the face of extreme episodic events.

Fish Growth

By 1997, the affected and unaffected areas of the mark-recapture section contained two distinguishable size-classes of fish: age 0 and adult (all fish older than age 0). Average brook trout size and individual growth were at their observed peaks, and average size and individual fish growth in the debris-flow-affected area was greater than in the unaffected area. Brook trout size and growth rate steadily decreased, and by 1999 there was no significant difference between the affected versus unaffected areas.

While increased growth rates have been observed for age-0 and adult salmonids occupying other disturbed areas (Elwood and Waters 1969; Lamberti et al. 1991; Letcher and Terrick 1998), decreased growth rates over time have not been documented. In these studies increased growth generally was attributed to increased water temperature, increased food supply, and/or decreased competition due to a low population density following the event. An increase in water temperature would not seem to be beneficial to a coldwater species so near the southern extent of its range, and it was beyond the scope of the present study to examine macroinvertebrate abundance or brook trout consumption. However, there was a strong negative relationship between brook trout growth and population density.

Density-dependent growth of brook trout has been observed in field (Hunt 1974) and laboratory studies (Marchand and Boisclair 1998), and has been examined through modeling (Marschall and Crowder 1996). Whether increased growth at low density is the result of increased food consumption or decreased agonistic interactions remains a point of debate (Marchand and Boisclair 1998). The postevent data provided a rare look at growth during periods of extremely high and extremely low densities for the Staunton River.

Increased growth immediately following the debris flow and its relationship to density may seem to indicate that suppressing population size could alter the fishery by providing fewer but faster-growing and ultimately larger fish. Donald and Alger (1989) found that reducing the number of fish in a lentic brook trout population increased fish growth. The relatively small increase in size they observed, however, would likely be of minimal importance to anglers. The same could be said of

the present study, where over the entire period the maximum fish size remained near 250 mm.

Although the differences in growth observed over time or between affected and unaffected areas may be of little importance to the typical angler, they may be ecologically significant. Increase in age-0 growth, such as that observed immediately following the flood, can decrease age-at-maturity or increase fecundity (Hutchings 1996) and suggests a mechanism that has developed to allow populations to quickly increase their numbers when decimated by events such as debris flows.

Instream Habitat

During the 1995 BVET habitat survey we noted that in many sections the stream was highly disordered, containing multiple, braided channels that made it difficult to distinguish the main channel (authors' observation). This was reflected in the increased total number of habitat units and the decreased average surface area during the 1995 survey. The immediately postevent Staunton River consisted of a large number of small-surface-area pools; these pools served to break riffles into small sections, effectively decreasing their average surface area as a result. The decreased total surface area of riffles in 1995 was also the result of the disordered channel. Water flowed in several small channels between pools instead of through a single main channel, resulting in a decreased estimate of the total riffle area and the total stream area in 1995. By 1999, the stream channel had become more typically organized, with a single main channel in most areas and a return to preevent levels for the total number of habitat units, average surface area, and total stream area.

The reorganization of the stream channel between 1995 and 1999 demonstrated the importance of high-flow events in channel adjustments (Reice et al. 1990). Several high-flow events experienced in the 4 years after the flood and debris flow reorganized the stream channel. The two largest events were in 1996 ($>8.50 \text{ m}^3/\text{s}$) and 1998 ($>2.83 \text{ m}^3/\text{s}$), and base flow ranged between $0.03 \text{ m}^3/\text{s}$ and $0.16 \text{ m}^3/\text{s}$ over the period of the study. High-flow events between 1995 and 1999 altered channel morphology and returned several of the measured variables to near-preevent conditions without the implementation of habitat manipulation projects.

Extreme floods and debris flows are commonly associated with changes in dominant substrate size (Elwood and Waters 1969; Reice et al. 1990; Dolloff et al. 1994; Swanson et al. 1998). Flood disturbance can help to maintain productive salmonid

habitat by decreasing the amount of fine substrate materials such as sand, silt, or clay from streams. These substrates are known to decrease salmonid egg survival when they are found in redds (Reeves et al. 1995; Kondolf 2000). Alternatively, extreme flood disturbance could conceivably remove not only fine substrates but the gravel substrates on which salmonids such as brook trout typically spawn (Jenkins and Burkhead 1994), damaging reproductive capabilities. The proportion of gravel substrate in the Staunton River decreased following the flood and debris flow, but within 3 years brook trout population density in the Staunton River recovered to preevent levels, indicating that suitable spawning habitat was not a limiting factor. By 1999 particle sizes had begun to shift toward the smaller particle scale and the amount of gravel substrate had returned to preevent levels.

The direct effects of flooding and debris flows and their impact on riparian areas accounted for the observed changes in LWD abundance. As would be expected, both the debris-flow-affected and unaffected areas saw increases in nearly all size-classes of LWD following the 1995 flood and debris flow. However, between 1995 and 1999, the debris-flow-affected area saw increases in only the medium-diameter LWD (sizes 2 and 5), whereas several size-classes increased or remained nearly steady in the unaffected area. The relatively intact riparian section of the unaffected area provided a direct source of LWD input that was lost when trees within 30 m of the stream were eliminated in the debris-flow-affected area. The only direct source of LWD that remained in the affected area was from the trees that had fallen across but remained suspended above the stream channel. The majority of these trees were of medium diameter (authors' observation) and as they were washed or broke and fell into the channel, they accounted for continued inputs of LWD into the debris-flow-affected area. This will be the only direct source of LWD inputs for the debris-flow-affected area for several decades, while trees in the riparian area grow to suitable sizes (Hornbeck and Kochenderfer 2000).

Past studies have related low amounts of LWD with decreased habitat diversity, low numbers of pools, and decreased salmonid density (Fausch and Northcote 1992; Flebbe and Dolloff 1995). While LWD can create a large number of pools through scour or damming of the channel in some streams (Harmon et al. 1986), observations made during the 1999 habitat survey indicated that no pools (0 of 105) in the debris-flow-affected area were

formed exclusively by LWD, 5% (5 of 105) were formed by a combination of LWD and rock, and the remaining 95% were formed by rock alone. Despite a higher input of LWD, similar results were found in the debris-flow-unaffected area where less than 1% (1 of 190) of pools were formed by LWD exclusively, 6% (11 of 190) were formed by a combination of LWD and rock, and the remaining 94% were formed by rock alone. Although LWD did not play a significant role in pool formation, the number of pools/km and population density were near to those of similar-size streams flowing through old growth forest where LWD did play a significant role in habitat formation (see Flebbe and Dolloff 1995 for comparison). Flebbe and Dolloff (1995) indicated that in some streams where LWD did not contribute significantly to habitat formation, large cobbles and boulders could provide a suitable surrogate, as appeared to be the case in the Staunton River.

Decreases in discharge are known to increase the number of habitat units, decrease the average surface area, and decrease the total stream area (Herger et al. 1996; Hilderbrand et al. 1999). In our study discharge was significantly lower in 1999 than 1995, but the total number of habitat units decreased, and average surface area and total stream area increased. In 1995 the channel consisted of a large number of small surface area habitat units. By 1999 the channel became more typically organized and consisted of a smaller number of large surface area habitat units. Any effect decreased flow may have had on estimates was overridden by large changes in channel morphology.

Synthesis

Fish populations in high-gradient streams, and the streams themselves, are to a large extent shaped by extreme flow events. On a geologic timescale, extreme floods and debris flows are common, and as such should not be perceived as catastrophic but rather as a normal, albeit unpredictable and dramatic, facet of stream ecology. Given the proper conditions, fish populations and stream habitat can quickly respond to these relatively short-lived, localized events. However, chronic disturbances, such as land use changes, global climactic changes, the introduction of exotic species, and acid rain, can increase the frequency and severity of such events and decrease the ability of fish and habitat to respond to them. Left unchecked, the effects of chronic disturbances can be much more detrimental to stream habitat

and fish population persistence than 'catastrophic' natural events.

Acknowledgments

Partial funding for this project was provided by the U.S. Geological Survey, Biological Resources Division, and the University of Virginia through Grant Number 5-29372. We thank personnel from the USFS Center for Aquatic Technology Transfer, including Keith Whalen, Kevin Leftwich, David Hewitt, Steve Quarles, John Moran, Kurt Newman, and dozens of technicians and volunteers. Sundar Dorai-Raj of the Virginia Tech Historical Consulting Center provided essential help with data analysis. Critiques by Art Bulger and two anonymous reviewers greatly improved the quality of this manuscript.

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