NOTES

Changes in Distribution of Nonnative Brook Trout in an Idaho Drainage over Two Decades

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Abstract.-Invasions of brook trout Salvelinus fontinalis are believed to threaten the aquatic fauna native to the cold streams and lakes of western North America. Although invasion is widespread, documentation of historic versus recent invasion rates throughout drainages is lacking. We compared brook trout distributions in 1996 to those as early as 1971 for 17 streams in the upper South Fork Salmon River, Idaho. In 1996, brook trout occurred in 11 of the streams. Adult ranges expanded at least 0.5 km upstream in 8 streams, and upstream invasion (1.2-2.4 km) occurred in 3 of those. No recent invasion was apparent in 10 streams that lacked dispersal barriers within 1 km of the South Fork Salmon River confluence or of previous distribution limits, including 4 streams containing at least some adult brook trout. We also compared distributions between 1993 and 1997 in two streams of the Weiser River drainage, Idaho, and found no changes in upstream distribution limits over that shorter time interval. Although invasion may be ongoing in some streams, brook trout do not appear to be relentlessly invading every accessible stream.

The invasion of cold streams and lakes by brook trout *Salvelinus fontinalis* has contributed to the decline of native fishes, amphibians, and invertebrates throughout much of the United States and Canada (Leary et al. 1993; Carlisle and Hawkins 1998; Dunham et al. 1999; Knapp and Matthews 2000). Preventing further invasion has become a major concern for many managers, particularly as mandates to preserve native fauna have increased (Kruse et al. 2001).

Invasion can be viewed as a cycle with three

phases: (1) arrival (including dispersal), (2) establishment, and (3) integration (Vermeij 1996). Establishment is defined as the presence of a locally reproducing population (Vermeij 1996). With positive population growth and additional dispersal, the cycle continues, and invasion progresses either continuously or intermittently. Different factors operating over increasingly long time scales can influence success or failure in each phase (Carroll and Dingle 1996; Moyle and Light 1996; Vermeij 1996). We use the term "distribution expansion" to describe situations in which brook trout had arrived since previous surveys but were not established.

While biologists have amassed copious information about brook trout biology, that knowledge has rarely been applied to understanding the mechanisms of invasion. The lack of understanding of the invasion process has hindered efforts to predict and minimize brook trout invasion. We lack some very basic information, such as current versus historic invasion rates, that is critical to determining the best strategies for minimizing the effects of brook trout on native fauna. Fausch (1989) suggested that brook trout have probably had ample time to "expand upstream to the limits of their capabilities" in streams where no major barriers exist. However, the supposition remains relatively unexplored, and the invasion rate in stream networks has been documented for only a handful of invasions and then over intervals of only a few years (e.g., Behnke 1992; Leary et al. 1993).

To investigate the patterns and the amount of recent invasion by nonnative brook trout, we examined changes in the upstream distribution limits of brook trout over 25 years in the upper South Fork Salmon River drainage, Idaho, and over 4 years in the Weiser River drainage, Idaho. We also looked for dispersal barriers near distribution lim-

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its to determine whether or not invasion was limited by an inability to disperse farther upstream.

Methods

Study area.—The majority of the study occurred in the upper South Fork Salmon River drainage, Valley County, Idaho, upstream of the Secesh River (Figure 1). The drainage is in the Idaho Batholith, a granitic landform "characterized by steep slopes, heavily dissected topography, and highly erodible soils" (for detailed land- and channeltype descriptions, see Platts 1979a; Platts et al. 1989). Annual precipitation ranges from 76 to 152 cm, and high flows in tributaries occur during spring snowmelt, occasional rain-on-snow events, and localized, intense summer rainstorms. The predominant physical alteration of the main stem and many tributaries prior to and during the study period was massive loading with fine sediments, which began in the late 1950s (Platts et al. 1989; Waters 1995).

We studied 17 South Fork Salmon River tributary streams in which brook trout invasions, if any, were assumed to be upstream directed because no population existed in a headwater lake (e.g., Adams et al. 2001). Study streams ranged from first to fourth order. In the study reaches, elevations ranged from 1,143 to 1,841 m, channel slopes from less than 1% to more than 26%, and wetted stream widths from 1.6 to 12.9 m during low flows (Adams 1999). Other fishes observed in study reaches included the bull trout S. confluentus, bull \times brook trout hybrids, westslope cutthroat trout Oncorhynchus clarki lewisi, native and introduced rainbow trout/steelhead O. mykiss, and rainbow \times cutthroat trout hybrids; chinook salmon O. tshawytscha, mountain whitefish Prosopium williamsoni, and shorthead sculpin Cottus confusus were observed occasionally.

Brook trout dispersal to the South Fork Salmon River and some tributaries occurred initially via human transport and subsequently proceeded without human assistance. Documented brook trout stocking occurred in the main stem and in some tributaries and headwater lakes from 1932 to 1972 (Idaho Department of Fish and Game, unpublished data), although undocumented stocking probably occurred both earlier and later. Because brook trout were scattered throughout the main stem of the upper South Fork (S. Adams, unpublished data; W. Platts, unpublished data) and are known to make long-distance movements (Gowan and Fausch 1996; Adams et al. 2000, 2001), we inferred that they had access to all of the study streams.

Historic data collection.—Data on brook trout distributions prior to the 1990s came primarily from extensive fish surveys conducted in 14 of the study streams from 1971 through 1974 (Table 1; Platts 1974, 1979b, and unpublished data). In 1971-1972, Platts used block nets and primacord (explosives) in 7-27 (median = 16), 15.2-m-long sites per stream. Sample sites were spaced evenly within each land type throughout a stream. The median distance between sites was 0.5 km, and the range for each stream was 0.3-0.9 km. Sampling began near the confluence with the South Fork and in most streams continued upstream until either (1) the stream was dry or too small to sample or (2) no fish were collected or observed at several consecutive sites upstream of a waterfall or other apparent barrier. In streams containing brook trout, a median of 10 sites (range = 2-13) were sampled upstream of the uppermost observation of brook trout.

In 1974, Platts conducted more intensive sampling via snorkeling and electrofishing in the downstream segments of some study streams (Table 1). Fish distributions in 11 streams, including 3 not sampled by Platts, were studied by other investigators in the 1980s (Table 1).

Recent data collection.—From 19 August to 1 October 1996, we revisited the 17 streams to determine if upstream brook trout distribution limits had changed detectably since previous surveys. We used daytime snorkeling to define the brook trout distribution limits within 0.5 km of the actual limit and randomized the sequence of drainages snorkeled. We intended to determine the presence or absence of brook trout, not to estimate densities or to determine all the year-classes present. However, we deliberately searched for age-0 fish, which were relatively easy to observe in stream margins and shallow, off-channel habitats during the day.

We snorkeled primarily in pools because brook trout tend to occupy low-velocity habitat units, even within steep stream reaches (Moore et al. 1985; Cavallo 1997; Magoulick and Wilzbach 1998), and we assumed that at low densities, brook trout would typically occupy the best habitat available to them. We also snorkeled side channel and lateral habitats, where available, because these are also preferred habitat for brook trout, especially for age-0 individuals (Moore et al. 1985; Cavallo 1997). We sampled only pools that we subjectively judged to be of moderate to high quality relative to other pools within each stream segment. Pools meeting our standards were those having (1) a maximum wetted width wider than the average



FIGURE 1.—Study streams and other major tributaries of the upper South Fork Salmon River, Idaho. All streams with names shown (except those in bold) were study streams. The known distribution of brook trout in tributaries in 1996 is shown by gray shading. Based on our observations and Platts' sampling, we presumed that brook trout were scattered throughout the main stem.

TABLE 1.—Presence (+ [or number when few were found]) or absence (-) of brook trout in tributaries of the upper South Fork Salmon River, Idaho, during previous surveys and the numbers of brook trout observed and sites sampled in 1996. The number of brook trout observed in 1996 is provided to give a general impression of abundance, but the data are suitable only for presence/absence interpretation.

Tributary	Platts 1971–1972 ^a	Thurow 1984–1985 ^b	Cascade Environ- mental Services 1989 ^d	Krassel 1993–1994 ^e	Number of brook trout observed in 1996	Number of sites sampled in 1996
Bear	+	+			25	6
Blackmare	1	-	+		8	4
Buckhorn	_	_	_		0	2
Little Buckhorn				_	0	4
West Fork	_	-	_	_	0	2
Cabin	+		+		11	3
Camp		2	_		1	4
Cougar	+	+			15	5
Curtis	-(+)	+			2	4
Trail	1				18	6
Dollar	+	+	+		6	4
Fitsum	_	_			0	3
Fourmile	_	-	_		0	3
Lodgepole	+(+)				7	3
Phoebe		+ c			0	2
Six-Bit	_				1	4
Tyndall	-				5	7

^a Symbols in parentheses are from 1974; others are from 1971-1972.

^b Snorkeled- and electrofished-only habitats typically used by steelhead trout (Thurow 1987).

^c The only brook trout observed were age-0 fish at the mouth, so this was not considered an extirpation.

^d Subsampled one to three, 200-m-long sites per stream by snorkeling and electrofishing (CES 1989).

^e Snorkeled a subset of each habitat type (methods in Overton 1997; unpublished data, U.S. Forest Service, Krassel Ranger District, McCall, Idaho).

width in the stream segment, (2) maximum depths equal to or exceeding the median pool depth in the stream segment, (3) low water velocities, and (4) fish cover provided by overhead or submerged large wood or vegetation, large substrate, turbulence, or depth. Variables were assessed visually while walking upstream, and because quality was judged relative to available habitat, parameters indicative of "quality" pools varied among stream segments.

We snorkeled three pools beginning near the previous upstream brook trout distribution limit or, if none were found previously, at the confluence with the South Fork. If brook trout were abundant, we moved upstream to the next site; otherwise, we snorkeled at least three more pools and one run. We then moved upstream 0.5–1.0 km, depending on fish densities and changes in channel morphology, and repeated the process. We continued sampling until no brook trout were observed in a site consisting of at least six pools and one run. We ended the survey there if we had at least one of the following three types of supporting evidence for having reached the distribution limit: (1) no brook trout were observed in the entire stream; (2) the brook trout distribution appeared to end at an obvious barrier such as a large falls (i.e., >6 m) and no brook trout were found above the falls in previous surveys; or (3) a similarity was found with results obtained by U.S. Forest Service biologists who conducted fish distribution surveys in the stream in 1996 and 1997 (see below). If we lacked supporting evidence, we returned downstream and snorkeled a 100-m-long reach approximately 0.25–0.50 km upstream of the uppermost brook trout sighting. We snorkeled 2–7 sites in each stream (Table 1) and at least one site upstream of our last brook trout sighting. We looked for potential dispersal barriers by walking 1 km upstream of our uppermost brook trout observation location.

In both Lodgepole and Trail creeks, Forest Service scientists (Rocky Mountain Research Station, Boise, Idaho) sampled 25–30 reaches by snorkeling in 1996 and 14 reaches by electrofishing in 1997. Reaches were short (range, 5.6–31.1 m; average, 20.7 m) and were separated by an average change in elevation of 9 m. The data were used as supporting evidence for our delineation of upstream distribution limits in the two streams.

We also assessed distribution changes over a shorter time interval (1993–1997) in two streams, the Little Weiser River and Dewey Creek, Adams County, Idaho. In 1993, fish distributions were de-

termined by day and night snorkeling (Adams and Bjornn 1997). In 1997, Forest Service scientists reassessed the distribution limits by electrofishing 18–19 short (20–38 m) reaches (D. Myers, U.S. Forest Service, Rocky Mountain Research Station, unpublished data). The average change in elevation between reaches was 21.5 m.

Data comparisons and potential bias.-We compared the upstream distribution limits of brook trout in 1996 with the most upstream observation of any brook trout in the earliest data available for each stream (see Table 1). We differentiated between the distribution expansion of adults and invasion, characterizing the latter as the presence of juvenile and adult brook trout where no brook trout occurred previously. Adults appear to be the primary upstream dispersers in the system (Adams et al. 2000), so we assumed that the presence of both adults and juveniles indicated local reproduction and thus establishment. Because earlier investigators did not necessarily target juvenile fish, we did not distinguish between the presence of only mature fish and reproducing populations in the historical data. We only discuss changes in distribution limits greater than 0.6 km, as smaller differences are probably more indicative of the spatial sampling scale than of meaningful changes in distributions.

The lack of patchiness among sites in our recent brook trout presence/absence data suggests that the level of sampling effort was adequate for defining the distributions of reproducing brook trout populations (see Discussion). Because our sampling had longer, and in some streams more closely spaced, sites than Platts', our probability of detecting brook trout was higher than his. However, the agreement in distribution limits in many streams suggests that his sampling adequately identified upstream distribution limits. Because we had a higher probability than did Platts of detecting brook trout near their upper distribution limits, any errors resulting from differences between methods should have led to overestimation of invasion and distribution expansion.

Results

We observed brook trout in 11 of the 17 streams (Table 1). Upstream distribution limits remained stable (no change > 0.6 km) in 8 streams containing brook trout and in 5 of the 6 streams lacking them (i.e., we found no brook trout in the latter set; Figure 1). In the remaining 4 streams, the distribution limits expanded 1.9-3.1 km upstream. Invasion was evident in 3 of the 4 streams where

distributions expanded but was more restricted than expansion in each case (Figure 2). Tyndall Creek was the only stream invaded that lacked brook trout in 1971–1972. In Curtis Creek no invasion was evident, and about 1 km of the range expansion may be attributable to differences in sample site locations between surveys.

In 4 of the 11 streams containing brook trout, the potential for invasion was limited by natural barriers to upstream migration that were within 1 km of the 1970s distribution limits (Figure 2). Adult brook trout distributions extended to one barrier in 1971 and to two more in 1996. Of the 7 brook trout streams lacking obvious dispersal barriers, brook trout distributions remained essentially unchanged in 3 and expanded upstream 1.9– 3.1 km in 4.

Elevations at the upstream distribution limit of brook trout ranged from 1,207 to 1,792 m (median = 1,654 m). Most range expansion and invasion occurred in the higher-elevation streams within the South Fork drainage (Figures 1, 2), and the three streams where we documented invasion were among the four with the highest brook trout distribution limits.

On a shorter time scale, brook trout distributions were virtually unchanged in the Little Weiser River and Dewey Creek between 1993 and 1997. No waterfalls or steep channel slopes appeared to prevent upstream dispersal beyond the 1993 distribution limit in either stream. Bull trout were the only fish upstream in both cases (Adams and Bjornn 1997).

Discussion

The minimal invasion over 25 years in most of the streams indicates that brook trout invasion is not continuously progressing throughout much of the drainage. Any bias between the recent and historic fish surveys should have led to overestimating distribution expansion (see Methods); thus, it is conservative to conclude that invasion was not extensive over the 25-year interval. However, invasion in three streams also illustrates that it can continue many decades after introduction. Measurable expansion of distributions occurred in several instances where mature brook trout were found upstream of previous limits but had not established reproducing populations that we could detect. Because upstream distribution limits did not recede in any streams, we suggest that the distribution limits were probably not fluctuating upstream and downstream over the years, as did both native brook trout and nonnative rainbow trout



FIGURE 2.—Amounts of distribution expansion and invasion by brook trout in tributaries of the South Fork Salmon River (SFSR), Idaho, since Platts' 1971–1972 surveys or the earliest other survey. Kilometer 0 represents the upstream distribution limit of brook trout from the earliest survey or, if no brook trout were found, the confluence with the SFSR. Asterisks indicate streams lacking brook trout in 1996. Streams are listed in order of increasing elevation at the confluence with the SFSR. Elevations (m) of upstream brook trout distribution limits are indicated on the right.

limits in the Smoky Mountains (Strange and Habera 1998).

Alternative patterns of invasion may occur in the drainage. Invasion may occur in pulses (Behnke 1992) when conditions are suitable, and newly established distributions are subsequently maintained (Moyle and Light 1996). Conversely, when factors that inhibit invasion in a stream are altered, a long period of slow invasion may resume. Adequate historic data were not available to assess physical or biotic changes that may have contributed to the recent invasions in three streams.

While natural dispersal barriers clearly limited invasion in some streams, the absence of invasion in other streams where no evident barriers existed indicates that factors other than dispersal ability limits invasion in some streams. However, in the latter streams, invasion could resume if conditions change. One approach to managing brook trout invasions has been to construct migration barriers (Thompson and Rahel 1998), sometimes without a prior understanding of whether or not the invasion has stalled. If an invasion is limited by factors other than dispersal, then barriers may be unnecessary and therefore an inefficient use of resources. More importantly, a barrier that constrains native fish populations (Gowan and Fausch 1996; Dunham et al. 1997) may make them less resilient or resistant to environmental variation and biotic interactions (Rieman and Dunham 2000). Native populations that previously inhibited invasion via biotic resistance (Griffith 1988; Baltz and Moyle 1993) could then become more vulnerable to invasion by any brook trout that pass the barrier, whether by natural or human means (e.g., via barrier failure or human endeavor; Behnke 1992; Thompson and Rahel 1998).

Invasion and range expansion were concentrated in the higher-elevation streams. While the pattern may be related to water temperature or hydrologic regime, other factors potentially confound such an interpretation. For example, the higher-elevation tributaries were typically smaller than those farther downstream. Rich (1996) found that, other factors being equal, brook trout were more likely to occur in smaller streams than large ones. Assessing how physical and biotic factors influence invasions is clearly an important issue but is beyond the scope of this study.

Because recent invasions have occurred and are evidently ongoing in some instances, managers must not become complacent about the security of native populations upstream of brook trout (Paul 2000). Yet factors other than dispersal limitations have evidently inhibited invasion in many South Fork Salmon River tributaries and are likely to influence the potential for future invasions and the ultimate implications for native fishes. Rather than operating under an assumption that brook trout will inevitably invade all accessible stream habitat, we should focus on understanding the factors that limit their invasion (Moyle and Light 1996). An improved understanding of the invasion process will allow us to better prioritize actions to minimize invasions and thereby become more efficient in our attempts to restore and manage native populations (Adams et al. 2001; Kruse et al. 2001).

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