Transactions of the American Fisheries Society 129:623–638, 2000

Movements of Nonnative Brook Trout in Relation to Stream Channel Slope

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Abstract.—We provide new insights on the ability of naturalized brook trout *Salvelinus fontinalis* to ascend steep, headwater streams in the western USA. We tested hypotheses that upstream movements by brook trout are limited or absent in reaches of steep streams and are more prevalent and longer in gradually sloping streams. We compared brook trout movements in headwater streams in Idaho at sites with varied channel slopes (averages of <1–12%). After eradicating fish from 200-m stream sections, we assessed immigration of marked fish into these sections. Contrary to our hypothesis, upstream movements were more prevalent than downstream movements during the summer, even in steep streams. Marked brook trout ascended stream channels with slopes of 13% that extended for more than 67 m and 22% for more than 14 m; they also ascended a 1.2-m-high falls. Nearly vertical falls, rather than steep slopes per se, apparently inhibited upstream movements. Our hypothesis that upstream movements would decrease with increasing channel slope was partially supported; fish did not move as far upstream in steep as in gradual sites, and upstream movements through steep channels were dominated by larger fish (>135 mm total length). Immigration by marked fish smaller than 95 mm was uncommon in all sites. Slopes up to 13% do not ensure against upstream dispersal, although other mechanisms may inhibit brook trout invasion in steep channels. In very steep channels, fewer dispersing fish and slower upstream movement rates may increase the time required for successful invasion and reduce its likelihood of occurrence.

Brook trout *Salvelinus fontinalis,* a char native to eastern North America, have been introduced to cold water streams and lakes throughout western North America (MacCrimmon and Campbell 1969; Meehan and Bjornn 1991) and have successfully invaded many waters beyond where they were intentionally stocked. They are presently the second most widely distributed salmonid species (native or introduced) in the interior Columbia River basin, surpassed only by introduced rainbow trout *Oncorhynchus mykiss* (Thurow et al. 1997). Brook trout have been implicated in reducing populations of some native salmonids (Fausch 1989; papers in Howell and Buchanan 1992; Leary et al. 1993; Dunham et al. 1999), as well as other vertebrate and invertebrate fauna (Dawidowicz and Gliwicz 1983; Bradford 1989; Bechara and Moreau 1992; Bradford et al. 1993).

Use of barriers to prevent brook trout invasion or reinvasion of streams is increasingly prevalent, but not, perhaps, always justified. Recently, concerns over declines in and local extirpations of bull trout *S. confluentus* and cutthroat trout *O. clarki* have led to expensive attempts to eradicate brook trout from streams and lead to the construction of barriers to prevent their reentry (Dambacher et al. 1992; Thompson and Rahel 1998). Artificial barriers have also been considered as a means to prevent brook trout from invading places they have not previously occupied (Kershner 1995; Thompson and Rahel 1998), even though the ability to predict future invasions is limited. Barriers may hinder movements of native fishes, however, which could disrupt adaptive migration and dispersal patterns (Gowan et al. 1994) and exacerbate declines in native fishes by increasing population fragmen-

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Received October 5, 1998; accepted October 13, 1999

tation and isolation (Young 1995b; Dunham et al. 1997). The virtue of constructing dispersal barriers to prevent invasion rests on the assumptions that (1) dispersal is inevitable, and (2) if dispersal occurs, invasion will follow. Conversely, assuming that stream segments upstream of steeply sloping reaches are immune to invasion assumes that brook trout will not ascend steep reaches.

Managing brook trout invasions in a manner that maximizes benefits to native fish populations will require better understanding of the mechanisms of invasion, including improved understanding of brook trout dispersal and its role in limiting invasions. Invasion requires both dispersal and establishment of a self-sustaining population. Either or both can limit the invasive ability of an organism in a given habitat (D'Antonio 1993; Hengeveld 1994). Closer attention to dispersal processes is necessary to determine under what conditions, or to what degree, dispersal actually limits the rate and extent of an invasion (Johnson and Carlton 1996). We use the term ''dispersal'' to describe one-way movements away from a home range (Lidicker and Stenseth 1992) or movements that lead to reproduction away from the fish's natal habitat. Other types of movements include those within a home range, round-trip migrations, or exploratory movements.

Little has been reported about brook trout movements and dispersal in steep, mountainous streams. Numerous studies have evaluated brook trout movements, but nearly all were conducted in gradual (≤2%) to moderate (>2 to <6%) stream slopes (Saunders and Smith 1955; reviewed in Gowan and Fausch 1996b). Although many of the studies included intrinsic biases against finding extensive movements (Gowan and Fausch 1996b), in most cases some fish were found farther than 3.2 km from release locations. Several authors concluded that movement was an important demographic process in the populations they studied (e.g., Flick and Webster 1975; Gowan et al. 1994). For example, in a gradually sloping stream in New York, up to 33% of brook trout marked at one location each year were recaptured 6.6 km upstream (Flick and Webster 1975). We know of only one published study of brook trout movements in steep streams: Moore et al. (1985) documented extensive brook trout movements in streams with slopes of 8–18% within the Great Smoky Mountains National Park. Marked brook trout moved more than 900 m upstream and downstream during the 4-year study, and several fish moved between tributaries. However, behaviors exhibited in southern populations cannot necessarily be extrapolated to western populations (Adams 1999:22–23).

Questions regarding dispersal abilities of brook trout arise, in part, from the observed distribution of the fish. In the western United States, brook trout are frequently most abundant in gradual to moderate channel slopes (Chisholm and Hubert 1986; Fausch 1989). Fausch (1989) hypothesized three mechanisms to explain why, in the presence of cutthroat trout, brook trout are less abundant in channels with steep slopes (>7%) than in those with more gradual slopes: (1) brook trout are poorer swimmers than cutthroat trout and would have difficulty ascending steep streams, (2) brook trout may not have had enough time to disperse into the steeper reaches, which are usually near the headwaters of streams, and (3) in steep streams, age-0 brook trout may compete poorly with cutthroat trout or may have low survival rates irrespective of the presence of the latter. He discounted the second mechanism because most brook trout were stocked 50–100 years ago, but considered the first and third to be plausible.

In this paper we report on an experiment designed to provide insight into Fausch's hypothesis that poor swimming ability limits brook trout prevalence in steeply sloped stream channels. As our primary objective, we tested the following hypotheses: (1) upstream movements are more prevalent and longer in gradually sloping than in steeply sloping streams, (2) brook trout will not ascend channels with slopes steeper than 8%, and (3) if brook trout do ascend steep streams, then within such streams, downstream movements are more prevalent and longer than upstream movements. Secondary objectives included (1) characterizing short-term barriers to brook trout movements, (2) identifying which brook trout size-classes moved the most, and (3) exploring how homing (considered a motivating factor) influenced movements in one steep stream. We examined these objectives by selecting study sites with average slopes that were gradual (<1% to 2%) or steep (6–12%), removing fish from 200-m-long stream sections, and comparing immigration of marked and unmarked brook trout from neighboring stream sections into the removal sections.

Study Area

The six experimental sites were in four tributaries of Johnson Creek, in the South Fork (SF) Salmon River drainage, Valley County, Idaho (Figure 1). We refer to a previously unnamed, north-flowing tributary of Sheep Creek as Hillbilly

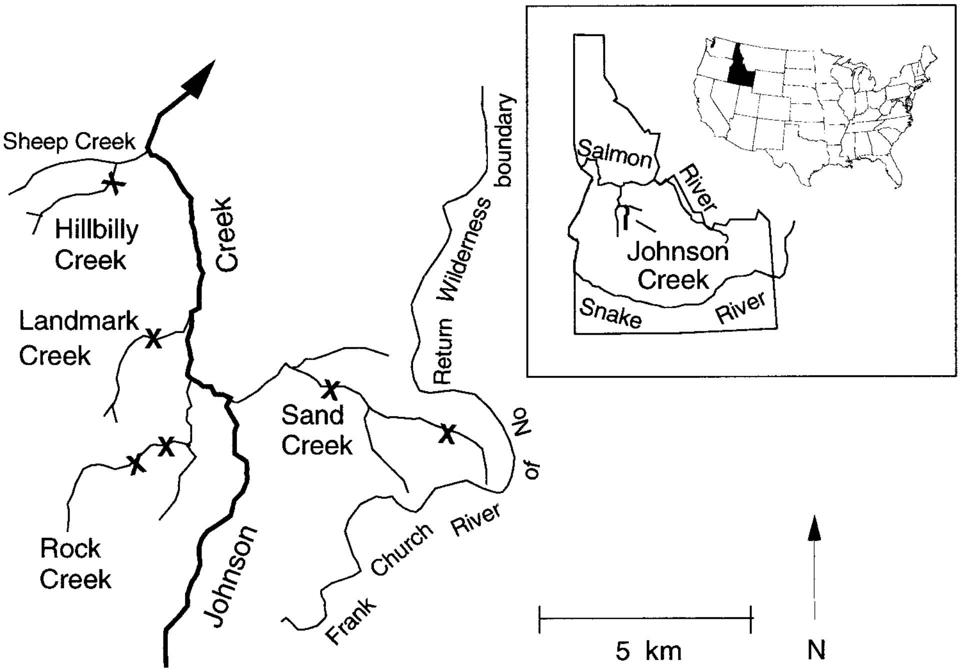

FIGURE 1.—Experimental sites **(X)** in the Johnson Creek drainage, Idaho. Hillbilly Creek was previously unnamed.

Creek. The two Sand Creek sites were about 5 km apart; the two Rock Creek sites were contiguous. Sites were chosen based on channel slope, sufficient length of relatively uniform channel morphology, and adequate brook trout densities. Stocking records indicate that brook trout were stocked in the SF Salmon River drainage from 1932 to 1972 (Idaho Department of Fish and Game, unpublished data), although unrecorded stocking presumably occurred earlier and perhaps later.

The study area was within the Idaho batholith (a granitic intrusion), where streams tend to have relatively high levels of fine sediments and low fertility (Platts 1979). All experimental sites were in small, low-conductivity streams with varying average channel slopes (1–12%; Table 1; Figure 2). At both the Hillbilly Creek and upper Sand

TABLE 1.—Stream channel and valley characteristics and thalweg lengths at the six experimental sites, Valley County, Idaho. Width (refers to wetted channel widths) and channel are averages for the entire site. Predominant substrates and valley confinement were visually estimated. Water conductivity, wetted stream width, and stream discharge were measured between late August and early September 1996, a period of low stream flows. Discharge was estimated by the midsection method (Harrelson et al. 1994) in each site. Stream order was determined by the Strahler method based on blue-line streams of U.S. Geological Survey topographic maps (1:24,000).

Stream site	Channel slope (%)	Channel pattern	Stream order	Width (m)	Low flow discharge (m^3/s)	Conductivity (μS/cm)	Elevation (m)	Reach length (m)	Predominant substrates[a]	Valley confinement[b]	Riparian habitat[c]
Lower Sand	<1	Tortuous	2	4.0	0.096	54.8	2,089	606	S, G	V	ME
Upper Rock	1	Meandering	2	3.3	0.035	40.4	2,060	603	G, S	L–M	FO, ME
Landmark	2	Meandering	2	2.6	0.015	30.9	2,039	622	S, G, C	M	FO
Lower Rock	6	Straight	2	3.1	0.031	39.8	2,033	455	G, C, B	M	FO
Upper Sand	9	Straight	1	2.9	0.038	60.6	2,213	602	C, G, B	M	CC
Hillbilly	12	Straight	1	2.5	0.012	37.7	1,981	403	B	H	BU

[a] Substrate types include sand (S), gravel (G), cobble (C), and boulder (B).
[b] Valley confinement types are very low (V), low (L), moderate (M), and high (H).
[c] Riparian types are meadow (ME), forest (FO), clearcut (CC), and burned forest (BU).

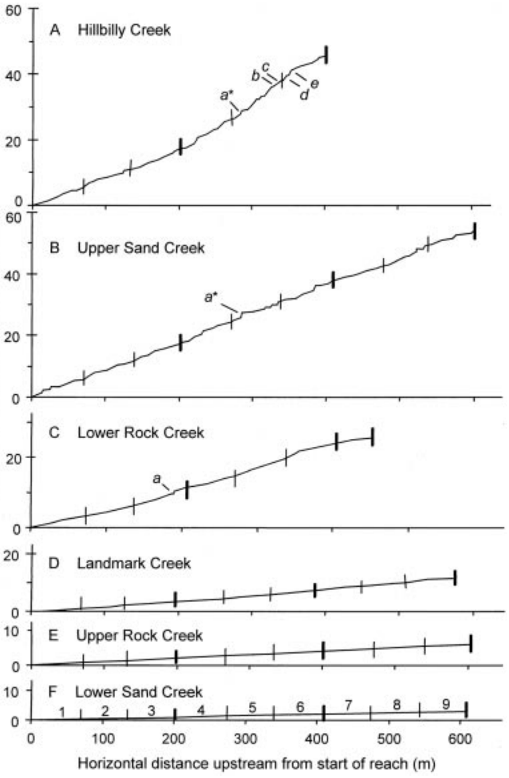

FIGURE 2.—Schematic profiles of experimental sites drawn approximately to scale in order of decreasing average channel slope (panels **A**–**F**). Large vertical steps are visible, but small steps are obscured by gradients measured over longer distances. Italicized, lowercase letters refer to potential dispersal barriers (see text). Asterisks indicate the uppermost locations where we saw marked fish that had been released downstream. Vertical lines indicate section (bold) and subsection breaks, and the lower Sand Creek profile (F) includes subsection numbers for reference. The sites in Hillbilly and lower Rock creeks lacked complete upstream marking sections (see text).

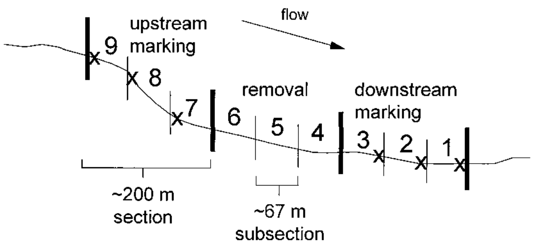

FIGURE 3.—Schematic diagram of a typical experimental site showing subdivisions into marking and removal sections (bold vertical lines) and numbered subsections (vertical lines). Locations where fish from each marking subsection were released after marking are shown **(X)**.

Creek sites, channel slopes exceeded 18% for at least 15 m. A 0.7-m-high falls (Figure 2C, step *a*) was just downstream of the removal section (see Methods) in the lower Rock Creek site.

The high elevation (average 2,069 m) forests were dominated by lodgepole pine *Pinus contorta,* and riparian vegetation along the sites varied from grass and forbs to conifer forests. The sites in Rock and Landmark creeks were surrounded primarily by lodgepole pine forests. At the upper Sand Creek site, the creek flowed through the middle of an approximately 35-year-old clear-cut with no streamside riparian vegetation buffer. The lower Sand Creek site was in an open meadow, where undercut banks provided most of the available cover. A dirt road paralleled the stream at the lower site, and fishing pressure was probably the highest at this site, although we never observed anglers at any site. The conifer forest surrounding the Hillbilly Creek site burned several years before the study.

Methods

Experimental design and field methods.—Our typical study site consisted of three 200-m-long sections: a ''removal section'' bounded by an upstream and downstream ''marking section'' (Figure 3). Each section was further subdivided into three subsections, allowing us to refine our estimates of distances that fish moved. Subsections were numbered consecutively beginning downstream (those numbers are noted in parentheses throughout the paper). We permanently removed all the brook trout that we could capture from the removal sections. In each marking subsection (SS), fish were captured, marked, and returned to the subsection where they were captured. Fish were released at the end of the subsection farthest from the removal section (Figure 3).

Exceptions to the above design occurred in the Hillbilly Creek and lower Rock Creek study sites. The upstream marking section of the lower Rock Creek site had only one subsection (SS 7), about 50 m long, because the channel slope flattened abruptly upstream. However, because the two Rock Creek sites were contiguous, movements could be assessed over both sites, allowing detection of movements over a longer distance. We had no upstream marking section in Hillbilly Creek because we found no brook trout upstream of step *d* (Figure 2A) in the uppermost removal subsection (SS 6). Due to the relatively low brook trout density, we captured few brook trout from the downstream marking section of Hillbilly Creek. Therefore, we uniquely marked fish from the removal section and translocated them to the downstream end of marking SS 3 (67 m downstream of the removal section), releasing them with the fish originally captured in SS 3.

We captured fish by electrofishing between 22 July and 8 August, 1996. Subsections being sampled were isolated with block nets, and three or four electrofishing passes were made in each subsection using one or two Smith–Root, backpack electrofishers. During first passes we used voltage settings as high as 1,100 V and 50 Hz, with a 1-ms pulse width, as recommended to reduce incidence of spinal injuries in low-conductivity waters (Fredenberg 1992). A frequency of 60 Hz was sometimes used in subsequent passes to improve capture efficiency. Higher settings were often used during the final pass in removal sections. At least 40 min elapsed between successive passes.

Before being marked, fish were held in perforated buckets in the stream until all electrofishing passes were complete (3–14 h). After fish from the marking sections were sedated in a solution of tricaine methanesulfonate (MS-222, Finquel), they were measured for total length (TL) with caudal fin compressed, given adipose fin clips, and marked with injections of visible implant fluorescent elastomer (Northwest Marine Technology, Inc.; Bonneau et al. 1995). Fish from removal sections, except for those in Hillbilly Creek that were moved to the downstream marking section (see above), were killed with an overdose of MS-222 and measured.

Whenever possible, unique marks (red or orange marks injected in the adipose eyelids or maxillaries and in the dorsal, caudal, or neither fin) identified the subsection where a fish was captured (Adams 1999). We were able to consistently mark the adipose eyelids or maxillaries of fish 50 mm or longer, but we could consistently mark fins only in fish exceeding 75 mm. In three trials, we quantified short-term survival and mark retention in samples of 24–25 fish (65–210 mm TL) by holding fish in perforated buckets in the stream for 21–25 h after marking.

Movements and recolonization were assessed by night snorkeling in removal subsections at approximately logarithmic intervals (2, 4, 8, 16, 32, and 64 nights after fish removals; as recommended by Sheldon 1984) between 24 July and 2 October 1996 and once the following summer (August 1997; see Adams 1999 for exact dates). The intervals between snorkeling differed slightly among sites for logistical reasons. The dive for night 32 at the lower Rock Creek site was canceled because the water was too shallow for effective snorkeling. One observer (S. Adams) conducted all the snorkeling samples by moving slowly upstream with an underwater flashlight, identifying fish and marks and estimating fish lengths to the nearest 10 mm. A bank observer, remaining several meters downstream, searched by flashlight for fish in shallow water (Bonneau et al. 1995).

Channel slopes, measured with a clinometer in gradually sloped sites and with a rod and level in steeply sloped sites, were averaged over both sites and subsections and, in some instances, over shorter stream lengths. We measured waterfall heights from water surface to water surface and subsection lengths along the thalweg.

Analyses.—We calculated initial minimum densities of fish by section and, when possible, by subsection. Densities were calculated from the actual number of fish captured during electrofishing. Because some fish undoubtedly eluded capture, actual densities were probably higher.

Most statistical analyses of fish movements were restricted to or repeated with data for brook trout 95 mm or longer for two reasons. First, most (91%) of the fish held to determine short-term survival, were 95 mm or longer. Although all seven smaller fish survived the 21-h period, we could not completely discount the possibility of high mortality among the smaller fish marked. Second, although we did capture many fish less than 95 mm by electrofishing and observe them while snorkeling, both techniques may have been slightly biased toward detection of fish 95 mm or longer. In most analyses, we used numbers, rather than percentages, to describe movements of marked fish because (1) we generally ‘‘resighted’’ (sighting of marked fish) a small percentage of the fish that we marked (Table 2), (2) the percentage of fish moving was apparently unrelated to the number marked (Table 2), (3) numbers of fish marked were similar upstream and downstream of removal sections, and (4) fish densities were not correlated with channel slope (Figure 4).

We assessed upstream versus downstream movements by comparing data on resightings (in removal sections) of fish marked upstream versus downstream. Calculating the total number of marked fish that moved into the removal reaches from downstream was not possible because marked fish were not individually identified. That is, usually we were unable to distinguish among individuals of a given mark group that were ob-

TABLE 2.—The number of brook trout (≥95 mm) that were marked and released in the downstream (3) and upstream (7) subsections (which were adjacent to the removal sections) and the range of percentages of those fish later observed in the removal sections on different nights. For Hillbilly Creek, we distinguish between fish originally captured in subsection (SS) 3 and the translocated fish, although all were released in SS 3. Streams are listed in order of decreasing channel slope. In the Hillbilly and upper Sand sites, we observed no marked fish that had moved upstream through the entire removal section.

	Originating downstream		Originating upstream[a]	
Site	Number of marked fish released in SS 3	Fish observed in removal section (%)	Number of marked fish released in SS 7	Fish observed in removal section (%)
Hillbilly (fish originally from removal section)	25	20–52		
Hillbilly (fish from marking SS 3)	13	8–38		
Upper Sand	14	14–28	20	0–5
Lower Rock	56	2–5	8	0
Landmark	34	12–18	33	0
Upper Rock	13	0–13	14	0
Lower Sand	10	10–60	16	0–6

[a] No data for Hillbilly Creek because there was no upstream marking section.

served iteratively during successive sampling periods, although we could sometimes identify specific fish based on a combination of marks, fish size, and unusual features. At all sites we could distinguish among marked immigrants from upstream based on unique features because few individuals were resighted. However, for fish originating downstream, we made minimum and maximum estimates of the numbers of marked immigrants. Minimum estimates included marked immigrants observed on the night with the most observations of marked fish for each site (the ''peak night'' for the site) plus marked fish observed on other nights that were known to be different from those observed on the peak night. Maximum estimates included observations of marked fish summed over all sampling nights, excluding any repeat observations of fish individually identified by unique features. Thus, some fish were probably counted more than once in maximum estimates. To avoid introducing a size bias in analyses of immigrant body lengths, we did not identify additional fish as unique based on length.

We conducted a separate analysis to determine

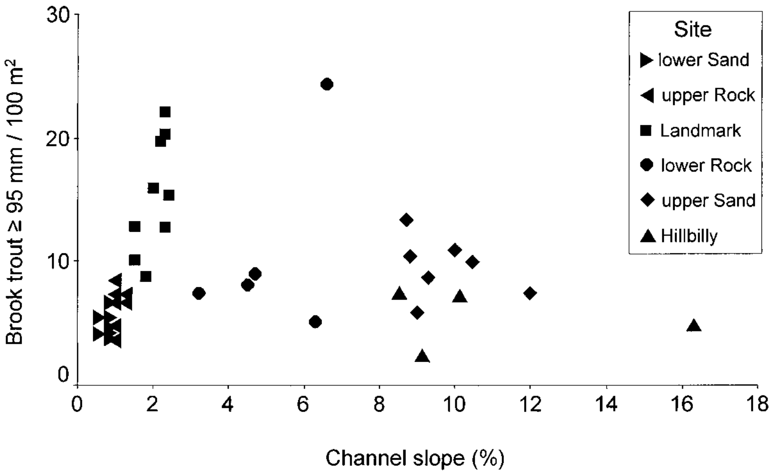

FIGURE 4.—Preexperimental densities (fish/100 m²) by subsection channel slope for brook trout 95 mm total length or longer captured in each marking subsection; we calculated a combined density for the entire removal section in every site (except Landmark Creek, for which the density of each subsection is shown). Two points each from the lower Sand Creek and upper Rock Creek sites were shifted to the left and right, respectively, for clarity.

whether the number of ''total immigrants'' (both marked and unmarked brook trout) in the upstream removal subsection, relative to the downstream subsection, was related to channel slope. The analysis also further addressed the question of whether downstream movements exceeded upstream movements in steep streams. We hypothesized that, if fish recolonizing the removal reach originated equally from upstream and downstream, the upstream removal subsection (SS 6) should contain about the same number of immigrants as the downstream removal subsection (SS 4). However, if fish were immigrating primarily from downstream, SS 6 would contain fewer immigrants than SS 4 because marked fish did not ascend the length of the removal reaches in the steepest sites.

We made the conservative assumption that all unmarked fish observed during the first night of observation were fish that evaded capture during electrofishing and were not immigrants. Therefore, the peak-night estimate of total immigrants in a subsection was calculated as the greatest number of brook trout observed in the subsection during any night of observation minus the number of unmarked brook trout observed in the subsection on the first night of observation. We computed the difference between the peak immigrants total in the lower removal subsection (SS 4) and the peak in the upper removal subsection (SS 6) and regressed the difference on site slope using simple linear regression.

Sizes of immigrants.—We used chi-square to test for differences between the length distribution of marked fish immigrating into removal sections and the length distribution of all fish marked. Proportions of all fish marked in each length category ($<$95, 95–134, and $>$134 mm) were used to calculate expected frequencies of marked immigrants. We limited the analysis to observations made in 1996 to minimize bias due to fish growth. Chi-square tests were conducted separately for fish pooled across the three steeply sloped and across the three gradually sloped sites. Tests were repeated without the smallest ($<$95-mm) size category.

Results

Brook trout were the only fish species at four of the sites. At the other two sites, Sand (lower) and Hillbilly creeks, rainbow trout were present at densities ranging from 0.2 to 11.5 fish/100 m^2 (median = 3.58 fish/100 m^2). Brook trout densities estimated during the initial electrofishing were highly variable within and between sites ranging from 3.6 to 128.3 fish/100 m^2 (median density = 15.9 fish/100 m^2). Densities were not significantly different between sites with steep versus gradual slopes for all sizes of fish (*t*-test: $P = 0.808$, $N = 6$) or for fish 95 mm or longer ($P = 0.810$, $N = 6$). Likewise, brook trout density by subsection was not significantly correlated with percent channel slope for all sizes of fish ($r = -0.0901$, $P = 0.586$, $N = 39$) or for fish 95 mm or longer ($r = -0.0240$, $P = 0.884$, $N = 39$; Figure 4).

Short-term fish survival and mark retention were adequate for assessing the objectives of the study. Survival of the 72 marked fish held overnight was 98.6%. Overnight loss rates of adipose eyelid marks ranged 2–13%, dorsal fin marks 0–27%, and caudal fin marks 5–8%. Nearly all fish were given two adipose eyelid or two maxillary marks, so the probability of losing both marks was less than 2%; in addition, adipose fin clips further identified fish as marked. For an individual that lost a fin mark, we conservatively assumed that the fish was originally captured in the marking subsection closest to the removal section.

Upstream Movements

Brook trout ascended steeper slopes than we had hypothesized. Marked brook trout moved upstream through an entire subsection with an average slope of 13% but did not move completely through two other subsections with 10% and 17% slopes. Marked fish also ascended a 14.5-m length of stream with a 22% slope and a 23-m length with 16% slope.

Minimum estimates of the number of fish moving upstream were generally comparable between steep and gradual channel slopes. Only in the sampling interval closest to night 5 did we find that significantly more marked fish had moved upstream in gradual than in steep sites (*t*-test: $P = 0.007$ after adjustment for multiple, nonindependent comparisons; Rice 1989). However, we infer that in sites with gradual slopes, marked fish moved through and beyond the removal sections, whereas in the two steepest sites, this almost certainly did not occur (see below). Thus, more fish than we estimated may have actually moved upstream in the gradual than in the steep sites.

Although upstream movement of fish was prevalent in all sites, marked fish did not move upstream as far in steep as in gradual sites. At the gradual sites and the lower Rock Creek site (6% slope), some marked fish moved upstream at least through the entire removal reach ($>$200 m). In Hillbilly Creek (12% slope), no marked fish were

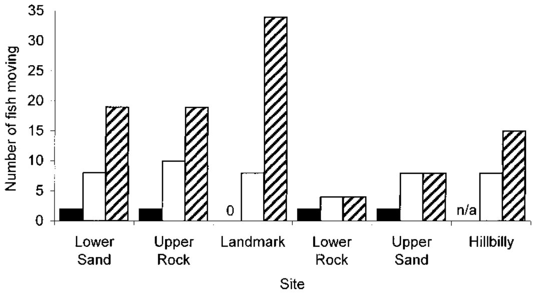

FIGURE 5.—Resightings (number of marked fish of all sizes observed) of fish in removal sections of each site that had moved downstream (closed bars) and minimum (open bars) and maximum (shaded bars) estimates of resightings of fish that had moved upstream, as observed in 1996. See text for explanation of estimates. Sites are in order of increasing channel slope from left to right.

resighted farther than about 150 m upstream from their point of release. In the two steepest sites, no fish released in the downstream marking section were observed farther than halfway up the removal section. Thus, we infer that fish did not move upstream through, and beyond, the removal sections in the two steepest sites.

Upstream versus Downstream Movements

Contrary to our hypotheses, marked fish moved upstream more than downstream, even in steep sites. At each site, 66–100% of resightings were fish marked within 200 m downstream. The minimum number of observations of immigrants 95 mm or longer that were marked downstream was significantly greater than the number marked upstream at all sites except Hillbilly Creek, which lacked an upstream marking section (paired *t*-test: $P = 0.004$, 4 df; Figure 5). The numbers of fish 95 mm or longer initially marked downstream and upstream of removal sections were not significantly different (paired *t*-test: $P = 0.627$, 4 df). At all sites, the percentage of fish marked in the nearest downstream subsection (SS 3) and resighted in the removal section greatly exceeded the percentage of fish marked in the nearest upstream subsection (SS 7) and later resighted in the removal section (Table 2). The results are unchanged, but more complicated to present, when fish from all marking sections are included (see Adams 1999: Chapter 2 for results with all marked fish).

Patterns of recolonization by both marked and unmarked fish supported the conclusion that at the steepest sites, upstream movements were shorter than at gradual sites but still predominated over downstream movements. We almost always observed more unmarked than marked fish in removal sections. However, in the two steepest sites, the numbers of fish in the upper removal subsections (SS 6) did not increase after the first night, and numbers in the middle subsections (SS 5) increased less than in the lower subsections (SS 4). Conversely, in the three gradual sites, SS 6 had as much or more recolonization than SS 4 (Figure 6). The regression of the difference between peak

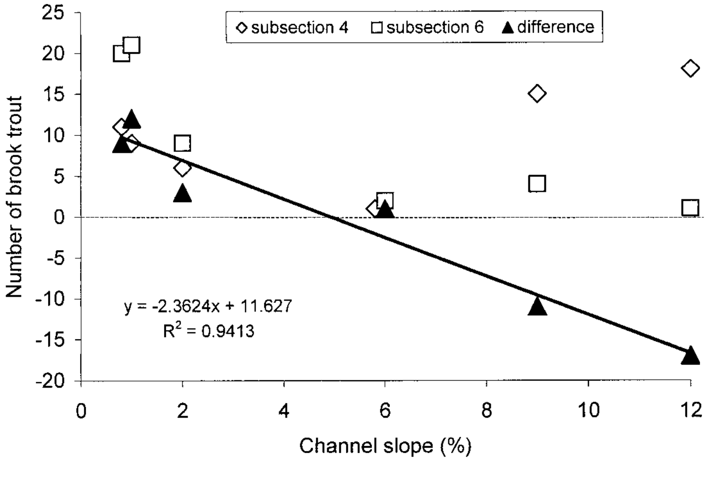

FIGURE 6.—Differences (solid triangles) between peak numbers of brook trout immigrants to upper and lower removal subsections (subsection 6 minus subsection 4). The linear regression line of the differences in peak numbers of immigrants between the subsections on channel slope of the site is shown. Only fish 95 mm total length or longer observed in 1996 were included. The Hillbilly Creek point includes "homing" fish (see text), but the regression was similar with those fish excluded.

numbers of immigrants to SS 4 minus peak numbers of immigrants to SS 6 on channel slope was highly significant ($R^2 = 0.94$, $P = 0.001$; Figure 6). At the upper Sand Creek site, the limited recolonization of SS 6 by unmarked fish further suggests that little downstream movement occurred during the summer; if downstream movements exceeding 200 m were prevalent, we expect that unmarked brook trout from upstream would have immigrated into SS 6.

Characteristics of Short-Term Barriers

Nearly vertical steps or falls rather than steep slopes per se apparently inhibited upstream movements by brook trout. At the upper Sand Creek site, we saw one brook trout (210 mm TL) that had ascended a 1.5-m high, complex falls (Figures 2B, step *a*; 7, upper). The falls had a 0.5-m-high upper step where the water passed over and through boulders and coarse and fine woody debris and a lower step of 0.7 m over boulders and bedrock. A small, high-velocity ''pool'' less than 0.2 m deep separated the two steps. In Hillbilly Creek, no marked fish were found upstream of a 1.1-m vertical falls over a large log (Figure 2A, step *a*). At the lower Rock Creek site, marked brook trout as small as 90 mm ascended a 0.7 m-high, nearly vertical falls over boulders and bedrock (Figure 2C, step *a*).

Based on initial locations, we suspect that during some periods the fish can ascend stream features they did not ascend during this study. We initially captured brook trout upstream of both falls described above, so we assume that some fish had ascended these and other large steps to colonize upstream areas. Due to the small size, steep slope, and remote location of the two steepest sites, we find it unlikely that fish were stocked upstream of the falls. Before our experiment, the upper distribution limit of brook trout in Hillbilly Creek was the middle of a series of four bedrock chutes (Figure 2A, steps *b*–*e*). Brook trout occurred upstream of two chutes with slopes of 26% (10.5 m long) and 23% (5.3 m; Figure 7, lower) but not upstream of chutes with slopes of 35% (3.8 m) and 23% (9.8 m). Each chute consisted of a series of steps (0.4–0.6 m high) interspersed with fast, shallow runs (most <0.3 m deep). The three downstream chutes each had a pool more than 0.5 m deep at the base.

We saw no evidence that brook trout moved upstream over low-flow obstacles during the high streamflows in spring 1997. During snorkeling in August 1997, we did not see marked fish that had ascended the largest steps in Sand (upper site) and Hillbilly creeks, nor was there any indication that unmarked fish had ascended the large step (Figure 2A, step *a*) in Hillbilly Creek.

FIGURE 7.—(Upper) Nearly vertical 1.5-m falls in Sand Creek (upper site), Idaho (see Figure 2B, step *a*), ascended by a marked 210-mm brook trout during summer 1996. (Lower) Bedrock chute in Hillbilly Creek, Idaho (Figure 2A, step *b*), with seven steps dropping a total of about 2.8 m over a distance of 10.5 m. Although recolonizing brook trout did not ascend to the bottom of the chute during the study, brook trout were initially found upstream of this and another similar chute.

Movements Longer than 200 m

Several observations indicated that some brook trout moved farther and faster than the experiment was designed to detect. After we marked fish in the downstream marking section of the lower Sand Creek site, a block net washed out overnight. The next day, we electrofished the two remaining sections and captured 22 brook trout marked downstream the previous day (we released them in downstream marking subsection 3). Four brook

TABLE 3.—Summary of chi-square analyses comparing immigration by marked brook trout of three total length (TL) categories. Observed frequencies represent marked immigrants sighted in removal sections, and expected frequencies are based on lengths of all brook trout marked at each site. Data were pooled across the three gradually sloped and across the three steeply sloped sites. Analyses were repeated without the smallest size-class.

Size class (mm)	All fish sizes			Fish ≥95 mm TL		
	Observed	Expected	χ^2	Observed	Expected	χ^2
Gradually sloped (≤2%) sites						
<95	1	11.9				
95–134	15	10.1		15	17.9	
>134	10	4.0	21.25[a]	10	7.1	1.64
Steeply slopes (≥6%) sites						
<95	1	22.4				
95–134	10	7.2		10	21.7	
>134	22	3.4	122.7[a]	22	10.3	19.6[a]

[a] Significant: $P < 0.005$.

trout (91–122 mm) had moved 400–600 m upstream in less than 24 h. The smallest brook trout recaptured (75 mm) had moved over 65 m upstream. We recaptured more marked brook trout during electrofishing in the removal sections than we observed in those sections during any subsequent snorkeling period. We infer that either marked fish moved completely through the removal sections before our first snorkel period, as suggested by the rapid movement rates, or we overlooked many marked fish while snorkeling.

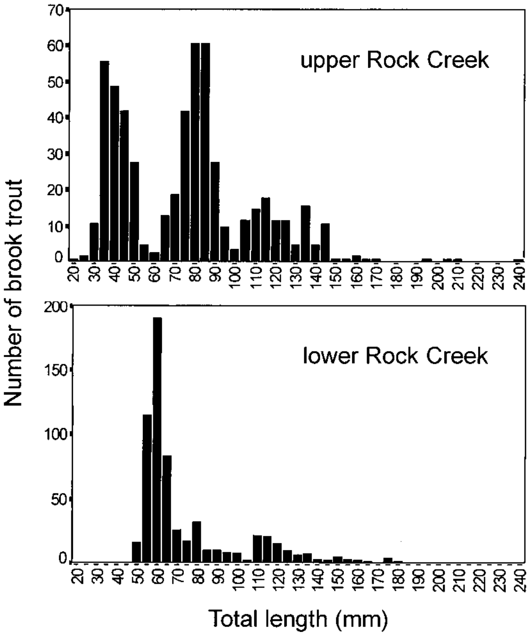

FIGURE 8.—Length frequencies of fish captured during electrofishing at the upper and lower Rock Creek sites, Idaho, in July and August 1996. The sites were contiguous, and a 0.7-m-high step separated the areas where most juvenile fish occurred in each. Note that vertical axes have different scales.

In Rock Creek, contiguous sites allowed us to detect fish movements over longer distances. At the upper Rock Creek site, 28% of all resightings were of fish marked farther than 200 m downstream. Those fish represent immigrants that would have been unmarked if we did not have an adjacent study site downstream. At the lower Rock Creek site, 21% of marked immigrants originated from farther than 500 m upstream.

Sizes of Immigrants

The larger fish predominated among the immigrants. In both gradual and steep sites, significant differences occurred between observed and expected distributions of marked immigrants in the three size-classes (Table 3). In each case, fewer marked immigrants than expected occurred in the smallest size-class. When only fish 95 mm or longer were considered, we found significant differences between observed and expected size distributions for the steep, but not for the gradual, sites (Table 3). The fish that ascended the 1.2-m step in Sand Creek (upper site) was one of the largest fish marked (all were <200 mm TL).

Differences in length distributions of fish between sites in Rock Creek (Figure 8) reinforce the observation of minimal dispersal by fish 95 mm or longer. Rearing areas in the adjacent lower and upper Rock Creek sites were separated by a 0.7-m-high falls (Figure 2C, step *a*). If young fish moved freely between sites, length distributions should have been similar between sites.

Homing

In Hillbilly Creek, a homing tendency appeared to influence fish movements. Higher percentages of translocated fish (i.e., those captured in the removal section and released downstream in marking SS 3) recolonized the removal section than did other fish that originated downstream (Table 2); thus, we assumed that the translocated fish were homing. On sampling nights 14 and 30, when the most resightings occurred, 38% of fish originally captured in SS 3 versus 52% of those translocated to SS 3 were resighted in the removal section. Although this was the steepest site, the translocated fish had the second highest percentage of any group of marked fish resighted in a removal section on a given night (Table 2).

Discussion

Upstream Movements in Steep Streams

We found that brook trout did ascend steep streams. During low summer streamflows, fish moved upstream through slopes at least as steep and long as 13% and 67 m and through steeper slopes over shorter distances. Although brook trout moved farther and in greater numbers through gradual slopes than through the steepest slopes studied, even at the steepest sites some moved upstream as much as 150 m (summer 1996). Fausch (1989) hypothesized that poorer swimming ability of brook trout, relative to cutthroat trout, may explain why brook trout are less prevalent in steep streams. Although, we do not have comparable data for cutthroat trout movements in steep streams, the ability of brook trout to ascend 13% slopes suggests that swimming ability, alone, does not explain why brook trout densities decrease in some streams as channel slopes become moderate to steep (Chisholm and Hubert 1986; Fausch 1989). Initial brook trout densities did not differ significantly between steeply and gradually sloping sites in our experiment, but we did not select sites randomly with respect to brook trout densities.

Brook trout have been documented in very steep streams elsewhere. In tributaries to the South Fork Salmon River, Idaho, brook trout occurred in the presence of native salmonids in channel slopes of 12–14% (Platts 1974). Allopatric populations have been documented in Idaho (Maret et al. 1997) and Nevada (Schroeter 1998) in slopes of 12–16%. Brook trout, in remnant populations restricted to headwater streams of the Great Smoky Mountains National Park, moved within channel slopes averaging 12–15% (Larson and Moore 1985). Our results suggest that nonnative brook trout in the western United States are also capable of colonizing such steep slopes from downstream. Within steep stream segments, however, brook trout tend to occupy habitats with gradual slopes (e.g., stair-stepped pools; Larson and Moore 1985; Adams, unpublished observations). Therefore, the specific configuration of channel slopes within segments and reaches probably influences the susceptibility of steep streams to brook trout invasion.

Brook trout ascended larger steps than we expected, but nearly vertical falls within steep stream sections appeared to inhibit upstream movement. The height of a step required to inhibit upstream movement during summer low flows depended on characteristics of the step and of the pool at the base. Complex steps over boulders and logs were ascended more readily than shorter, more vertical steps over bedrock ledges. Brook trout ascended steps up to 1.2 m high during our study, and based on their preexperiment distribution, we assume that some ascend larger steps occasionally. Thus, we find it unlikely that artificial barriers can be constructed that will selectively allow passage of native trout and char while impeding brook trout.

Apparently, motivation to move upstream through very steep slopes was high in the translocated fish in Hillbilly Creek (*motivation* is used in the sense of internal and external factors stimulating a behavior; Beer 1972; Lidicker and Stenseth 1992). Others have also reported that the behavior of translocated salmonids can be strongly influenced by a tendency to home (Armstrong and Herbert 1997; but see Saunders and Smith 1962). Although we cannot conclude that brook trout were incapable of ascending the steepest slopes in Hillbilly Creek, the translocated fish in Hillbilly Creek would presumably have returned all the way to their site of capture if they were capable.

Upstream versus Downstream Movements

We were surprised to find upstream movements of marked fish more prevalent than downstream movements in steep sites, but the result conforms to directions of seasonal movement patterns observed in studies of more moderately sloped streams. Upstream movements of brook trout older than age 0 are generally more common and more extensive than downstream movements during the summer (McFadden 1961; Saunders and Smith 1962; Flick and Webster 1975; Riley et al. 1992; Gowan and Fausch 1996b), although downstream movements may be more important in the winter

(Smith and Saunders 1958; Saunders and Smith 1962; Flick and Webster 1975; Chisholm et al. 1987; Gowan and Fausch 1996b). The frequency of upstream movements by brook trout in other studies was most pronounced during the spring, with a secondary peak occurring in the fall (Smith and Saunders 1958; Flick and Webster 1975; Gowan and Fausch 1996b), which suggests that factors motivating or allowing migratory movements vary seasonally. In some streams, conditions allowing passage over obstacles may occur only during infrequent windows of time lasting from hours to weeks (Grainger 1953). For example, after Nagel (1991) repatriated brook trout into a Tennessee stream, very high spring discharges apparently allowed the fish to ascend a vertical drop that was 1.2 m high at low flows (J. Nagel, personal communication).

In the two steepest sites, we found no marked fish that had moved upstream into the upper portions of the removal sections during 1996, even though brook trout initially occupied those areas. We predicted that brook trout would ascend low-flow barriers during high spring flows when the heights of vertical steps were minimized and side channels around low-flow barriers developed. However, despite relatively high streamflows during spring snowmelt in 1997, the following August we found no marked brook trout above the obstacles they had failed to ascend in 1996. Possible explanations are that opportunities for upstream fish passage do not occur annually, motivation for dispersal was limited, or fish ascended the steps but we did not detect them. We suggest that brook trout may ascend certain stream features only during brief occurrences with infrequent return intervals (e.g., exceptionally high snowmelt runoff) when abiotic conditions allow passage during a period when the fish are motivated to disperse. Alternatively, temporary features such as a waterfall over a large log (e.g., step *a* in Hillbilly Creek) may create obstacles that fish cannot ascend until the feature itself changes, in which case dispersal into the upstream habitat may be delayed for many years.

Our analysis of total immigrants (marked and unmarked) supported our observations that upstream movements predominated even in steep streams. If downstream movements were prevalent at the upper Sheep Creek site during the study, we would expect to see similar numbers of fish in the upper (SS 6) and lower (SS 4) removal subsections. We do not think that fish would have preferentially established residence in SS 4 rather than SS 6 because of differences in habitat quality between the subsections. Although we could not calculate initial fish densities in the two subsections, observations of fish captures during electrofishing and of habitat conditions lead us to believe that the two subsections were comparable.

Our use of unmarked fish to assess immigration is justified by increases in their numbers over time at all sites. At three sites the numbers of unmarked brook trout 95 mm or longer observed in removal sections at least doubled between the first night that we snorkeled and the nights that followed that same summer. Thus, we inferred that unmarked fish immigrated into the removal sections. Unmarked fish could have originated from three sources: (1) fish in removal sections missed during electrofishing, (2) fish from the marking sections missed during electrofishing, and (3) fish from beyond the study sites. Although we did not quantify long-term mark-retention, loss of marks cannot explain the unmarked fish in removal sections because all marked fish were also given adipose fin clips. No fin regeneration was evident until the last sampling date, one year after marking.

Distances Moved

Our results agree with those of earlier workers who found that brook trout often do not restrict their activity to small home ranges within streams (McFadden 1961; Shetter 1968; Gowan and Fausch 1996b). Some marked fish moved at least 600 m, the longest distance over which we could have detected movements. Observations of marked fish immigrating into removal sections of each Rock Creek site from the adjacent site and of overnight movements at the lower Sand Creek site provided direct evidence of fish moving farther than 400 m in channel slopes of 1–6%. The rapid movements we observed are probably not attributable to our handling of the fish. Earlier studies indicated that electrofishing, marking, and holding brook trout in streams did not detectably influence movements, and in particular, did not increase emigration (Smith and Saunders 1958; Moore et al. 1985; Riley et al. 1992; Gowan and Fausch 1996b). Furthermore, recolonization of removal sections by relatively large numbers of unmarked fish suggests that colonists frequently dispersed from locations farther than 200 m away, where we did not electrofish. Our observations at the lower Sand Creek site confirmed that immigration could be rapid, at least in sites with gradual slopes. Thus, we inferred that many of the unmarked fish observed on the first night of snorkeling could have been immigrants. Similarly, Gowan and Fausch (1996a) found that most immigrants to 250-m sections of ‘‘improved’’ habitat came from beyond the adjacent 250-m study sections in Colorado streams.

Sizes of Immigrants

Upstream movements in steep streams were primarily restricted to larger brook trout. At all sites, immigrants into removal sections were predominantly 95 mm or longer. In steeper channel slopes, extensive movements involved only larger fish. Gowan and Fausch (1996b) also observed that brook trout that moved were generally longer than those that remained in home sections. Because swimming performance increases with fish length, we suspect that steep channel slopes inhibited movements of small more than large fish. Only adult brook trout were found in several streams in the South Fork Salmon River drainage (Adams 1999: Chapter 3), including Hillbilly Creek, which is consistent with the observation that upstream dispersal was dominated by relatively large individuals. Similarly, the largest rainbow trout were the first to invade streams in Great Smoky Mountains National Park (Larson et al. 1995).

Movements by age-0 brook trout appear to be highly variable, but summer downstream movements may be more prevalent in age 0 than in older individuals (Hunt 1965; Phinney 1975). However, we found little evidence of movements longer than 67 m in either direction by marked age-0 fish. In Rock Creek the different length-frequency distributions for age-0 and age-1 fish above and below the small falls supports this observation. The length differences could have been due to (1) distinct subpopulations of juveniles with little movement between them, or (2) differential downstream dispersal by faster or slower growing individuals. However, the paucity of resightings of small marked fish ($<$100 mm) suggests that movements between sites by small fish was minimal in both directions. Hunt (1965) reported that the relative importance of upstream versus downstream movements by age-0 brook trout in Lawrence Creek, Wisconsin, varied by stream section but that, overall, downstream movements were predominant. However, Lawrence Creek has a moderate slope and supports faster growth so that the age-0 fish were similar in length to age-1 or 2 fish in our experiment. The smaller length-at-age in our study populations and steeper slopes at some sites may have inhibited movements by younger fish.

Movements, Dispersal, and Invasion

Although steep channels (at least up to 13% slope) do not inherently form barriers to brook trout dispersal, they may slow the invasion process by reducing dispersal rates. The combination of conditions necessary to motivate and allow brook trout to ascend steps typical of steep streams may occur infrequently. Numerous factors, including highly variable environmental conditions, can influence the likelihood of a population becoming established (Crowl et al. 1992). Average slopes of 9% or greater over distances of 400 m can apparently decrease the number of fish moving upstream and the movement rates. When the number of dispersers is small, demographic factors (such as the sex of dispersers) become increasingly important to the probability of successful invasion (Lewis and Kareiva 1993; Kot et al. 1996). Therefore, multiple dispersal events may be required before an upstream population is established. Thus, while invasion may occur more slowly where dispersal is difficult, steep stream reaches do not necessarily prevent brook trout invasion indefinitely, especially where gradual reaches favorable to reproduction occur upstream.

Movement and dispersal (as we use the terms) are not synonymous, but distinguishing between them is difficult. Homing to streams, lakes, or specific sites for various purposes has been shown in many salmonids, including chars (Arctic char *S. alpinus*: Johnson 1980; brook trout: Power 1980; Näslund 1992; bull trout: Swanberg 1997), but few studies have attempted to determine the degree of straying in these fishes. The degree to which mobile brook trout home to specific natal sites for spawning is unknown but is of primary importance to understanding dispersal in the context of invasions. Exploratory movements that do not result in spawning in a new location are probably of minor relevance to the invasion process. Although we cannot conclude that the fish in our study were actually dispersing, many were clearly capable of dispersing through steep slopes.

For fish to disperse through a given stream reach, they must have both adequate swimming ability and the necessary proximate motivating factors. The observation that translocated fish tended to move upstream more than most other groups of fish suggests that motivating factors are important to fish movements. Motivations for salmonid movements are poorly understood, although a number of papers offer insights into possible factors stimulating movements (reviewed in Gowan et al. 1994; Northcote 1997). To be able to predict dispersal patterns that may lead to invasion, we will need to know the physical swimming abilities of fish and understand more about factors motivating dispersal (Schlosser and Angermeier 1995). The latter could greatly advance our understanding of relationships between abiotic and biotic ecosystem changes and brook trout invasion of streams.

Management Implications

Biases in selection of fish survey sites may be responsible, in part, for the perception that brook trout are primarily creatures of gradually sloping streams. In attempting to gather data for a meta-analysis, we found that fish surveys are often not conducted within or above very steep stream reaches (i.e., $>10\%$). Such reaches may be considered unlikely to support salmonids, unimportant for recreational fishing, or of limited importance to fish production. While the latter two assumptions may be true, we have shown that steep reaches can be important dispersal corridors. A better understanding of fish production and dispersal in steep channels will improve our understanding of invasion processes. Gradual stream reaches are often interspersed among steep reaches and may facilitate invasions by serving as productive ‘‘stepping stones’’ if colonized by brook trout dispersing upstream through the steeper reaches. In addition, small, steep headwater stream segments are the last refuges of many remnant native salmonid populations in the West (e.g., papers in Young 1995a). Thus, invasion of such areas by brook trout constitutes a threat out of proportion to the amount of habitat invaded. Biological surveys of steep reaches could help identify and track incipient invasions.

We have discounted poor swimming ability as a sole explanation of limited brook trout invasion in steep streams. Other likely limitations include low reproductive success or juvenile survival (Fausch 1989), biotic resistance by interactions with other fishes, and limited motivation for dispersal through steep reaches. Numerous management activities that result in physical or biotic changes to stream ecosystems could influence all of these factors. Identifying how these factors operate and which are most critical will require continued exploration into the complexities of invasions by brook trout, as well as other stream fishes, and will provide insights into how human activities alter the susceptibility of habitats to invasion or the invasive abilities of fishes.

Acknowledgments

K. Gillogly, P. Hanna, D. Horan, and J. McGlathery (Rocky Mountain Research Station, RMRS); B. Kibler and T. Koch (U.S. Fish and Wildlife Service); and M. Bauer assisted with field work. D. Myers (RMRS) provided endless logistical support. D. Peterson, B. Gresswell, and S. Moore provided comments that greatly clarified the manuscript. The Cascade Ranger District, Boise National Forest, provided housing and other logistical support. This research was supported primarily by funds provided by the USDA Forest Service, Rocky Mountain Research Station. S. Adams received additional support from a University of Montana, Division of Biological Sciences, honors predoctoral fellowship, and from the Western Division, American Fisheries Society.

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