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ECOSYSTEMS

Geography of Invasion in Mountain Streams: Consequences of Headwater Lake Fish Introductions

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ABSTRACT

The introduction of fish into high-elevation lakes can provide a geographic and demographic boost to their invasion of stream networks, thereby further endangering the native stream fauna. Increasingly, remaining populations of native salmonids are concentrated in fragmented headwater refugia that are protected by physical or biological barriers from introduced fishes that originate in the pervasive source populations established at lower elevations. Although fish introduced near mainstem rivers frequently encounter obstacles to upstream dispersal, such as steep slopes or falls, we found that brook trout (*Salvelinus fontinalis*) dispersed downstream through channel slopes of 80% and 18-m-high falls. Thus, headwater lake stocking provides source populations that may be capable of invading most downstream habitats, including headwater refugia of native fishes. The extent of additional area invasible from lakes, beyond that invasible from downstream, depends on the geography of the stream network, particularly the density and distribution of headwater lakes and their location relative to barriers inhibiting upstream dispersal. In the thermal and trophic environments downstream of lakes, fish commonly grow faster and thus mature earlier and have higher fecundity-at-age than their counterparts in other high-elevation streams. The resulting higher rates of population growth facilitate invasion. Larger body sizes also potentially aid the fish in overcoming barriers to invasion. Trout introductions to high-elevation headwater lakes thus pose disproportionately large risks to native fishes—even when the place of introduction may appear to be spatially dissociated from populations of the native species. Mapping the potential invasible area can help to establish priorities in stocking and eradication efforts.

Key words: invasion; dispersal; landscape; demography; conservation; nonnative fish; salmonids; lake; stream.

INTRODUCTION

Interactions with nonnative species are one of the leading causes of species extirpations and declines in freshwater ecosystems (Miller and others 1989; Allan and Flecker 1993; Kruse and others 2000). Salmonid fishes, including salmon and trout (*Oncorhynchus* spp. and *Salmo* spp.) and char (*Salvelinus* spp.), have been introduced to freshwater ecosystems worldwide. As a result, nonnative fishes have become numerically dominant over native salmonids across large regions. For example, introduced rainbow trout (*O. mykiss*) and nonnative brook trout (*Salvelinus fontinalis*, a char native to eastern North America) are now the two most widespread salmonids in the interior Columbia River basin of the Pacific Northwest (Thurow and others 1997). Nonnative fish invasions originating in relatively

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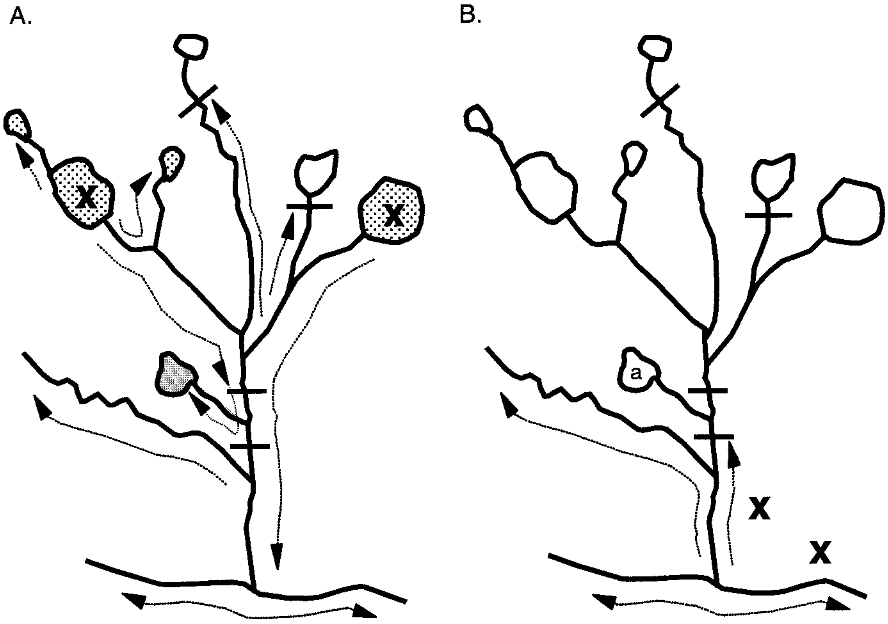

Figure 1. Schematic diagram of a hypothetical drainage with brook trout introductions in headwater lakes **(A)** vs downstream **(B)**. Arrows and dashed lines indicate the direction and extent of invasions from locations of introductions (Xs). Bars bisecting the streams indicate physical barriers to upstream dispersal, and stippled lakes contain brook trout. In panel B, all habitat upstream of barriers provides refugia from nonnative fishes. Stocking fish in lake "a" would affect substantially less of the stream network than would stocking fish in the remaining, upstream lakes.

low-elevation habitats have had a negative impact on native aquatic fauna in large portions of many drainages. In this paper, we address the additional invasion of headwater stream refugia that can result from fish stocking in headwater lakes and explore some implications for native stream fishes.

Fisheries managers have stocked fishes (including species native to the region) in mountain lakes throughout the western United States and Canada since the late 1800s, primarily to provide sport fishing. Similar practices have been followed in Scandinavia since the 12th century or earlier (Nilsson 1972) and continue in headwater lakes worldwide. Much of this stocking occurs in lakes within designated wilderness areas, national parks, and other conservation areas. An estimated 95% of all high-mountain lakes in 11 western states lie upstream of Pleistocene-age barriers to fish colonization and were thus naturally fishless (Bahls 1992). However, about 60% of the lakes and 95% of the deeper, larger ones now contain trout or char (Bahls 1992). Many lakes have been repeatedly stocked regardless of whether self-sustaining fish populations were already present or became established after initial introductions (for example, see Evans and Willox 1991). Brook trout are particularly easily established in lakes, probably because they will spawn in either inlet or outlet streams or in areas of groundwater upwelling within lakes (Reimers 1958).

Stocked fishes potentially influence native fishes via predation, competition, spread of diseases or parasites, inducement of behavioral changes, and hybridization (Miller and others 1989; Krueger and May 1991; Stewart 1991; Crowl and others 1992). The introduction of numerous salmonid species has caused dramatic changes in community composition, trophic organization, and the population structures of stream communities (Moyle and others 1986; Kreuger and May 1991; Crowl and others 1992; Flecker and Townsend 1994). Many populations of native fishes in small high-elevation streams may be relatively unstable due to slow growth, late maturity, low fecundity, and low survival during harsh winter conditions, and those isolated above barriers cannot be supported or recolonized by the immigration of fish from other areas. Such populations may be ill-equipped to withstand the additional stresses imposed by an introduced species. For these reasons, some scientists have argued that fish should not be introduced into sites where they could contact native fishes downstream (Krueger and May 1991; Lee and others 1997). Fish invasions of headwater stream networks that were historically fishless probably have even more profound ecosystem effects, as discussed in other papers in this issue.

Headwater streams and lakes situated above barriers to upstream fish dispersal often historically provided either (a) refuges for native, nonfish stream fauna (for example, amphibians, invertebrates) from native fishes or (b) populations of native fishes isolated from the effects of downstream communities, which now often include nonnative fishes (Figure 1). Worldwide, such isolated populations represent the entire remaining distribution of native species in many drainages where nonnative fishes have invaded downstream segments (Power 1980; Townsend and Crowl 1991; Crowl and others 1992; Closs and Lake 1996; Kruse and others 2000). Even where dispersal barriers are absent, headwater streams frequently serve as strongholds for native salmonids (Larson and Moore 1985; Fausch 1989; Larson and others 1995; Dunham and others 1997). For example, unlike most other native fishes in the South Fork Salmon River basin of Idaho, the densities of native bull trout (*S. confluentus*) and westslope cutthroat trout (*Oncorhynchus clarki lewisi*) increased at higher elevations (Platts 1979). These native species are typically found upstream of introduced brook trout (Fausch 1989; Adams and Bjomn 1997; Dunham and others 1999).

Most studies of the effects of high-mountain lake fish stocking have focused on biotic effects within the lakes. However, studies that have looked beyond the individual lake scale have shown drainage- or regional-scale impacts on amphibians from fish stocking in headwater lakes (for example, see Knapp and Matthews 2000; Pilliod and Peterson 2001). Because of the importance of headwater stream refugia and the potential for nonnative fishes stocked in headwaters to spread throughout entire drainages (Lee and others 1997), the consequences of headwater fish introductions on aquatic communities downstream of stocked lakes warrants additional attention.

Our objective was to describe the influence of headwater lake fish stocking on invasion potential in a landscape context. We focused our analysis on brook trout for several reasons: (a) They have been widely introduced to, and have readily established populations in, both lakes and streams, (b) they appear to have detrimental effects on numerous native species, and (c) they are easily distinguishable from all native species in the Rocky Mountains. We used the following three approaches to examine mechanisms for brook trout invasion from headwater lakes into stream networks: (a) inference of downstream and upstream movements from present-day distributions and known stocking locations, (b) projections of potential invasible area with a geographic information system (GIS) and simple rules of invasibility based on channel morphology, and (c) examination of demographic advantages for fish in lakes and lake outlets relative to other high-elevation stream habitats. Dispersal and demographic rates are important determinants of fish invasion beyond stocking locations, and we use results to show that both can be influenced by the location of stocking within a watershed.

METHODS AND RESULTS

Downstream and Upstream Fish Movements

Methods. We collected data in the field and from other biologists to assess the downstream dispersal of brook trout in lake-outlet streams. We summarized surveys of fish distributions for which we could infer downstream dispersal from lakes. Fish introductions were well documented in some drainages, but in others, we inferred where introductions had occurred based on present fish distributions and stream morphologies. Because we were interested in movements through steep channel slopes, we analyzed downstream-directed invasions in lake-outlet streams containing channel slopes exceeding 10%. We included streams in the data set only if they met at least one of the following criteria: (a) Brook trout were documented as previously stocked or recently present in a headwater lake feeding the stream, (b) no brook trout populations occurred in a lower mainstem river near the stream or in a neighboring stream that would likely act as a source population for an upstream-directed invasion, or (c) brook trout occurred upstream of an impassable falls (more than 3 m high) or of a stream reach with a channel slope exceeding 17% for at least 100 m.

In mark–recapture experiments, marked brook trout moved upstream through a 67-m-long reach with an average slope of 13% (Adams and others 2000). Over 1 year, no fish moved completely through two other subsections with 10% and 17% slopes, but brook trout occurred upstream of both reaches during initial sampling, suggesting that they had invaded upstream through those slopes at one time. One marked brook trout (210 mm long) ascended a 1.5-m-high, complex falls; however, no marked fish were found upstream of a 1.1-m vertical falls (Adams and others 2000). We believe that our slope criteria, as stated in (c), is a conservative estimate of barriers to upstream brook trout dispersal and that flatter slopes and smaller falls frequently inhibit upstream invasion.

We conducted fish distribution surveys in three stream systems in Idaho and Montana during 1996 and 1997 (Appendix A). In the two Idaho streams, we determined the absence or presence of brook trout by daytime snorkeling in sequences of five to seven pools and one run at intervals of 0.5 to 1.0 km along the stream (see Adams 1999 for details). In Montana, we collected fish by multiple-pass electrofishing without block nets in seven evenly spaced 100-m-long reaches in Moore Creek and two additional reaches in the South Fork (SF) Little

Joe River, downstream of the confluence with Moore Creek.

We obtained additional data for streams with downstream-directed invasions from other biologists. The methods used for fish sampling are described in Appendix A. Distances over which channel slopes were measured varied from about 30 to 100 m, but slopes were often reported as averages for stream segments delineated by changes in channel morphology and location of tributary junctions.

The maximum channel slope that brook trout dispersed through downstream was determined either from on-site channel slope measurements or United States Geological Survey (USGS) 1:24,000 scale topographic maps, whichever indicated the steepest slope. Map-derived slopes were calculated over 100–200 m of stream. We report the heights of the highest known waterfalls over which brook trout dispersed downstream (Appendix A). Because short, steep drops are not usually apparent at a 1:24,000 map scale and field crews seldom walked the entire lengths of streams, the slopes and waterfalls reported should be considered minimum estimates of the steepness of features traversed by brook trout in each stream.

On 1:24,000 scale maps, we measured the distances that brook trout from lake-origin populations had dispersed or invaded downstream. We only included distances to the mouths of lake-outlet streams or to reaches where we were confident that the brook trout were descendants of fish in the lake of interest. For eight streams where we had adequate data, we measured distances between the most downstream location with evidence of successful brook trout reproduction (detection of age 0 individuals) and the most downstream observation of older brook trout in the stream and assumed that individual fish had likely traveled the entire distance (Adams 1999).

We collected data on the channel slopes ascended by fish moving upstream in 13 tributary drainages of the upper SF Salmon River (Valley County, Idaho) in 1996 by using the snorkeling methods described above (Adams 1999). The stream segments surveyed ranged from first to fourth order (Strahler) with wetted widths from 1.7 to 12.9 m and channel slopes from less than 1% to 23%.

Results. Neither steep slopes nor waterfalls prevented brook trout from dispersing downstream. We found evidence of 15 cases where brook trout had dispersed downstream over channel slopes exceeding 20% (Figure 2 and Appendix A). The most extreme conditions traversed included one stream reach with an 80% slope and another with an 18-m-high waterfall.

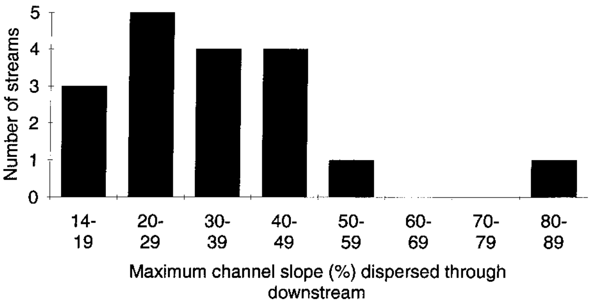

Figure 2. Approximate maximum channel slopes through which lake-origin brook trout or their progeny dispersed downstream.

In some streams with downstream-directed invasions, adult brook trout occupied reaches with 19% to 23% slopes (Table 1). In four of seven streams, brook trout were observed in the steepest reaches sampled. However, in Lick Creek, no fish were observed in apparently suitable habitat (large pools) within a very steep reach (channel slopes of 17% to 24% and numerous falls), even though brook trout occurred both upstream and downstream of the reach. Absence of age 0 or yearling-size individuals probably indicates that the brook trout did not reproduce successfully in such steep reaches. In upstream-directed invasions, the steepest reach where we found brook trout had an average slope of 17% over 70 m (Table 1).

Brook trout distributions extended as far as 22 km downstream of lakes in stream systems where no apparent downstream source populations existed (Figure 3 and Appendix A). We inferred that individual brook trout moved farther than 15 km downstream in Warm Springs Creek and 8 km in Old Man Creek through stream segments where no evidence of reproduction was found. Discussions with biologists who provided data indicated that brook trout were occasionally observed farther downstream than we report in some drainages. In contrast, brook trout were abundant and reproducing in Elizabeth Creek 0.5 km downstream of Ice Lake, but they were not found in any of the nine reaches sampled farther downstream.

Geographic Projections

Methods. We used a GIS to characterize potential brook trout colonization from headwater lakes in two morphologically different drainages—the SF Salmon River, Idaho, and the Big Hole River, Montana. We classified all stream segments as potentially invasible from one of three sources: (a) headwater lakes only, (b) mainstem and headwater sources, or (c) neither. We used the following rules

Table 1. Channel Slope and Wetted Stream Width of the Steepest Reach where Brook Trout Were Found and Slope of the Steepest Reach Sampled in Idaho Streams where Brook Trout Occupied Channels Slopes greater than 10%

Stream	Maximum Slope with Brook Trout (%)	Maximum Slope Sampled (%)	Average Wetted Width in Reach with Brook Trout (m)
Downstream-directed invasions			
Gedney Creek	23[a]	28	4.2
Moore Creek	19[b]	19	1.8
S. F. Blackmare Creek	~19[c]	~19	7.1
Lizard Creek	16[a]	16	5.0
Running Creek	15[a]	15	6.6
Rainbow Creek	12	14	2.0
Lick Creek	10[c]	24	8.1
Upstream-directed invasions			
Hillbilly Creek	17[d]	17	2.8
Bear Creek	13[b]	13	3.5
Upper Sand Creek	12[e]	12	2.3
Cabin Creek	12[c]	12	3.8

Some streams with downstream-directed invasions were excluded because the resolution of channel slope data was inadequate. Streams with upstream-directed invasions are a subset of 13 brook trout streams studied in the South Fork Salmon River drainage (Adams 1999).

[a] Slope measured over 150 m

[b] Slope measured over 100 m

[c] Slope measured over approximately 30 m

[d] Slope measured over 70 m (includes 34 m of 20% slope with brook trout)

[e] Slope measured over 60 m

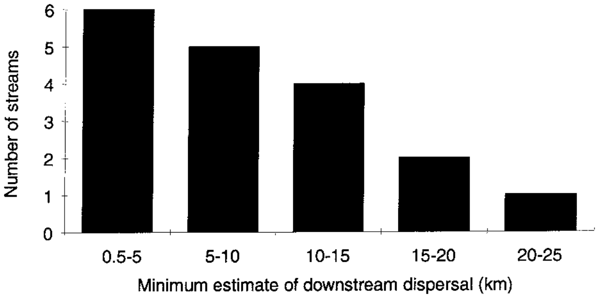

Figure 3. Minimum estimates of distances downstream from lakes that brook trout in lake-origin populations occurred in Idaho and Montana streams. This does not imply that individual fish moved the distances shown; both dispersal and colonization may be reflected.

for classification: (a) brook trout could disperse downstream through any slope and over any waterfalls, (b) they could disperse upstream until they met a dispersal barrier, (c) invasions could originate from all headwater lakes and from all tributary confluences with the mainstem rivers, and (d) intermittent streams could be used as dispersal corridors (Figure 1 illustrates rules a and b). Any of three conditions constituted a dispersal barrier: (a) a channel slope of 17% or greater measured in the field, (b) a channel slope of 17% or greater over 100–200 m of stream on a USGS 1:24,000 scale topographic map, or (c) a known barrier (for example a waterfall greater than 2.5 m or a permanently dry stream reach). The downstream-most dispersal barrier in each stream and barriers upstream of lakes were digitized in a GIS. We tallied stream segment lengths by category within each basin.

Results. The relative lengths of stream potentially invasible from headwater compared to mainstem sources was strongly dependent on the drainage basin morphology, specifically the locations of barriers to upstream dispersal and the distribution of headwater lakes (Figure 4). Due to the steep headwater streams and numerous hanging valleys in the SF Salmon River drainage, brook trout could disperse into more than a third of the basin only from headwater stocking locations (Table 2). Warm Lake was the only lake invasible from the mainstem, and three entire tributary drainages were inaccessible to brook trout moving upstream. Conversely, in the upper Big Hole River drainage, headwater lake stocking had little predicted impact on the basin area accessible to brook trout relative to area accessible from mainstem sources (Table 2).

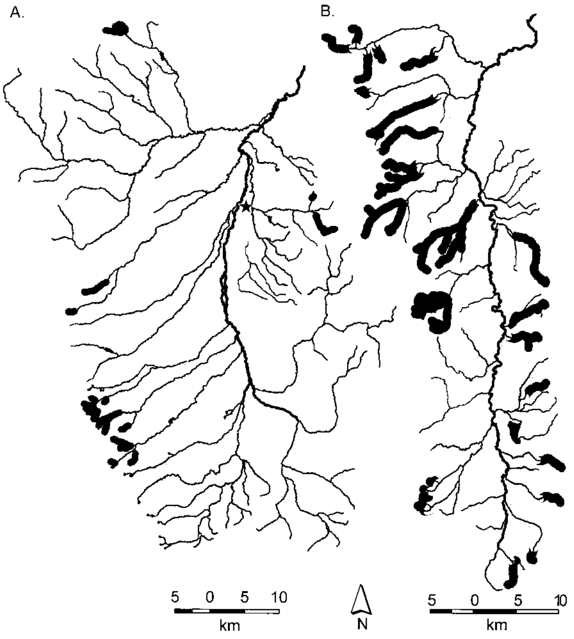

Figure 4. Areas potentially invasible from brook trout source populations in mainstem locations and headwater lakes (*light gray shading*) and additional areas invasible only from source populations in headwater lakes (*dark shading*). Areas classified as not invasible are not shaded. Most named streams and all lake-outlet streams in each drainage were analyzed. In the upper Big Hole River drainage, Montana **(A)**, 946 km of stream were invasible from downstream and 46 km were invasible from upstream, with 53 km not invasible. The star indicates Wisdom, Montana. In the upper South Fork Salmon River drainage, Idaho **(B)**, 199 km of stream were potentially invasible from mainstem and 151 km were invasible from headwater lake sources; 101 km were not accessible from either source.

The paucity of dispersal barriers resulted in numerous lakes being predicted as invasible from downstream and only a few short headwater reaches of streams being inaccessible to brook trout from downstream sources. The major exceptions in the Big Hole drainage were several streams where a lack of surface-water connection to the mainstem prevented invasion from downstream sources (B. Roberts personal communication).

Demographic Patterns

Methods. We compared length at age, age at maturity, and fecundity of brook trout in a lake-outlet stream system (Moore Creek/SF Little Joe River, Montana) and a nearby stream lacking a headwater lake (Twelvemile Creek, Montana). We collected all size classes of brook trout present in September and October 1997 and aged fish by examining annual growth rings on sagittal otoliths (ear bones) (Adams 1999). Sex and maturity of the fish were determined, and eggs from mature females were preserved and counted. Stream temperatures were inversely related to elevation in Twelvemile Creek, but nearly the opposite pattern existed in Moore Creek due to the headwater lake influence (Figure 5B).

Results. Age 0 brook trout in the uppermost reach of Moore Creek (50–150 m downstream of Moore Lake) grew significantly faster than those in any other reach sampled in Moore Creek, the SF Little Joe, and Twelvemile Creek (ANOVA, d.f. = 12, $P < 0.001$, LSD post hoc comparisons $P < 0.001$) (Figure 5A). Length-at-age was highly correlated with mean August stream temperature among all six reaches in both streams. The correlation was strongest for the youngest fish ($r = 0.996$ for age 0, 0.902 for age 1, and 0.831 for age 2 fish) (Figure 5). Faster-growing brook trout in the two reaches nearest the outlet of Moore Lake matured at least 1 year earlier (males at age 1, females at age 2) than individuals in the lower four reaches of Moore Creek and the upper two reaches of Twelvemile Creek (Adams 1999). Fecundity was positively correlated with female body weight ($r > 0.8$ for both streams).

DISCUSSION

The rate and spatial extent of stream fish invasions may be influenced by many factors, including dispersal rates and options, demographic rates in the invasion front, and demographic pressures in potential source populations. Headwater lake stocking potentially affects each of these factors, resulting in more stream area being invasible from headwater than downstream source populations. Although we focused on brook trout, we expect similar results for other salmonid fishes stocked in high-elevation lakes.

Headwater lake stocking allows fish access to more stream area within a watershed than does mainstem or low-elevation stocking. Limited dispersal ability is the most obvious mechanism potentially restricting upstream dispersal and invasion by fishes in steep streams. Most mathematical models used for predicting invasions (for example diffusion models) assume equal dispersal by organisms in all directions and locations (Hastings 1996; Kot and others 1996). However, for lotic organisms, dispersal is primarily linear and often differs in rate and frequency in each direction and at different locations along the dispersal route (Johnson and Carlton 1996). Brook trout dispersed through much

Table 2. Predicted Stream Lengths and Percentage of Stream Length that Brook Trout Could Invade from Headwater vs Mainstem Source Populations within the Upper Basins of the SF Salmon River, Idaho, and the Bighole River, Montana

Source Location	SF Salmon River km (%)	Bighole River km (%)
Mainstem and headwaters	199 (44)	946 (91)
Headwaters only	151 (33)	46 (4)
None	101 (22)	53 (5)
Total	451	1045

Mainstem river lengths are not included. Stream segments were predicted as invasible based only on ability of fish to disperse to the segment. Predictions are conservative with respect to stream length invasible only from headwater locations.

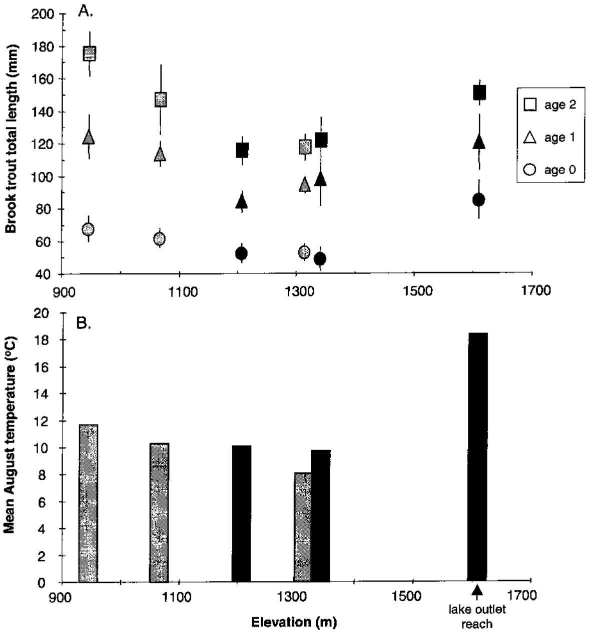

Figure 5. Brook trout length-at-age **(A)** and mean August 1997 stream temperature **(B)** vs elevation in two Montana streams. Twelvemile Creek (*gray symbols*) has no lake, whereas Moore Creek (*black symbols*) is a lake-outlet system. Lengths are mean total lengths (± 1 standard deviation) of age 0–2 brook trout. Only data from stream reaches where temperatures were recorded are shown, but the trends are the same with all fish sampling reaches included (Adams 1999). Fish were collected between 11 September and 6 October 1997. Annual thermal regimes, where recorded, followed similar patterns. The upper temperature recorder in Moore Creek was about 50 m downstream of Moore Lake.

steeper streams in a downstream than upstream direction. In downstream-directed invasions, where dispersal ability was not limiting, brook trout sometimes occupied reaches with much steeper slopes than those they dispersed through in upstream-directed invasions. This finding shows that dispersal ability, and not an inability to occupy steep slopes, limits upstream brook trout invasion of very steep (at least 17%) streams.

Downstream movements in very steep streams may also increase the rate and extent of invasion by forcing the colonization of new habitat. Animals often make exploratory forays into multiple new habitats before dispersing (Woolfenden and Fitzpatric 1984; Holekamp and Sherman 1989). However, if fish move downstream over features that prevent their return "home," their exploratory movements or passive displacements automatically and involuntarily become dispersal. Such individuals may be more likely to colonize distant or less suitable habitats than fish originating in suitable habitat lower in a drainage. In the southern Appalachian Mountains, brook trout that moved downstream over waterfalls had some of the longest movements documented by Moore and others (1985). We inferred that brook trout moved over 15 km downstream in some of the steep lake-outlet streams we studied.

Although brook trout disperse widely, invasion may not be inevitable everywhere they have access. Several SF Salmon River tributaries that were open to invasion from mainstem sources did not contain brook trout (Adams 1999). In other instances, brook trout were found for several kilometers downstream of lakes, but there was little evidence of reproduction in the streams. Further research on accessible stream networks that have not been invaded may produce useful insights into the invasion process. Understanding the sources of variation in dispersal and colonization will provide insight into the mechanisms of both downstream- and upstream-directed invasions and will help us to better manage fishes and habitat in ways that limit further invasions.

Demographic processes can be important determinants of invasion (Hastings 1996) and of the ultimate distribution and population structure of a species (Carter and Prince 1981; Caughley and others 1988; Carey and others 1995). We believe that the increased growth rate of fish in lakes and lake-outlet streams increases the rate or extent of invasion over the invasion rates in streams that lack lakes. When fish densities are not excessively high, salmonid growth rates in mountain lakes and lake-outlet streams are typically higher than those in headwater stream segments that lack the thermal and trophic influences of lakes (Domrose 1963; Haraldstad and others 1987; Hayes 1995). Faster growth results in larger, earlier-maturing, more fecund fish (See, for example, Northcote 1981; Elliott 1994; Downs and others 1997). Our assessment of brook trout in Moore Creek confirms that a high-elevation lake can substantially increase fish growth and fecundity. Matrix projection modeling results suggest that the observed differences in brook trout fecundity and age at maturity among stream reaches in our study were sufficient to create large differences in population growth rates (Adams 1999). Also, larger brook trout appear to be the primary dispersers in steep streams (Adams and others 2000); therefore, increased length-at-age of fish from lake-influenced habitats may increase their dispersal ability or tendency. Even in the Big-hole River drainage, where headwater lake stocking only marginally increases the amount of accessible habitat, lake stocking may still increase the stream invasion rates by altering fish demographics.

Faster growth of brook trout in lakes or lake-influenced streams also potentially increases their impact on native species. Behavioral interactions among salmonids are typically size-dependent, with larger fish often having an advantage in interspecific interactions (Chapman 1966; Noakes 1980; Nakano and others 1998; but see Rose 1986). Because salmonids are gape-limited predators, faster growth should allow them to consume larger prey (including juvenile native fishes) at an earlier age. Thus, bigger fish in streams should be better competitors and predators as well as better invaders.

Headwater stream invasions have important implications for native fishes. Brook trout have replaced or contributed to declines in native bull trout populations via hybridization and possibly competition or other mechanisms (papers in Howell and Buchanan 1992; Leary and others 1993; Nakano and others 1998). In many drainages, brook trout have displaced or replaced native cutthroat trout in streams, although the specific mechanisms remain unknown (Griffith 1988; Fausch 1989; De Staso and Rahel 1994; papers in Young 1995; Dunham and others 1999). Lahontan cutthroat trout (*O. c. henshawl*) are typically restricted to stream segments upstream of brook trout, and their downstream distribution limit occurs at significantly higher elevations in streams that contain brook trout than in those that do not, suggesting a negative interaction between species (Dunham and others 1999). Bechara and Moreau (1992) showed that in small streams, brook trout can have a top-down influence on benthic invertebrates, which has the potential to influence food availability for native fishes. The impacts from other salmonids commonly introduced to high-mountain lakes, including rainbow and cutthroat trout, are similar but also include introgression among native and nonnative subspecies and stocks (Henderson and others 2000; Kruse and others 2000). Even where outlet stream systems function as sink habitats (Pulliam 1988; Schlosser and Angermeier 1995) or dispersal corridors supporting little reproduction, competition and predation by nonnative fishes can strongly affect the stream communities (McFadden 1961; Hawkins and Sedell 1990).

Compared to upstream-directed invasions, invasions from headwater sources may result in greater overlapping distributions and the potential for adverse interactions between native fishes largely restricted to headwater areas and nonnative fishes (for example, native bull or cutthroat trout and brook trout). In drainages where large areas are invasible only from headwater sources (for instance the SF Salmon River), headwater lake stocking of nonnative fishes potentially decreases the available refuge area for native fauna, thereby increasing opportunities for the displacement of native species. The probability of maintaining strong headwater populations of native fishes to sustain or refound other populations thus can be severely diminished when headwater stocking adds top-down dispersal opportunities for nonnative species.

Management Implications

The demand for recreational fishing in high-mountain lakes is the primary motivation for stocking nonnative fishes such as brook trout. It is important to consider, however, that stocking of a mere handful of lakes could allow nonnative fishes access to nearly an entire stream network. Consideration of the invasion geography could be useful in prioritizing lakes to protect or rehabilitate. For example, when a nonnative species already occurs downstream of a migration barrier, stocking lakes that are a short distance upstream of the barrier (assuming that other barriers occur farther upstream) will risk less than stocking lakes far upstream of the barrier (Figure 1). Similarly, the stream area negatively affected by nonnatives could be minimized by stocking multiple lakes in one tributary basin instead of one lake each in multiple basins. Similar analyses could help in prioritizing lake-stream networks for the eradication of nonnative fishes (see Knapp and Matthews 1998). Systems where nonnative fishes have emigrated from headwater lakes and occupy, but have not successfully colonized, the outlet streams should be considered good candidates for eradication projects. For example, Ice Lake is the only lake known to contain brook trout within a large area of the North Fork Clearwater River, Idaho, and as of 1996, the species had colonized little of Elizabeth Creek, the outlet stream (Appendix A). Brook trout eradication from Ice Lake would remove the one extant population with potential for invading a large drainage area. We believe systematic landscape-level analyses will reveal opportunities for defusing invasion threats in the montane regions of western North America and for reducing conflict between fisheries management and native species conservation programs.

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REFERENCES

Adams SB. 1999. Mechanisms limiting a vertebrate invasion: brook trout in mountain streams of the northwestern USA [dissertation]. Missoula (MT): University of Montana.

Adams SB, Bjornn TC 1997. Bull trout distributions related to temperature regimes in four central Idaho streams. In: MacKay WC, Brewin MK, and Monita M. editors. Proceedings of the Friends of the Bull Trout Conference proceedings. Calgary (Alberta): p 371–80. Bull Trout Task Force c/o Trout Unlimited Canada.

Adams SB, Frissell CA, Rieman BE. 2000. Movements of nonnative brook trout in relation to stream channel slope. Trans Am Fish Soc 129:623–38.

Allan JD, Flecker AS. 1993. Biodiversity conservation in running waters: identifying the major factors that threaten destruction of riverine species and ecosystems. BioScience 43:32–43.

Bahls P. 1992. The status of fish populations and management of high mountain lakes in the western United States. Northwest Sci 66:183–93.

Bechara JA, Moreau G. 1992. Top-down effects of brook trout (*Salvelinus fontinalis*) in a boreal forest stream. Can J Fish Aquat Sci 49:2093–103.

Carey PD, Watkinson AR, Gerard FFO. 1995. The determinants of the distribution and abundance of the winter annual grass *Vulpia ciliata* ssp. *ambigua*. J Eco 83:177–87.

Carter RN, Prince SD. 1981. Epidemic models used to explain biogeographical distribution limits. Nature 293:644–45.

Caughley G, Grice D, Barker R, Brown B. 1988. The edge of the range. J Animal Eco 57:771–85.

Chapman DW. 1966. Food and space as regulators of salmonid populations in streams. Am Nat 100:345–57.

Clearwater BioStudies Inc. 1993. Habitat conditions and salmonid abundance in Meadow Creek, North Fork Ranger District, summer 1992. Orofino (ID): USDA Forest Service, Clearwater National Forest.

Clearwater BioStudies Inc. 1995a. Habitat conditions and salmonid abundance in the Stanley and Dutch creek drainages, Lochsa Ranger District, summer 1994. Orofino, (ID): USDA Forest Service, Clearwater National Forest.

Clearwater BioStudies Inc. 1995b. Habitat conditions and salmonid abundance in the upper Boulder Creek drainage, Lochsa Ranger District, summer 1994. Orofino (ID): USDA Forest Service, Clearwater National Forest.

Clearwater BioStudies Inc. 1997a. Habitat conditions and salmonid abundance in selected streams within the Black Canyon area, North Fork Ranger District, summer 1996. Orofino (ID): USDA Forest Service, Clearwater National Forest.

Clearwater BioStudies Inc. 1997b. Habitat conditions and salmonid abundance in streams within the Old Man Creek drainage, Lochsa Ranger District, summer 1996. Orofino (ID): USDA Forest Service, Clearwater National Forest.

Closs GP, Lake PS. 1996. Drought, differential mortality and the coexistence of a native and an introduced fish species in a south east Australian intermittent stream. Environ Bio Fishes 47:17–26.

Crowl TA, Townsend CR, Mcintosh AR. 1992. The impact of introduced brown and rainbow trout on native fish: the case of Australasia. Rev Fish Bio Fisheries 2:217–41.

De Staso J III, Rahel FJ. 1994. Influence of water temperature on interactions between juvenile Colorado River cutthroat trout and brook trout in a laboratory stream. Trans Am Fisheries Soc 123:289–97.

Domrose RJ. 1963. Age and growth of brook trout, *Salvelinus fontinalis*, in Montana. Proc Montana Acad Sci 23:47–62.

Downs CC, White RG, Shepard B. 1997. Age at sexual maturity, sex ratio, fecundity, and longevity of isolated headwater populations of westslope cutthroat trout. North Am J Fisheries Manage 17:85–92.

Dunham JB, Peacock MM, Rieman BE Schroeter RE Vinyard GL. 1999. Local and geographic variability in the distribution of stream-living Lahontan cutthroat trout. Trans Am Fisheries Soc 128:875–89.

Dunham JB, Vinyard GL, Rieman BE 1997. Habitat fragmentation and extinction risk of Lahontan cutthroat trout. North Am J Fisheries Manage 17:1126–33.

Elliott JM. 1994. Quantitative ecology and the brown trout. New York: Oxford University Press.

Evans DO, Willox CC. 1991. Loss of exploited, indigenous populations of lake trout, *Salvelinus namaycush*, by stocking of non-native stocks. Can J Fisheries Aquat Sci 48 (Suppl 1): 134–47.

Fausch KD. 1989. Do gradient and temperature affect distributions of, and interaction between, brook charr (*Salvelinus fontinalis*) and other resident salmonids in streams? Physiol Ecol Japan 1:303–32.

Flecker AS, Townsend CR. 1994. Community-wide consequences of trout introduction in New Zealand streams. Ecol Applic 4:798–807.

Griffith JS. 1988. Review of competition between cutthroat trout and other salmonids. In: Gresswell RE, editor. Status and management of interior stocks of cutthroat trout. Bethesda, (MD): American Fisheries Society. p 134–40.

Haraldstad Ø, Jonsson B, Sandlund OT, and Schei TA. 1987. Lake effect on stream living brown trout (*Salmo trutta*). Archiv Hydrobiol 109:39–48.

Hastings A. 1996. Models of spatial spread: is the theory complete? Ecology 77:1675–9.

Hawkins CP, Sedell JR. 1990. The role of refugia in the recolonization of streams devastated by the 1980 eruption of Mount St. Helens. Northwest Sci 64:271–4.

Hayes JW. 1995. Importance of stream versus early lake rearing for rainbow trout fry in Lake Alexandrina, South Island, New Zealand, determined from otolith daily growth patterns. NZ J of Marine Freshwater Res 29:409–20.

Henderson R, Kershner JL, Toline CA. 2000. Timing and location of spawning by nonnative wild rainbow trout and native cutthroat trout in the South Fork Snake River, Idaho, with implications for hybridization. North Am J Fisheries Manage 20:584–96.

Holekamp KE, Sherman PW. 1989. Why male ground squirrels disperse. Am Sc 77:232–9.

Howell PJ, Buchanan DV, editors. 1992. Proceedings of the Gearhart Mountain bull trout workshop. Corvallis (OR): Oregon Chapter of the American Fisheries Society.

Johnson LE, Carlton JT. 1996. Post-establishment spread in large-scale invasions: dispersal mechanisms of the zebra mussel *Dreissena polymorpha*. Ecology 77:1686–90.

Knapp RA, Matthews KR. 2000. Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. Conserv Biol 14:428–38.

Knapp RA, Matthews KR. 1998. Eradication of non-native fish by gill netting from a small mountain lake in California. Restor Ecol 6:207–13.

Kot M, Lewis MA, van den Driessche P. 1996. Dispersal data and the spread of invading organisms. Ecology 77:2027–4.

Krueger CC, May B. 1991. Ecological and genetic effects of salmonid introductions in North America. Can J Fisheries Aquat Sci 48(Suppl 1):66–77.

Kruse CG, Hubert WA, Rahel FJ. 2000. Status of Yellowstone cutthroat trout in Wyoming waters. North Am J Fisheries Manage 20:693–705.

Larson GL, Moore SE. 1985. Encroachment of exotic rainbow trout into stream populations of native brook trout in the southern Appalachian Mountains. Trans Am Fisheries Soc 114:195–203.

Larson GL, Moore SE, Carter B. 1995. Ebb and flow of encroachment by nonnative rainbow trout in a small stream in the southern Appalachian Mountains. Trans Am Fisheries Soc 124:613–22.

Leary RF, Allendorf FW, Forbes SH. 1993. Conservation genetics of bull trout in the Columbia and Klamath River drainages. Conserv Biol 7:856–65.

Lee DC, Sedell JR, Rieman BE, Thurow RF, Williams JE, Burns D, Clayton J, Decker L, Gresswell R, House R, and others. 1997. Broadscale assessment of aquatic species and habitats. In: Quigley TM, Arbelbide SJ, editors. An assessment of ecosystem components in the interior Columbia Basin and portions of the Klamath and Great basins. Portland (OR): US Forest Service PNW-GTR-405. p 1057–497.

McFadden JT. 1961. A population study of the brook trout, *Salvelinus fontinalis*. Wildl Monogr 7:1–73.

Miller RR, Williams JD, Williams JE. 1989. Extinction of North American fishes during the past century. Fisheries 14(6):22–38.

Moore SE, Larson GL, Ridley B. 1985. Dispersal of brook trout in rehabilitated streams in Great Smoky Mountains National Park. J Tenn Acad Sci 60:1–4.

Moyle PB, Li HW, Barton BA. 1986. The Frankenstein effect: impact of introduced fishes on native fishes in North America. In: Stroud RH, editor. The role of fish culture in fisheries management. Bethesda (MD): American Fisheries Society. p 415–26.

Nakano S, Kitano S, Nakai K, Fausch KD. 1998. Competitive interactions for foraging microhabitat among introduced brook charr, *Salvelinus fontinalis*, and native bull charr, *Salvelinus confluentus*, and westslope cutthroat trout, *Oncorhynchus clarki lewisi*, in a Montana stream. Environ Biol Fishes 52:345–55.

Nilsson NA. 1972. Effects of introductions of salmonids into barren lakes. J Fisheries Res Bd Can 29:693–7.

Noakes DLG. 1980. Social behavior in young charrs. In: Balon EK, editor. Charrs: salmonid fishes of the genus *Salvelinus*. The Hague: Dr. W. Junk. p 683–701.

Northcote TG. 1981. Juvenile current response, growth and maturity of above and below waterfall stocks of rainbow trout, *Salmo gairdneri*. J Fish Biol 18:741–51.

Pilliod D, Peterson CR. 2001. Local and landscape effects of introduced trout on amphibians in historically fishless watersheds. Ecosystems 4: 322–333.

Platts WS. 1979. Relationships among stream order, fish populations, and aquatic geomorphology in an Idaho river drainage. Fisheries 4(2):5–9.

Power G. 1980. The brook charr, *Salvelinus fontinalis*. In: Balon EK, editor. Charrs, salmonid fishes of the genus *Salvelinus*. The Hague: Dr. W. Junk Publishers. p 141–203.

Pulliam HR. 1988. Sources, sinks, and population regulation. Am Nat 132:652–61.

Reimers N. 1958. Conditions of existence, growth, and longevity of brook trout in a small, high-altitude lake of the eastern Sierra Nevada. Calif Fish Game 44:319–32.

Rose GA. 1986. Growth decline in subyearling brook trout (*Salvelinus fontinalis*) after emergence of rainbow trout (*Salmo Gairdnen*). Can J Fisheries Aquat Sci 43:187–93.

Schlosser IJ, Angermeier PL. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation. In: Nielsen JL, editor. Evolution and the aquatic ecosystem: defining unique units in population conservation. Bethesda (MD): American Fisheries Society Symposium 17. p 392–401.

Stewart JE, 1991. Introductions as factors in diseases of fish and aquatic invertebrates. Can J Fisheries Aquat Sci 48: 110–117.

Thurow RF, Lee DC, Rieman BE. 1997. Distribution and status of seven native salmonids in the interior Columbia River basin and portions of the Klamath River and Great Basins. North Am J Fisheries Manage 17:1094–110.

Townsend CR, Crowl TA. 1991. Fragmented population structure in a native New Zealand fish: an effect of introduced brown trout? Oikos 61:347–54.

Woolfenden GE, Fitzpatric JW. 1984. The Florida scrub jay: demography of a cooperative-breeding bird. Princeton (NJ): Princeton University Press.

Young MK, editor. 1995. Conservation assessment for inland cutthroat trout. General technical report RM-GTR-256. Fort Collins CO: USDA Forest Service.

Appendix A. Stream Morphology and Fish Data

Table A1. For streams with downstream-directed invasions, maximum channel slope and height of known falls over which brook trout dispersed

Stream	Drainage	Max Slope (%)	Height of falls (m)	km Downstream	Brook Trout in lake	Stocking date(s)	Fish Sample Method	Source of Data
SF Blackmare Creek	SF Salmon R, ID	26—site	n/a	11.7-m	yes[a]	1937[b]	DS	This study
Lick Creek	SF Salmon R, ID	24—site	12	17.0-m	yes[a]	1935–72[b]	DS	This study
Moore Creek	St. Regis R, MT	19—site	3.5	3.2-m	yes	ND	E/NS	This study
Warm Springs Creek	MF Salmon R, ID	14—map	n/a	22.4-m	yes	ND	E/DS	C. Zurstadt[c] unpublished
Slate Creek	Salmon R, ID	22—site	n/a	13.4	yes[d]	ND	DS	K. Munson[e] unpublished
Lizard Creek	Selway R, ID	30—map	n/a	8.5	yes[d]	1947[d]	DS	P. Green[f] unpublished
Rhoda Creek	Selway R, ID	50—map	3	18.8 min.	yes[f], no[d]	ND	DS	P. Green[f] unpublished
Running Creek	Selway R, ID	30—map	10	9.3 min.	yes	ND	DS	P. Green[f] unpublished
Buck Lake Creek	Selway R, ID	40—map	18	10.8 min	yes[d]	1940–47	DS	P. Green[f] unpublished
WF Gedney Creek	Selway R, ID	40—map	n/a	5.8 min.	yes[d]	1948	DS	P. Green[f] unpublished
Surprise Creek	Lochsa R, ID	38—site	n/a	10.7-m	ND	ND	DS	(Clearwater BioStudies Inc. 1995b)
Stanley Creek	Lochsa R, ID	48—site	n/a	7.5	yes[d]	ND	DS	(Clearwater BioStudies Inc. 1995a)
Old Man Creek	Lochsa R, ID	24—map	n/a	4.0-min.	yes[d]	1940[d]	DS	(Clearwater BioStudies Inc. 1997b)
Old Man Lake Creek	Lochsa R, ID	37—map	n/a	2.7-m	yes[d]	1940[d]	DS	(Clearwater BioStudies Inc. 1997a)
Chimney Creek	Lochsa R, ID	48—map	n/a	4.9-m	yes[d]	1940[d]	DS	(Clearwater BioStudies Inc. 1997a)
Elizabeth Creek	NF Clearwater, ID	80—site	n/a	0.5	yes[d]	ND[g]	DS	(Clearwater BioStudies Inc. 1993)
Meadow Creek	NF Clearwater, ID	24—map	n/a	8.2-min.	yes[d]	ND	DS	(Clearwater BioStudies Inc. 1993)
Rainbow Creek	SF Clearwater, ID	14—site	n/a	3.4-m	yes	1937–46	E	(D. Mays unpublished data)[h]

Distance brook trout were found downstream of putative lake source is indicated: min. is a minimum estimate of downstream occurrence when either sampling was not conducted downstream or the entry of other tributaries prevents determination of the source of fish found further downstream—m indicates that brook trout occurred all the way to the mouth of the lake outlet stream. Presence of brook trout at the mouth or in steep slopes does not imply that reproduction is occurring there. The stocking dates of the headwater lakes are indicated.

ND, no data available; max, maximum; DS, day snorkel; NS, night snorkel; E, electrofish (day)

[a] *Don Anderson, Idaho Department of Fish and Game, McCall, personal communication.*

[b] *S. Clark, Idaho Department of Fish and Game, Boise, unpublished*

[c] *Lowman Ranger District, Boise National Forest, Lowman, Idaho*

[d] *E. Shriever and P. Murphy, Idaho Department of Fish and Game, Lewiston, Unpublished*

[e] *Slate Creek Ranger District, Nez Perce National Forest, Idaho*

[f] *Nez Perce National Forest, Grangeville, Idaho*

[g] *Stream included based on criteria (c) (see Methods)*

[h] *Crooked River Ranger District, Nez Perce National Forest, Idaho*