

# Mechanisms Limiting a Vertebrate Invasion: Brook Trout in Mountain Streams of the Northwestern USA

by

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Committee Chair: Dr. Christopher A. Frissell

# Abstract

I used multiple approaches to study brook trout invasions in mountainous streams of Idaho and Montana, USA. After studying marked fish in experimental reaches and fish distributions throughout a drainage, I concluded that larger brook trout (95mm) moved more than smaller ones and were probably responsible for most dispersal leading to invasion. Contrary to earlier hypotheses, poor swimming ability did not prevent brook trout from ascending streams with channel slopes of 13 % over 67 m. During the summer, brook trout moved upstream more than downstream even in the steepest experimental areas. Nearly vertical drops in steep reaches rather than steep slopes *per se*, prevented upstream movements. In downstream-directed invasions (originating from headwater lakes), brook trout apparently dispersed downstream through 80 % slopes and over 18-m-high waterfalls and occupied steeper stream channels than they appear capable of ascending.

In the South Fork Salmon River drainage, Idaho, little change in upstream brook trout distribution limits occurred over 25 years. In the three streams where invasion occurred, the average apparent invasion rate was 5 to 11 m per year, suggesting that invasion may have occurred in pulses. Dispersal ability clearly limited invasion in several streams, but not in others. Invasion of accessible habitat is not necessarily inevitable in the short term (several decades), but because brook trout can ascend steep streams, more area is accessible than commonly assumed and may ultimately be invaded.

Brook trout annual growth rate (measured by length at age) declined upstream in a non-lake-fed stream but increased upstream in a lake-fed stream and was correlated with stream temperature in age classes 0 and 1. Later maturation and reduced fecundity associated with slow growth were sufficient to substantially reduce upstream subpopulation growth rate unless compensated by increased survival. Life-stage simulation analyses indicated that early age class survival rates and early maturation had strong effects on population growth. In the non-lake-fed stream, patchier recruitment of age 0 fish and slower growth upstream likely contributed to creating the distribution limit. Patterns and processes observed were consistent with the idea that source-sink dynamics help to sustain distributions of brook trout in streams.

# Dedication

To Casey Adams Quinn, age 4, who has gained his great knowledge of the world in less time than this research has taken.

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# Chapter I. Introduction, Synthesis, and Literature Review

## General Introduction

Invasions by nonnative species have become a major force reshaping many biological communities and a serious threat to the maintenance of biotic integrity worldwide. Biological invasions are cited second only to land use changes as a cause of extinctions, and the two often interact strongly (Miller et al. 1989; D'Antonio and Vitousek 1992). While land use changes are reversible in some instances, species invasions generally are not (D'Antonio and Vitousek 1992; Allan and Flecker 1993). Moreover, aquatic habitat restoration efforts that are successful by abiotic standards may be failures in terms of restoring biotic integrity if they facilitate invasion by nonnative species (e.g. Jude and DeBoe 1996).

Exotic species affect native biota through a variety of mechanisms (reviewed for fishes by Moyle et al. 1986; Allan and Flecker 1993). Introduced species can directly affect native species via predation (mosquito fish, Meffe 1984; brown tree snake, Savidge 1987), competition and interference (*Carpobrotus edulis*, D'Antonio 1993), and hybridization (rainbow x cutthroat trout, Miller et al. 1989; Krueger and May 1991; bull x brook trout, Kanda 1998). Indirect effects include habitat alteration (carp, Allan and Flecker 1993), introduction or spread of diseases (avian malaria, Brown 1989; reviewed for freshwater fauna by Stewart 1991; western toads, Blaustein et al. 1994) and parasites (fishes, Allan and Flecker 1993), and growth reduction resulting from behavioral changes (Resetarits 1995; Kiesecker and Blaustein 1998). Some effects, such as changes in disturbance regimes, actually represent changes in ecosystem function (e.g. feral pigs and grass/fire cycle, D'Antonio and Vitousek 1992).

As with other taxa, fish introductions have occurred on a global scale. More than 160 exotic species occur in 120 countries (reviewed by D'Antonio and Vitousek 1992), and many more fishes have been moved to new habitats within countries. Twenty of the 46 fish species in New

Zealand are exotic. In the continental United States, introduced fishes generally constitute less than 10% of the fish species in drainages east of the continental divide but 35 to 59% in the west (Moyle et al. 1986). Introduced species more frequently dominate the faunal assemblages of western than eastern streams. For example, nonnatives comprised about 39 % of the total taxa (includes species, subspecies, and races) in the upper Columbia River basin (northwestern USA), and nonnative outnumbered native species in about 20 % of the watersheds analyzed (from Figure 4.18, Lee and others 1997).

Endangerment of aquatic fauna is relatively high compared to other ecosystems and introduced species have contributed to this endangerment (Allan and Flecker 1993). While most fish extinctions in North America during the 20th century have had multiple causes (Frissell 1993; Young 1995b), species introductions contributed to 68% of the extinctions and hybridization (often linked to introduced species) to 38% (reviewed by Miller et al. 1989). The rate of establishment by exotic fishes in the USA continued to rise in the 1980's, due in part, to demand by anglers (Moyle et al. 1986).

Brook trout *Salvelinus fontinalis*, a char native to eastern North America, were widely introduced, beginning in the late 1800's, resulting in established populations in cold-water streams and lakes throughout the western U.S. and Canada (MacCrimmon and Campbell 1969). Most western states have drastically reduced or completely stopped stocking brook trout, but in Oregon extensive stocking of brook trout in headwater lakes

continues (personal communication, Terry Farrell, Oregon Department of Fish and Wildlife). Bahls (1992) estimated that 70 % of the mountain lakes in Oregon contained brook trout. At a watershed scale, brook trout were the second most widely distributed fish species in the upper Columbia River basin, surpassed only by nonnative rainbow trout (Lee and others 1997).

Brook trout have often been implicated in the demise of native salmonids, particularly bull trout *S. confluentus* (Buckman et al. 1992; Dambacher et al. 1992; Markle 1992; Ratliff and Howell 1992; Leary et al. 1993; Rieman and McIntyre 1993; Adams 1994) and cutthroat trout *Oncorhynchus clarki* spp. (Griffith 1988; Fausch 1989; Behnke 1992; De Staso and Rahel 1994). Statements that brook trout displace native species are generally followed by the qualification that the mechanisms of displacement are unclear (Young 1995b). However, in many circumstances, the process in question may be replacement (nonnative species invading *after* declines in native) rather than displacement (nonnative *causing* declines of native)(Griffith 1988). The distinction is important both for mechanistic understanding of the invasion process and for guiding management responses to potential invasions.

Understanding the mechanisms controlling invasion is critical to predicting invasion success for a given species and habitat, but such predictive capacity will not come easily. Invasion involves two components, dispersal and establishment, and either or both can limit the invasive ability of a plant or animal in a given habitat (D'Antonio 1993). Moreover, the factor(s) limiting invasion can vary over surprisingly small spatial scales (D'Antonio 1993). Additional factors can influence persistence time once an exotic species has invaded a habitat (Meffe 1984; Larson et al. 1995). Abiotic and biotic characteristics of the new location, as well as the ecology of the nonnative species, will determine success of establishment (Crowl et al. 1992)(Table 1). If the physical or biotic environment is only occasionally suitable for brook trout reproduction, rearing, or survival, invasion may proceed more slowly than in a more constant environment. Conversely, Gowan et al. (1994) suggested that dispersal rates may be higher in streams with more spatial or temporal variability, which could conceivably contribute to faster brook trout invasion in unstable stream systems.

The need for better understanding of the mechanisms of brook trout invasion is highlighted both by declines in native salmonids and by expensive and potentially harmful actions taken to prevent invasions. The assumptions that 1) brook trout invasion of accessible habitat is inevitable and 2) they displace native salmonids, has led managers to construct dispersal barriers to prevent further brook trout invasion (Young 1995b). Besides frequently being ineffective due to structural inadequacy or social rebellion (people moving fish upstream)(Behnke 1992; Thompson and Rahel 1998), artificial barriers may disrupt adaptive movements (Gowan et al. 1994) and increase isolation of native fishes (Dunham et al. 1997). Understanding the biotic and abiotic conditions or changes in conditions that promote versus inhibit invasion, the frequency and rates of ongoing invasions, and the factors influencing the persistence of established populations can allow more effective approaches to several management goals: 1) minimizing or reversing invasions, 2) prioritizing populations of native species for conservation, and 3) planning biologically effective restoration strategies for native species/assemblages. With the results of my research, I begin to fill gaps in our knowledge regarding factors inhibiting invasion and rates of ongoing invasions. However, due to the spatially and temporally changing nature of the limiting factors, and perhaps changes in the invaders themselves, accurate predictions of brook trout invasions will probably always be elusive.

Chapters in this dissertation are organized as potentially publishable units, so some repetition occurs. The "terminology" section below is applicable to all chapters. The "literature review" section is slightly redundant with chapters 2-4 but presents a more cohesive review of the literature on brook trout movements. Chapter 2 describes a mark-recapture experiment designed to compare up- and downstream movements by brook trout in stream reaches with average slopes ranging from < 1 to 12 %. In Chapter 3, I report the amount of invasion in tributaries of the South Fork Salmon River, Idaho, over a 25 year period, and make inferences about factors inhibiting invasion based on the patterns of invasion, or lack thereof. In Chapter 4, I compare dispersal and invasion in streams invaded from headwater lake source populations versus downstream source populations to further explore dispersal limitations and reproduction as factors limiting invasion. Chapter 5 summarizes detailed brook trout demographic data collected in two contrasting Montana streams, one invaded from the downstream end and the other from a headwater lake. In Chapter 6, I present population modelling results to explore the possibility that the upstream brook trout distribution limits (in one of the Chapter V streams) could be determined by a combination of slow fish growth in upstream reaches and source-sink population dynamics.

## Terminology

Some terms that are defined loosely in ecological literature and that I use throughout the dissertation are defined here for clarity. A nonnative species is one that did not naturally, or historically, occur in a location. "Movement" includes a variety of behaviors including travels within a home range, round trip migrations within a season or a lifetime, and explorations beyond the home range (Stenseth and Lidicker 1992). "Dispersal" refers to movements that are unidirectional away from the home range (Lidicker and Stenseth 1992) or that lead to reproduction in another location. Exploratory movement becomes dispersal (or indistinguishable from it) when an organism fails to return "home" for whatever reason (Lidicker and Stenseth 1992). Establishment is the formation of a self-maintaining population at a site. "Invasion" is a result of both dispersal to a site (or introduction by humans) and establishment of a reproducing population there. Downstream-directed invasions occur where fish were introduced into a headwater lake and subsequently dispersed downstream, resulting in secondary invasion of the outlet stream. Conversely, upstream-directed invasions are the result of fish dispersing upstream from a source population lower in a drainage. Colonization is similar to invasion but does not necessarily involve an introduced species and can include habitat that was only temporarily unoccupied by the species (after Sheldon 1984).

## Synthesis

I used observational, experimental, and modelling approaches to investigate the mechanisms and limitations of brook trout invasions in mountain streams. The overarching conclusions are that invasion is limited by different factors in different locations, and that complex suites of factors operating on a variety of processes can contribute to limiting invasion. Extreme or lethal conditions are not necessary to limit invasion, rather, subtle declines in demographic rates can apparently be sufficient to create a distribution limit.

Dispersal ability, which has been assumed to be important in limiting invasion of steep streams, is a prime example of a factor with varying, site-dependent importance in limiting invasion. In some streams, such as those with complete barriers to upstream migration (e.g. waterfalls), dispersal ability was clearly the dominant factor preventing further invasion. However, in other streams where brook trout invasion had stalled, or never started, dispersal ability was evidently not a limiting factor. Several streams repeatedly received wandering or dispersing brook trout, but were not invaded. Brook trout ascended slopes of 13 % over at least 67 m and steeper slopes over shorter distances. Brook trout will disperse downstream over precipitous channel slopes (80 %) and high (18 m) waterfalls. In downstream-directed invasions, brook trout occupied channels with steeper slopes than those they ascended in upstream-directed invasions.

Detailed study of demographic processes and population structure in one stream, combined with population modelling, indicated that a gradual upstream decline in fish growth rate was probably a major contributor to creation of the upstream distribution limit. Also, near the upstream limit, the incidence of reaches in which I observed no age 0 fish increased. Source-sink population dynamics may have been important in maintaining the brook trout distribution in the stream. Thus, all factors that caused declines in fish growth, reduced recruitment of age 0 fish, and inhibited dispersal from source areas may have contributed to limiting invasion in the stream. If source-sink dynamics typify stream populations of brook trout, then reproductive excesses in source areas, reproductive deficits in sink areas, and the proximity and connectivity between source and sink areas will all influence the extent of invasion, immensely complicating the task of determining what limits invasion in some systems.

Brook trout typically mature early and die young. In modelling brook trout populations, I found that early maturity and survival in early age classes strongly influenced population growth rates. Survival of adult age classes generally had little effect. It appears that where conditions allow rapid growth, brook trout are well adapted to sustaining populations under conditions of high fishing mortality. However, some salmonids native to the area (e.g. bull trout and westslope cutthroat trout) mature later and are typically longer-lived. Thus, fishing may favor brook trout over native species and contribute to species replacement in some systems.

Some results also provided insights into the mechanisms of invasion. Based on both experimental and observational results, it appears that movements over long distances and through moderate to steep slopes are primarily the domain of larger, older brook trout. Swimming ability typically increases with fish size, so increased fish growth and survival could also result in larger fish that have better dispersal abilities. Such a change could particularly facilitate invasion in steep streams where the ability to ascend nearly vertical drops should increase with fish size. The very slow rate of invasion in some streams suggests that invasion may occur in pulses rather than as a steady process. Brook trout are probably capable of ascending some stream features (e.g. falls or short, steep drops) only occasionally. High streamflows during periods of strong motivation for dispersal may result in fish ascending features that have prevented dispersal for seasons or years.

## Implications for management

Any changes to a watershed that may increase brook trout growth rate or survival of early age classes may increase invasion as a result of increased population growth rate. Increases in stream temperature (up to about 15 oC) and the quality and/or quantity of food available (e.g. via increased nutrient loading and reduced shading) are expected to result in faster brook trout growth. The role of other fish species in influencing growth rate and survival of brook trout in streams is not known.

Some fish distribution patterns I observed provided circumstantial evidence that biotic resistance may be important in limiting or preventing invasion in some streams. If biotic resistance minimizes invasion, then maintenance of strong populations of native fishes is critical to minimizing invasion. Habitat degradation, as well as fishing, can contribute to declines of native populations and thus, may facilitate invasion. Also, if blocking movements of native fishes reduces their population growth rate, then creating a physical barrier to prevent brook trout dispersal may ultimately set the stage for more extensive invasion if (or when) the barrier is breached.

Creation of brook trout source areas, characterized by high growth and survival rates, may cause expansion of distributions in distant, but connected, stream segments. Therefore, the potential for increased offsite invasion should be considered in analyses of any projects that have the potential to create or expand source areas. Invasion of marginal stream environments may be as much a function of proximity and connection to source areas as of characteristics of the marginal environment itself.

## Future research

Useful avenues of research that could increase understanding of brook trout invasion processes can be placed into three general categories: reach-scale demographic processes, population and metapopulation processes, and landscape associations. The theme of understanding how and to what degree interspecific interactions influence invasion recurs in all categories.

Demographic processes include birth, death, immigration, and emigration. Factors that influence brook trout growth, and thus birth processes, while far from completely understood, are probably the best studied of the three. The potential effect on growth of increased nutrient loading following watershed disturbance warrants research. Interspecific influences on growth in natural settings (e.g. not in labs or small cages) remain a mystery. The importance of reach- and habitat-level variations in survival have not been explored, to my knowledge, and may provide important clues to the limitations on invasion. Interspecific interactions relevant to invasion seem likely to be expressed in survival rates of early age classes. The role of fishing mortality in facilitating invasion and species replacement or displacement is an extremely important avenue of research.

Movements are an intuitively obvious process to consider in invasions. I have shown that swimming ability of brook trout in steep streams is better than has been commonly assumed. Yet understanding the linkage between the ability to ascend a stream reach and actually colonizing a new location will require extensive research, some of which is likely not feasible with present techniques. Furthermore, beyond the initial inoculation of a reach with brook trout, the importance of dispersal to maintaining distributions of invading stream fishes has received minimal attention. Four questions are particularly relevant to understanding the linkages between movements and dispersal leading to reproduction. How much of the documented movement results in dispersal? How much dispersal results in successful reproduction? What factors influence whether or not a fish

returns to its natal area after moving away? What factors motivate dispersal? I believe that the last two questions are the most important. We know that some movement results in fish reproducing in new habitats. What is critical to management of stream ecosystems is understanding how human activities influence fish dispersal. Human activities undoubtedly have some effect on whether fish leave their natal habitat and on whether they remain in a new location.

Population-level processes warranting research include metapopulation processes, understanding how new populations are established or re-established, understanding influences on the persistence of nascent populations, and source-sink dynamics at several scales within populations. The latter could be effectively studied by selectively blocking migrations or by removing source populations. Dispersal processes in large rivers and invasion of neighboring streams are virtually unexplored.

Landscape associations are large scale features of the habitat that are repeatedly associated with invasion, or lack thereof. If such associations exist, they would be useful for predicting invasion. If source-sink processes are integral to invasion, developing an ability to predict source areas based on habitat features (e.g. gradual channel slopes, groundwater upwelling, and lateral complexity) would be invaluable. Identifying the importance of proximity to a source area for invasion of less ideal habitat would further refine our predictive abilities. On a finer scale, determining the importance and characteristics of reproductive nodes may increase our knowledge of both the mechanisms of and the limitations to invasions. Our knowledge of invasion in marginal habitats would be increased by simply including steep stream reaches and headwater stream segments in routine stream fish surveys.

Finally, investigating biotic resistance to invasion is extremely important to understanding invasion and to appropriately managing streams to conserve native fishes and minimize invasion. Understanding of biotic resistance to invasion will require research at a variety of scales from interactions among individual fish to reach- or stream-scale manipulations to analyses of species distributions and population structures over large areas.

Of all of the research ideas mentioned, I suspect that the highest ratio of information to effort could come from the investigation of source-sink processes. The research effort could be coordinated with management efforts to eliminate brook trout from source areas, such as lakes, or to construct barriers to migration. Streams that contain no fishes other than brook trout are good candidates for large scale population manipulations. As an added benefit, the results of source-sink studies are likely to be applicable to conservation of native salmonids as well.

## Literature Reviews

### Brook trout movements

Movement by stream salmonids is "a potentially common and important phenomenon" (Gowan et al. 1994). Funk (1957) introduced the idea that stream fish populations may often consist of a relatively sedentary component and a more mobile component of wide ranging individuals. He also suggested that the degree of movement depends on habitat and season. The degree of movements by salmonids is important to invasion as it presumably reflects dispersal ability, if not dispersal tendency. Goldwasser et al. (1994) demonstrated that even a few wide ranging individuals greatly increased the rate of spread of a simulated population, and including variability of individual movements resulted in even faster spread.

The conclusions reached in studies of fish movement are often relative to the research methods used (Gowan et al. 1994). While many mark-recapture studies conclude limited movement by stream fishes, nearly all radio telemetry studies indicate some individuals moving long distances (Gowan et al. 1994). Studies of wild (native or naturalized) brook trout movements to date can be separated into four categories according to the methods employed: 1) mark and recapture with minimal manipulations; 2) mark and recapture with alterations of fish communities, populations, or habitats; 3) radio telemetry (one study); and 4) defaunation and recolonization.

#### Mark-recapture without manipulations

I reviewed seven studies of brook trout movement in which the only manipulation was the capture and marking of fish (Table 2). All were in streams with "low" to "moderate" channel slopes. In all studies reviewed, at least one fish was located farther than 1.6 km from the tagging location, and in most, fish were found farther than 3.2 km away. Shetter (1968) found 12% of recaptured fish between 1.6 and 17.7 km from the tagging site. In the steepest stream (up to 1.6%) studied by Shetter (1968), all recaptures of marked fish were made within 1.6 km, indicating that channel slope may have influenced movement.

In general, recaptures of marked fish indicated that a substantial proportion of each population moved less than several hundred meters. However, proportions of unmarked immigrants, changes in standing stocks, and captures of fish in weirs revealed that movement was an important process in most, if not all, brook trout populations studied (Holton 1953; Saunders and Smith 1955; McFadden 1961; Hunt and Brynildson 1964; Hunt 1965; Shetter 1968).

The role of fish density in stimulating movements was unclear. McFadden (1961) found more movement upstream into a refuge area (with no fishing) than downstream out of it even though density in the refuge was 79% higher than in the downstream sections. Hunt (1965) observed greater movement by age 0 brook trout among sections as densities of that age class increased. The lack of a clear relationship between density and emigration may reflect, in part, a failure to quantify the habitat area actually suitable for a given size class of fish.

#### Mark-recapture with manipulations

Three studies that employed weirs to estimate fish movements after various ecosystem manipulations all concluded that upstream movements of brook trout were more common than downstream movements (Table 3)(Saunders and Smith 1962; Flick and Webster 1975; Riley et al. 1992). Flick and Webster (1975) observed both long migrations and localized movements.

The motivations for brook trout movements remain elusive, but these studies resulted in numerous hypotheses about factors that stimulate movements. Some studies contained circumstantial evidence that higher fish densities resulted in more fish movement. The creation of a pond that increased "living space" resulted in the virtual cessation of emigration from a small stream (Smith and Saunders 1967). Saunders and Smith (1962) found that transplanted fish left sites more often than did prior residents. Riley et al. (1992) hypothesized, based on their results, that primarily subordinate fish were moving and that the most subordinate moved downstream. Habitat quality appeared to influence emigration and/or immigration rate (Saunders and Smith 1962; Riley et al. 1992). More immigrants resided in experimentally improved sites in Colorado streams, but the increased immigration and/or decreased emigration did not occur during the summer when weirs were in place (Riley et al. 1992).

Only one study, conducted in the GSMNP, examined brook trout movements in steep (8 - 18% slope) streams (Moore et al. 1985). Even in such steep slopes, some brook trout moved more than 900 m during the four year study, and several moved between tributaries.

Moore et al. (1985) noticed that after removing rainbow trout from high gradient (15%) stream reaches where they were sympatric with brook trout, the latter moved upstream into vacant habitat but not into allopatric brook trout populations. The authors concluded that an upstream brook trout population may serve as a biological barrier to dispersal by downstream brook trout. However, they did not discuss why rainbow trout had not invaded these areas, leaving open the possibility of some undetected physical or chemical deterrents to dispersal. Laboratory studies of chemodetection and behavior suggest that brook trout and other chars prefer water conditioned by the presence of conspecifics to unconditioned water (Selset and Døving 1980; Foster 1985; Olsén 1985; Keefe and Winn 1991; Sveinsson and Hara 1995).

### Radio telemetry

Chisolm et al. (Chisholm et al. 1987) used radio telemetry to follow the winter movements of brook trout in high elevation (>2,990 m) Wyoming streams. Seven fish tagged in four meadows all remained in the meadows from October through March. All were active, moving between pools, throughout the period. Net distances traveled ranged from 0 to 206 m and were biased downstream. Eight fish were radio tagged in October in a moderately steep (>4%) reach 50 to 310 m upstream of a beaver pond. The area was bounded by a waterfall upstream and a beaver dam downstream. Within two weeks, six of the fish moved an average of 163 m downstream to the pond, where they remained throughout the 127 day study. Two fish resided in lateral pools in the steep reach and had net movements of about 35 m.

### Repatriation

Nagel (1991) repatriated brook trout into a gently sloping segment of a Tennessee stream occupied by nonnative rainbow trout and reduced densities of the latter each summer for three years. Within one year, brook trout had moved at least 1.5 km upstream, apparently aided by high flows (J. Nagel, personal communication). By the third year, reproducing populations of brook trout were sympatric with rainbow trout both upstream and downstream of the reduced-density section.

In summary, movements of several kilometers or more apparently occur in many brook trout populations. Habitat size and quality apparently have some influence on seasonal and ontogenetic movements, but their role in stimulating movement is still unclear. In some studies, habitat seemed to influence emigration more than immigration, implying that fish were exploring and stopped only when they found appropriate conditions. The proximity of suitable summer, winter, and spawning habitats also appeared to influence seasonal movements. The relationship between density and movement was not entirely consistent, but higher densities were generally at least weakly associated with greater movement. The following avenues of research could improve our ability to link what is known about movements to the invasion process: 1) determine motivations for dispersal, 2) distinguish between migration and dispersal, and 3) examine reproductive success of dispersers in a new environment.

## Influence of impoundments on upstream fish communities: the importance of source populations

Fish assemblages in upstream reaches can be strongly influenced by assemblages (McDowall 1998) and disturbances (Pringle 1997) downstream. For example, more warmwater fish species occurred in mainstem tributaries than in similar sized streams near a drainage headwaters, possibly due to immigration from a richer species source pool in the mainstem (Osborne and Wiley 1992). Frequently, conditions in an unoccupied or recently invaded habitat are analyzed for characteristics conferring invasibility while characteristics of the source habitat and population are disregarded (Sheldon 1987). Characteristics of source, receiving, and intervening matrix communities can all exert control over the invasion process (Lidicker and Stenseth 1992)(Chapter 3). Habitat and/or faunal changes in downstream source or matrix areas can influence the invasion of distant, unchanged habitats upstream (Pringle 1997).

The influence of impoundments on upstream fish communities provides a classic example of downstream-upstream linkages. Changes in species composition, age and size structure of populations, sex ratio, and fish behavior were observed in tributary streams after filling of reservoirs downstream (Ruhr 1956; Crisp et al. 1984; Erman 1986; Winston et al. 1991). In some instances, fish populations in the reservoir and tributary streams had source-sink relationships (e.g. Ruhr 1956), whereas in other cases, one large population apparently occupied both habitats (Erman 1986).

Ruhr (1956) documented large populations of four nonnative fish species ("lake fish") occupying streams upstream of reservoirs but not unimpounded streams in Tennessee. The lake fishes reportedly had little or no reproduction in the streams and apparently emigrated from the reservoirs due to population pressures there. Surprisingly, in unobstructed streams, population size did not decrease with increasing distance from the reservoir for up to 120 miles (where the study ended). In streams with features inhibiting, but not entirely preventing dispersal, small populations of some lake fishes occurred above the barriers.

Crisp et al. (1984) found that the distribution of bullheads (*Cottus gobio* L.) extended farther upstream after than before downstream impoundment. No habitat changes were evident upstream. The densities of brown trout (*Salmo trutta*) fry in the same streams increased 300 to 1100%, probably due to the larger size of spawners from the reservoir. Also, larger spawners presumably buried their eggs deeper, rendering them less susceptible to spates. This may explain why the two flashiest streams experienced the greatest changes in fish populations after impoundment.

## MECHANISMS LIMITING A VERTEBRATE INVASION:

Increased trout populations in the uppermost stream sections were apparently supported by immigration from the middle and downstream reaches where lake-dwelling brown trout spawned.

Damming of the Speed River, Ontario, led to upstream changes in species composition and, possibly, production (Penczak et al. 1984). Two years after damming, fish production at a site 5 km upstream of the reservoir was 3.5 times higher than the pre-impoundment level, but no estimate of natural interannual variation in production was presented. Three species were present in the upstream reach that were not found there prior to impoundment, and one species had disappeared from the site. Other species present before impoundment held different ranks of relative density and biomass after impoundment. The changes were attributed to the effects of fishes emigrating from the reservoir.

In Sagehen Creek, California, the stream reach directly above a reservoir experienced instability in the fish community after impoundment (Erman 1973; Erman 1986). Brook trout in the lower reach, and two other species in the entire stream, were rare or absent 13 years after impoundment (Erman 1986). Two more species had extreme fluctuations in absolute and relative abundances, possibly due to changing conditions in the reservoir and/or to interactions with each other. Effects on communities in the middle and upper reaches were slight, but Erman suggested that stabilization of reservoir levels might increase upstream encroachment.

Winston et al. (1991) observed that four cyprinid species, all common elsewhere in the drainage, were absent upstream of a reservoir. Two other minnow species were 10 times more abundant above the reservoir than in nearby streams. Six other species were also more abundant above than below the impoundment. Fish species richness was lower upstream of the reservoir than downstream or in similar streams.

The profound influences that downstream activities can have on upstream populations is one illustration of the importance of the source population characteristics to invasion. In this study, I consider two aspects of source populations: location relative to potentially invadable habitats and demographics. Certainly much more remains to be learned about the role of source populations in invasions in general. In particular, understanding processes or conditions in source areas that motivate dispersal could vastly improve our understanding of brook trout invasions.

Table 1. Some factors likely to influence invasions by lotic fishes. Most factors are temporally variable.

### **Dispersal**

#### Abiotic

- physical barriers, e.g. waterfalls, dams
- habitat in source area
- habitat between source population and receiving habitat (corridor)
- distance from source to receiving habitat

#### Biotic

- swimming/jumping ability of invading species (size dependent)
- fish density in source habitat
- food availability in source habitat
- presence, density, and population structure of other fishes/predators in source, corridor, and receiving habitats
- health and condition of dispersers

### **Establishment** (conditions in receiving habitat)

#### Abiotic

- suitable habitat for various life stages: spawning, rearing, adult, overwinter
- temperature regime
- disturbance regime (also influences persistence)

#### Biotic

- number, maturity, fecundity and survival of dispersers
- food availability
- predation
- competition
- other behavioral interactions

-disease/parasitism

-Allee effect if small number of dispersers

Table 2. Summary of mark and recapture studies of movement by wild brook trout in which no manipulations other than marking fish were employed. Abbreviations are: "yr." = year; "recaps." = fish recaptured after marking; "mod." = moderate; NR = not reported.

Location	Average stream gradient	Number marked	Recaptures	Study duration	Methods	Conclusions	Source
Montana	< 1%	87	17 % (15 fish)	1.25 yr.	Recaps by electrofishing and creel surveys in and outtagging location. 1 fish moved of marking sections.	21 recaps. within 183 m of 3.7 km upstream.	(Stefanich 1952)
Montana	"low"	4216 wild & hatchery fish (3 spp.)	0.15% of wild fish (17 brook trout)	1 yr.	Recaps. obtained by electrofishing in marking sections.	Recaps. of wild fish indicated little movement. 28 brook trout moved > 152 m from marking location. 5 "trout" (species NR) moved > 1.6 km. High turnover of fish. Hatchery brook trout moved throughout the 4 km study area.	Holton 1953
New Brunswick(sea-run)	"low"	611 age 0 1197 older	6.4 % 17.4 %	8 yrs.	Electrofished 411 m. Recaps. obtained by creel surveys and electrofishing in and out of marking section, and with weirs downstream.	6.4% of age 0 fish in the study section after 1 year. 17.4 % of age 1+ fish recaptured in same creek. Of age 1+ fish in study section, 41-61 % were immigrants. Extensive immigration and emigration.	Saunders and Smith 1955
Wisconsin	"mod."	87% of all trout	NR	3 yrs.?	Marked fish from headwaters to a pond (5.3 km). Electrofished in September and April. Recaps. via complete creel census.	A few fish moved >3.2 km up- or downstream. More up- than downstream movement in headwaters. Standing stock considerably influenced by movement.	McFadden 1961
Wisconsin	"mod."	55 - 87% of all fish	>3900 adults; >3500 age 0	5 yrs.	Methods similar to McFadden (1961) but age 0 were marked in June, and sites were re-sampled in September.	Age 0 immigrants contributed up to 11 % of population per section. 1,303 age 0 fish immigrated to and 2,248 emigrated from headwater "refuge" during summers.	Hunt and Brynildson 1964
Wisconsin	"mod."	NR	8500 - 22,000 per year	4 yrs.	Similar to Hunt and Brynildson (1964) but studied only age 0 fish.	Age 0 fish from each section recaptured in all sections. In summer, age 0 fish moved down- more than upstream. Up- versus downstream movement varied by section.	Hunt 1965
Michigan	0.5 to 1.6%	3,310 (>17.8 cm)	346 (10.4%)	33 yrs.	Fish collected by seining and electrofishing in 4 km of Hunt Cr. and part of the Au Sable R.. Anglers provided recaps.	65% of recaps. were within 152 m of marking location; 12% were between 1.6 and 17.7 km away. 1 recap. in another creek. All Hunt Cr. recaps. within 1.6 km.	Shetter 1968

Table 3. Summary of mark and recapture studies on movement by wild brook trout in which fish populations, communities, or habitats were manipulated. "Recaps." are fish recaptured after marking.

Location	Average channel slope	Number marked	Recaptures	Study duration	Methods	Conclusions	Source
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MECHANISMS LIMITING A VERTEBRATE INVASION:

New Brunswick	"low"	691	>600 (repeat recaps)	2 yrs.	1-way and reciprocal transplants of all ages of native brook trout into vacant and occupied habitats during summer 1.	4 fish moved up to 2 km to "home" sites over one year. Transplants moved up- more than downstream. Transplants left sites more than prior residents.	Saunders and Smith 1962
New York	<0.1%	1000's	NR	13 yrs.	19 km study reach with 5 weirs operated May to November. Fish caught by weir, angling, traps and electrofishing. Marked fish >15 cm and some smaller fish. Non-salmonids removed each year.	Movements were biased upstream. 50-70% of all weir captures were in spring and < 10% in summer. "Long migrations" and localized movements occurred. After 7 years, movements by all species virtually ceased.	Flick and Webster 1975
Tennessee	8 - 18%	1702	25% (422)	4 yrs.	Contiguous 300 m sections electrofished annually. Up to 300m upstream and 900 m downstream of marking sections sampled for recaps. Some dispersal barriers existed. Rainbow trout removed from all sites 1st year and some sites later years.	83% of recaps. were within 300 m of marking section. 7.9% of recaps. had moved >900 m up- or downstream. Several fish moved between tributaries. Limited movement by age 0 - 1 fish.	Moore et al. 1985
Colorado	1 - 2.4%	~ 95 % of fish per section	22 - 42 %	4 yrs.	Electrofished adjacent 250 m sections . Cover and pool volume artificially increased in treatment sites. 2 streams had weirs in summers.	Several fish moved > 500 m. Movements differed between streams and years. Sections with improved habitat had more immigrants, but not due to summer movements.	Riley et al. 1992
Colorado	2.0 - 2.7%	4,005	28 %	4 yrs.	Methods similar to Riley et al. (1992); 2 streams. Weirs operated summer to fall for 3 years and intermittently for 1 year. Electrofished sites 4,500 m apart.	59% of fish moved 50 m (up to 3,380 m). Numerous fish moved 2 km. Highest movement rates in spring, then fall. Moving fish were longer but in poorer condition than average.	(Gowan and Fausch 1996b)

## Chapter II. Movements of Nonnative Brook Trout in Relation to Stream Channel Slope

### Abstract

I provide new insights on the ability of naturalized brook trout (*Salvelinus fontinalis*) to ascend steep, headwater streams. I tested the hypothesis that poor swimming ability prevents upstream dispersal by brook trout in steep streams and explains the paucity of brook trout invasions in such streams (Fausch 1989). I compared brook trout movements in sites with channel slopes ranging from < 1 to 12 % in headwater streams in Idaho. After removing fish from 200 m stream reaches, I assessed immigration of marked fish into the reaches. During the summer, upstream movements were more prevalent than downstream movements, even in steep streams. Marked brook trout ascended stream channels with slopes of 13 % over 67 m and 22 % over 14 m and ascended a 1.2 m-high falls. Nearly vertical falls, rather than steep slopes *per se*, apparently inhibited upstream movements. 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). Immigration by marked fish smaller than 95 mm was uncommon in all sites. While other mechanisms may inhibit brook trout invasion in steep channels, slopes up to 12 % do not ensure against upstream dispersal. However, in very steep channels, fewer dispersers and slower upstream movement rates may increase the time required for, and reduce the likelihood of, successful invasion.

# Introduction

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. In Press), as well as other vertebrate and invertebrate fauna (Dawidowicz and Gliwicz 1983; Bradford 1989; Bechara and Moreau 1992; Bradford et al. 1993). While much has been learned about habitat use and demographics in established brook trout populations, the mechanisms of, and limitations to, invasions have received little attention.

The ability to predict the biotic and abiotic conditions under which brook trout are likely to expand their distribution in a drainage is crucial to efficient application of limited resources for conserving and restoring native salmonids in the western USA. Many conservation plans for native trout rest on the untested assumption that steep channel slopes preclude invasion by brook trout from downstream sources. Recently, concern over declines in and local extirpations of bull trout (*S. confluentus*) and cutthroat trout (*O. clarki*) has led to attempts to eradicate brook trout from streams and to the construction of barriers to prevent their re-entry (Dambacher et al. 1992; Thompson and Rahel 1998). Artificial barriers have also been considered as a means to prevent invasion by brook trout in places where they have not previously occurred (Kershner 1995; Thompson and Rahel 1998), even though biologists' ability to predict future invasions is limited. Barriers may hinder movements of native fishes, which could disrupt traditional migration and dispersal patterns (Gowan et al. 1994) and exacerbate declines in native fishes by increasing population fragmentation and isolation (Young 1995b; Dunham et al. 1997). Furthermore, removing a fish species from a stream and preventing recolonization are expensive, labor intensive processes if they can be accomplished at all (Moore et al. 1986; Gresswell 1991; Thompson and Rahel 1998).

Invasion requires both dispersal and establishment of a self-sustaining population. Either or both can limit the invasive ability of a plant or animal 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).

Numerous studies have evaluated brook trout movements, but nearly all were conducted in gradual (< 2 %) to moderate (> 2 - < 6 %) stream slopes (Saunders and Smith 1955; reviewed in Gowan and Fausch 1996b). Although many of the studies were biased toward finding limited movement (Gowan and Fausch 1996b), some fish were found farther than 3.2 km away from release locations in most studies. 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). 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).

I know of only one published study of brook trout movements in steep streams. Moore et al. (1985) examined brook trout movements in streams with slopes of 8 to 18 % within the Great Smoky Mountains National Park (GSMNP). Marked brook trout moved more than 900 m up- and downstream during the four year study, and several moved between tributaries. Ecological comparisons between brook trout in southern (e.g. GSMNP) and western regions of the USA should be made cautiously, however. Substantial genetic differences apparently exist between populations in the southern and northern portions of the native range (Stoneking et al. 1981). Since northeastern populations were presumably the ultimate source of most brook trout introduced into the western USA, populations in the southern and western regions of the USA may have substantial genetic, physiological, and ecological differences. Thus, behaviors of brook trout in GSMNP are not necessarily relevant to populations in the West.

Questions regarding dispersal abilities of brook trout arise, in part, from the observed distribution of the fish. In the West, 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 the lower abundance of brook trout in channels with steep (>7 %) than with more gradual slopes in the presence of cutthroat trout: 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 since most brook trout were stocked 50 to 100 years ago, but considered the first and third plausible.

In this paper I report on an experiment designed to test Fausch's first hypothesis. I conducted a fish removal and recolonization experiment to compare the tendency of brook trout to move through steep versus gradual channel slopes. I also identified short-term barriers to upstream movements. I compared numbers and sizes of fish moving and distances moved, as well as the rate of immigration into stream reaches from which fish were removed. I predicted that upstream movement would decrease with increasing channel slope and that downstream movement would be more prevalent than upstream movement in steep sites. I expected to find little, if any, upstream movement in the two steepest sites.

## Study Area

The six experimental sites were located in four tributaries of Johnson Creek (Valley County, Idaho), a major tributary of the East Fork of the SF Salmon River (Figure 1). I refer to a previously unnamed, north-flowing tributary of Sheep Creek as Hillbilly Creek. Stocking records indicate that brook trout were stocked in the SF Salmon River drainage from 1932 to 1972 (unpublished data, Idaho Department of Fish and Game, Boise), although unrecorded stocking presumably occurred earlier and/or later. Historically, native bull, cutthroat and steelhead/rainbow trout, and chinook salmon (*O. tshawytscha*) probably inhabited at least several of the study sites.

The study area is located within the Idaho batholith, where streams tend to have relatively high levels of fine sediments and low fertility (Platts 1979a). The high elevation (average 2,069 m) forests were dominated by lodgepole pine (*Pinus contorta*). All experimental sites were in small, low-conductivity streams with channel slopes varying from less than 1% to 12 % (averaged over entire sites) (Table 1, Figure 2). In both the

Hillbilly Creek and upper Sand Creek sites, channel slopes exceeded 18 % for at least 15 m. All six sites were accessible to cattle until 1993, when all cattle grazing in the upper Johnson Creek drainage ceased.

The two Rock Creek sites were contiguous. The upper site was in a gradually sloping channel with abundant gravel substrate in a moderately confined, wooded valley. The lower site was in a steeper, moderately confined, wooded valley with gravel, cobble and boulder substrate. A 0.7 m-high falls (Figure 2C, step 1) was located just downstream of the removal reach (see Methods) in the lower site.

The two Sand Creek sites were about 5 km apart. At the upper site, the creek dropped steeply through the middle of an approximately 35 year old clearcut with no streamside riparian vegetation buffer. The substrate was primarily cobble, gravel and boulder. The lower site was in a meadow with little woody vegetation along the stream. Undercut banks provided most of the available cover. The dominant substrates were sand and gravel. A dirt road paralleled the stream at the lower site. Fishing pressure was probably the highest at this site, although I never saw anglers at any site.

The Hillbilly Creek site was in a steep, boulder-dominated channel flowing through a confined valley that had burned several years previously. Due to topographic shading, Hillbilly Creek received little direct sunlight. The Landmark Creek site was in a moderately confined valley in a lodgepole pine forest. The substrate was primarily sand, gravel and cobble.

## Methods

I removed fish from 200 m stream reaches and compared brook trout movements into those reaches in sites with gradual (2 %) versus steep (6 %) slopes. Six sites were divided into six to nine contiguous 67 m sections (Figure 3). All fish were removed from sections 4 through 6 ("removal sections") of each site. Sections 1-3 and 7-9 were the downstream and upstream "marking sections", respectively. Section numbers are indicated in parentheses throughout the paper. Lower Rock Creek, a steep site, had only one upstream marking section (7), about 50 m long, because the channel slope flattened abruptly upstream of the section. However, the upper Rock Creek site began immediately upstream of the lower site, so movements could be assessed over both sites. I had no upstream marking sections in Hillbilly Creek because no brook trout were found upstream of step 11 (Figure 2A) in the uppermost removal section (6).

Three or four electrofishing passes were made separately in each 67 m section using one or two electrofishers and block nets. A battery powered electrofisher was set up to 600v and a generator powered one up to 1100 volts. During first passes I used a frequency of 50 Hz or less with a 1ms 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. Higher settings were often used during the final pass in removal sections. At least 40 minutes passed between successive electrofishing passes. All electrofishing was done between 22 July and 8 August, 1996.

Fish were held in perforated buckets in the stream for 3 to 14 hours after electrofishing. Fish from the marking sections were sedated in a solution of tricaine methanesulfonate (MS-222, Fiquell) until they lost equilibrium (approximately three to four minutes). They were then measured for total length (TL) with the caudal fin compressed, given adipose fin clips, and marked by S. Adams with injections of Visible Implant Fluorescent Elastomer (Northwest Marine Technology, Inc.®, Shaw Island, WA) (Bonneau et al. 1995). Fish from each marking section were released at the end of the section furthest from the removal sections (Figure 3). Fish from removal sections were killed with an overdose of MS-222, measured, and retained for other analyses. Because I captured few brook trout in the downstream marking sections of Hillbilly Creek, I marked fish from the removal sections and released them at the downstream end of section 3, along with the fish originally captured in section 3.

Whenever possible, fish were given a mark unique to their section of capture. Red or orange marks were injected in various combinations of locations, including adipose eyelids, maxillary, dorsal fin, and caudal fin. Fish as small as 50 mm were consistently marked in the adipose eyelid or maxillary, but only fish > 75 mm were consistently given fin marks. A sample of 24 to 25 fish (65 to 210 mm TL) from each of two removal sections in Landmark Creek and from one removal section in upper Sand Creek were marked and held in perforated recovery buckets instream for 21 to 25 hours to quantify short-term survival and mark retention.

Movements and recolonization were assessed by night snorkeling in the removal sections at approximately logarithmic intervals (2, 4, 8...64 nights after fish removals) (as recommended by Sheldon 1984) and once the following summer (about 380 nights after removal). The intervals between snorkeling differed slightly among sites for logistical reasons. The dive for night 32 in lower Rock Creek was canceled because the water was too shallow for effective snorkeling. Sites were snorkeled between 24 July and 2 October, 1996 and between 12 and 15 August, 1997. I also snorkeled one downstream marking section (3) in Landmark Creek and one upstream marking section (7) in upper Sand Creek in August 1997. One diver (S. Adams) conducted all sampling by snorkeling slowly upstream with an underwater flashlight, identifying fish and marks and estimating 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).

Section lengths were measured along the thalweg. Channel slope was measured with a clinometer in 1996 and again in the steep sites with a rod and level in 1997. Channel slopes were calculated by section and site. For steep sites, I averaged 1996 and 1997 values since measurements from the two methods differed slightly. Heights of cascades were measured from water surface to water surface. Wetted stream widths were measured in late August. Discharge was estimated by the mid-section method (Harrelson et al. 1994) in each site between 30 August and 3 September, 1996, a period of low stream flows. Stream order was determined by the Strahler method based on blue-line streams of U.S.G.S. topographic maps (1:24,000). Water samples were taken from each site in mid-August, 1996, for conductivity measurements.

Since marked fish were not individually identified, I was often unable to distinguish among individuals with a given mark observed during successive sampling periods. I distinguished among marked immigrants originating upstream because there were so few individuals. However, for fish originating downstream I 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). I included marked fish

observed on other nights only if I identified them as unique from those observed on the peak night (e.g. based on length). For the total number of fish moving I identified unique fish based on marks and/or size. For comparisons of sizes of fish immigrating versus those marked, I identified additional fish as unique based only on marks so that I did not introduce a size bias. Maximum estimates included observations of marked immigrants summed over all sampling nights, excluding only fish that were clearly observed on multiple nights.

Several statistical analyses were restricted to data on fish 95 mm for two reasons. First, 90.5% of the fish held to determine short-term survival, were 95 mm. Although all seven small fish survived the 21+ hour period, I could not completely discount the possibility of high mortality in the smallest marked fish. Second, both electrofishing and snorkeling may have been slightly biased toward detection of fish >94mm. However, I did capture or observe many fish <95 mm with each technique.

Chi-square tests were used to test for differences in the length-frequencies of marked fish immigrating into removal sections versus all fish marked. Fish were assigned to length groups of < 95 mm, 95-134 mm, and > 134 mm. Proportions of all fish marked in each category were used to calculate expected frequencies of marked immigrants. I 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 "< 95 mm" size category.

I compared the number of fish 95 mm immigrating into lower versus upper removal sections in various slopes by regressing the differences between the two on channel slope. I estimated the channel slope in lower Sand Creek as 0.8 %. I estimated the peak number of immigrants ( $I_i$ ) into each section by adjusting for fish observed on the first night:

$$I_i = A_i - U_i;$$

$A_i$  = # all brook trout observed in section  $i$  on peak night (night with most fish in section  $i$ );

$U_i$  = # unmarked brook trout observed in section  $i$  on 1st snorkel night;

The unmarked brook trout observed on the first snorkel night were conservatively assumed to be fish that were missed during electrofishing rather than immigrants. I computed the difference between the peak number of immigrants in the lower removal section ( $I_4$ ) and the peak number in the upper removal section ( $I_6$ ) and regressed the difference on site slope using simple linear regression.

## Results

Brook trout densities during initial electrofishing were highly variable within and between sites. Densities of brook trout captured while electrofishing ranged from 3.6 to 128.3 fish/100 m<sup>2</sup> (median density = 15.9 fish/100 m<sup>2</sup>). Densities of rainbow trout captured in the lower Sand Creek and Hillbilly Creek sites ranged from 0.2 to 11.5 rainbow trout/100 m<sup>2</sup> (median = 3.58 fish/100 m<sup>2</sup>). Brook trout were the only fish observed in the other four sites, except for one rainbow trout and one longnose dace (*Rhinichthys cataractae*) in lower Rock Creek. I found no significant differences in estimated, pre-experiment densities of brook trout between sites with steep versus gradual slopes when I considered all sizes of fish (t-test,  $p = 0.808$ ,  $N = 6$ ) or only fish 95 mm ( $p = 0.810$ ,  $N = 6$ ). Likewise, brook trout densities by section were 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 ( $r = -0.0240$ ,  $p = 0.884$ ,  $N = 39$ )(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 %. Mark-retention in each body location improved with marking experience. Loss rates of adipose eyelid marks ranged from 2 to 13 %, dorsal fin marks from 0 to 27 % and caudal fin marks from 5 to 8 %. Nearly all fish were given two adipose eyelid or two maxillary marks, so the probability of losing both marks was less than 2 %. Loss of a fin mark led to the conservative conclusion that the fish was originally captured in the marking section closest to the removal section. Several "recaptured" fish were missing marks, and in 1997, some marks were difficult to see due to tissue growth.

Contrary to my predictions, marked fish moved upstream more than downstream, even in steep sites (Appendix A). At each site, 66 to 100% of observations of marked immigrants were of fish originating within 200 m downstream. The minimum number of observations of marked immigrants 95 mm originating downstream was significantly greater than the number originating upstream at all sites (paired t-test,  $p = 0.004$ ,  $N = 5$ ; Hillbilly Creek was excluded from the comparison since there were no upstream marking sections)(Figure 5). Numbers of fish 95 mm that were initially marked downstream versus upstream of removal sections were not significantly different (paired t-test,  $p = 0.627$ ,  $N = 5$ ). In all sites, the percentage of fish marked downstream (section 3) and later observed in the removal reach greatly exceeded the percentage of fish marked upstream (section 7) and later observed in the removal reach (Table 2). In most analyses, I used numbers, rather than percentages, of marked fish moving since 1) I generally "recaptured" a small percentage of the fish that I marked (Table 2), 2) numbers of fish marked were similar up- and downstream of removal reaches, 3) the percentage of fish moving was apparently unrelated to the number marked (Table 2), and 4) fish densities were not correlated with channel slope (Figure 4).

The minimum estimates of the number of fish moving upstream were generally comparable in steep versus gradual channel slopes. Only in the sampling interval closest to "night 5" did I observe significantly more marked immigrants from downstream in sites with gradual than with steep slopes (t-test,  $p = 0.007$  after adjustment for multiple, non-independent p-values, Rice 1989). However, I infer that in gradual slopes, marked fish moved through and beyond the removal sections, whereas in the two steepest sites, this almost certainly did not occur. Thus, more fish than I estimated may have actually moved upstream in the gradual than in the steep sites.

Although upstream movement of fish was prevalent in all sites, fish did not move upstream as far in steep as in gradual slopes. In the gradual sites and in lower Rock Creek (6 % slope), some marked fish moved upstream at least through the entire removal reach (> 200 m). In Hillbilly Creek (12% slope), no marked fish moved more than about 150 m upstream. No fish released in the lower marking sections (1-3) of the two steepest sites were observed farther than half way up the middle removal section (5). Thus, I infer that fish did not move upstream through, and beyond, the

removal sections in the two steepest sites.

Patterns of recolonization by both marked and unmarked fish confirmed that upstream movements predominated, even in the steepest sites, but that upstream movements were shorter in the steepest sites. The upstream removal sections (6) were recolonized by marked and unmarked fish as fully as the downstream sections (4) in gradual sites, but not steep sites. The regression of the difference between immigrants to the lower section (14) minus immigrants to the upper section (16) on channel slope was highly significant ( $R^2 = 0.94$ ,  $p = 0.001$ ) (Figure 6). In both the upper Sand Creek and Hillbilly Creek sites, the numbers of fish in the upper removal sections (6) did not increase after the first night, and numbers in the middle sections (5) increased less than in the lower sections (4). In the three gradual sites, the upper removal sections (6) had as much or more recolonization than the lower (4) sections (Figure 6). The lack of recolonization of the upper section and limited recolonization in the middle section of upper Sand Creek by unmarked fish is further evidence that little downstream movement occurred during the summer; if downstream movement was prevalent, unmarked brook trout from upstream would have immigrated into the upper removal section (6). In lower Rock Creek, there was no increase in fish numbers in the uppermost removal section (6) during the summer, but some marked brook trout did move completely through the site. Most fish counts in lower Rock Creek declined with time, possibly due to a more extreme loss of habitat area with declining streamflows than in other sites.

Our use of unmarked fish to further assess immigration is justified by increases in their numbers over time. In three sites, the numbers of unmarked brook trout 95 mm observed in removal sections at least doubled between the first night that I snorkeled and some later snorkeling date. Thus I inferred that unmarked fish immigrated into the removal reaches after I removed fish. The removal sections of upper Rock Creek had particularly high numbers of unmarked fish during the first snorkel period (night 2), but even so, numbers increased up to 2.5 times by later sampling dates the first summer.

Brook trout ascended steeper slopes than I expected. Marked brook trout moved upstream through one 67 m stream section with an average slope of 13%. However, they did not move completely through two other sections with 10 and 17% slopes. Marked fish ascended 14.5 m of stream with a 22% slope and 23 m with a 16% slope. In the middle removal section (5) of Hillbilly Creek, brook trout were initially observed in a 34 m length of stream with an average slope of 20%, but I never saw marked immigrants that far upstream. In lower Rock Creek, marked brook trout as small as 90 mm ascended a 0.7 m-high, nearly vertical falls over boulders and bedrock (Figure 2, step 1).

Nearly vertical steps or falls, rather than steep slopes *per se*, apparently inhibited upstream movements by brook trout. In upper Sand Creek, I saw one brook trout (210 mm TL) that had ascended a 1.5 m high, complex falls (Figure 2B (step 13)). 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 7). I initially captured brook trout upstream of both falls and so assume that some fish had ascended these, and other large steps, to colonize upstream areas.

The upper, pre-experiment, distribution limit of brook trout in Hillbilly Creek occurred in the middle of a series of four bedrock chutes (Figure 2A, steps 9 to 12). Brook trout occurred above two chutes with slopes of 26 and 23% over distances of 10.5 and 5.3 m, respectively, but not above two similar chutes with slopes of 35 and 23% over distances of 3.8 and 9.8 m, respectively. Each chute consisted of a series of steps from 0.4 to 0.6 m high with short, fast, shallow runs (most < 0.3 m deep), interspersed. The three downstream chutes each had a pool deeper than 0.5 m at the base.

I saw no evidence that brook trout moved upstream over low-flow obstacles during the high spring stream flows in 1997. During snorkeling in August 1997, I did not see marked fish that had ascended the largest steps in upper Sand and Hillbilly creeks, nor was there any indication that unmarked fish had ascended the large step (step 7) in Hillbilly Creek. In general, fewer marked fish were observed in removal sections during snorkeling in 1997 than in 1996. In the Landmark Creek and upper Sand Creek marking sections snorkeled in 1997, I saw 9 and 20%, respectively, of the larger fish (95 mm) marked in the sections in 1996. Smaller percentages of fish from those sections were observed in the removal reaches of the respective streams.

Several observations indicated that some, and perhaps many, brook trout moved farther and faster than the experiment was designed to detect. In the lower Sand Creek site, I marked fish only in the downstream marking sections (1-3) on 31 July 1996. The block net between the downstream marking reach and the removal reach (between sections 3 and 4) washed out overnight. On 1 August, after replacing the block net, I electrofished the remainder of the site (sections 4-9) and captured 22 brook trout marked downstream the previous day (I later released them downstream of the removal sections). Four brook trout (91 - 122 mm TL) had moved 400 to 600 m upstream in less than 24 hours. The smallest brook trout recaptured (75 mm TL) moved over 65 m upstream in less than 18 hours. I recaptured more marked brook trout during electrofishing in the removal sections than I observed in those sections during any subsequent snorkeling period. I infer that either marked fish moved completely through the removal sections before my first snorkel period, as suggested by the rapid movement rates, or I overlooked many marked fish while snorkeling. Because the two Rock Creek sites were contiguous, I could detect movements of marked fish over longer distances there than at other sites. In upper Rock Creek, 28% (3 to 6 fish) of all observations of marked fish were of fish marked further than 200 m downstream, and 14% (2 to 4 fish) originated farther than 500 m downstream, below two small falls. Those fish represent what would have been unmarked immigrants if I did not have an adjacent study site downstream. In lower Rock Creek, 21% (2 fish) of marked immigrants originated upstream further than 500 m.

The larger (and presumably older) fish in the populations dominated the pool of immigrants. In both gradual and steep sites, significant differences occurred between observed and expected length-frequencies 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 > 94 mm were considered, I still found significant differences between the remaining two size classes for the steep, but not for the gradual sites (Table 3). The fish that ascended the 1.2 m step in upper Sand Creek was one of the largest fish marked (all were < 200 mm TL).

The difference in length-frequency distributions of fish between sites in Rock Creek (Figure 7) further supports that dispersal by age 0 and 1 fish (< 95 mm TL) was minimal. Rearing areas in the adjacent lower and upper Rock Creek sites were separated by a 0.7 m high falls. If young fish

moved freely between sites, length-frequency distributions should have been similar between sites.

Motivation appeared to influence the incidence of upstream movement in the steepest site. In Hillbilly Creek, a higher percentage of fish that originated in the removal sections recolonized those sections than of fish that originated downstream (Table 2). On sampling nights 14 and 30, when the most marked fish were observed, 38 % of fish originally captured in section 3 versus 52 % of those originally captured in the removal sections were observed in the removal sections. Although this was the steepest site, the "homing" fish had the second highest percentage of any group of marked fish immigrating into removal sections on a given night. The highest percentage (60%) was in lower Sand Creek, the most gradually-sloping site.

## Discussion

I found that brook trout do ascend steep streams. During low summer streamflows, brook trout moved upstream through slopes at least as high as 13 % over 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, some moved upstream 150 m even in the steepest sites during the summer of 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. I do not have comparable data for cutthroat trout movements in steep streams, however, the ability of brook trout to ascend 13 % slopes suggests that swimming ability, alone, does not explain why brook trout densities decrease as channel slope increases above 4% in some streams. Furthermore, in contrast to some previous findings (Chisholm and Hubert 1986; Fausch 1989; but see Kozel and Hubert 1989), I did not find significant differences in brook trout densities between steeply- and gradually-sloping sites.

Brook trout have been documented in very steep streams from several other locations. In tributaries to the South Fork Salmon River, Idaho, brook trout occurred in the presence of native salmonids in channel slopes of 12 to 14 % (Platts 1974). Allopatric populations have been documented in Idaho (Maret et al. 1997) and Nevada (Schroeter 1998) in slopes of 12 to 16 %. In the GSMNP, brook trout in remnant populations were restricted to, and moved about in, headwater streams where average channel slopes were 12 to 15% (Larson and Moore 1985). Our results suggest that nonnative brook trout in the West are also capable of colonizing such steep slopes from downstream. Within steep stream reaches, however, brook trout tend to occupy habitats with gradual slopes (e.g. stair-stepped pools, Larson and Moore 1985; S. Adams, unpublished observations). Therefore, the configuration of channel slopes at a within-reach scale likely influences the invasibility of steep streams.

Brook trout ascended larger steps than I expected, but nearly vertical falls within steep stream reaches appeared to be what generally inhibited upstream movement. The height of a step required to inhibit upstream movement during summer low flows apparently depended on characteristics of the step and of the pool at the base. Complex steps over boulders and logs were ascended more readily than lower, more vertical steps over bedrock ledges. Brook trout ascended steps up to 1.2 m high during the study, and based on their pre-experiment distribution, I assume that some ascend larger steps occasionally. Thus, I find it unlikely that artificial barriers can be constructed that will passively allow passage of native trout and char, but not of brook trout.

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 I 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 in lower Sand Creek, provided direct evidence of fish moving farther than 400 m in channel slopes of 1 to 6 %. The rapid movements I observed are probably not attributable to 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 unmarked fish indicated that colonists frequently dispersed from locations farther than 200 m away, where I did not electrofish. Although I did not quantify long-term mark-retention, loss of marks cannot explain the unmarked fish in removal sections since all tagged fish were also given adipose fin clips, and no fin regeneration was evident until the last sampling date. Fish escaping capture during electrofishing undoubtedly accounted for some unmarked fish, however increases in fish numbers over time were evidence of immigration. Our observations in lower Sand Creek suggested that immigration could be rapid, at least in low gradient sites. Thus, I inferred that many of the unmarked fish observed on the first snorkel night 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.

Although I was surprised to find upstream movements more prevalent than downstream movements in steep sites, the result conforms to the seasonal movement patterns observed in studies of more moderately-sloping 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).

Upstream movement by brook trout in other studies was most pronounced during the spring with a secondary peak in the fall (Smith and Saunders 1958; Flick and Webster 1975; Gowan and Fausch 1996b), suggesting that motivation for moving varies seasonally. In some streams, conditions allowing passage over obstacles may occur only during infrequent windows of time lasting from hours to weeks. For example, after Nagel (1991) repatriated brook trout into a Tennessee stream, very high spring discharge apparently allowed the fish to ascend what at low flows was a "four foot vertical drop" in the stream (J. Nagel, personal communication). Sea-run Arctic char had to ascend a waterfall at the head of the tidal influence before migrating up the Sylvania Grinnell River in Canada. During the late summer and early fall when motivation to migrate upstream was high, the char could ascend the falls only during high "spring tides", occurring for several hours of several days, twice per month (Grainger 1953). In the two steepest sites, I found no marked fish that had moved upstream into the upper halves of the removal reaches during 1996, even though brook trout initially occupied parts of those areas. I suspected that brook trout may ascend low-flow barriers during high, spring flows when the heights of vertical steps were minimized, side channels around low-flow barriers developed, and motivation was high. However, despite relatively high

streamflows during spring snowmelt in 1997, the following August I found no marked brook trout above obstacles that they had failed to ascend in 1996. Possible explanations are that opportunities for fish passage do not occur annually, motivation for dispersal was limited, or fish ascended the steps but I did not detect them. I 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 and motivation for dispersal is high. Alternatively, temporary features such as a waterfall over a large log (e.g. step 7 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 years.

Upstream movements in steep streams were primarily the domain of mature brook trout. In all sites, immigration into removal reaches was dominated by fish 95 mm. In steep channel slopes, extensive movements were more restricted to larger fish. Gowan and Fausch (1996b) also observed that brook trout that moved were generally longer than those that remained in home sections. Since swimming performance increases with fish length, I suspect that steep channel slopes inhibited movements of small more than large fish. Only adult brook trout were found in several streams in the SF Salmon River drainage (S. Adams, unpublished data), including Hillbilly Creek, consistent with the observation that upstream dispersal was dominated by mature individuals. Similarly, the largest rainbow trout were the first to invade streams in GSMNP (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, I found little evidence of movements longer than 67 m in either direction by age 0 fish. In Rock Creek, the different length-frequency distributions for age 0 and 1 fish above and below the small falls corroborated my results from marked fish that age 0 and 1 fish did not move as much as older fish. The length differences could have been due to differential downstream dispersal by faster or slower growing individuals. However, the paucity of recaptures of marked fish smaller than 100 mm suggests that movements between sites by small fish was minimal in both directions. I only saw substantial recolonization by age 1 fish (unmarked) in one section of upper Rock Creek. Hunt (1965) reported that the relative importance of up- 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 the lengths of age 0 fish there were similar to those of age 1, and possibly age 2, fish in my experiment. The smaller length-at-age in my study populations, and steeper slopes in some sites, may have inhibited movements by younger fish.

Movement and dispersal (as I use the terms) are not synonymous, but distinguishing between them is difficult. Although homing to streams, lakes, or specific sites, for various purposes has been shown in many salmonids, including chars (Arctic char, Johnson 1980; brook trout, Power 1980; Näslund 1992; bull trout, Swanberg 1997), 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 likely of only minor relevance to the invasion process. I cannot conclude that fish I observed moving were actually dispersing.

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). Interannual variation in the incidence of brook trout movement (Flick and Webster 1975; Gowan and Fausch 1996b) suggests that at least some movements are stimulated by environmental, population, or individual conditions that are variable among years. Fish density and food availability (Hunt 1965; McMahon and Tash 1988; Riley et al. 1992), inter- and intraspecific behavioral interactions (Saunders and Smith 1962; Flick and Webster 1975; Keefe and Winn 1991), ontogenetic changes in foraging or habitat requirements (Smith and Saunders 1958; Smith and Saunders 1967) and the size, quality, and spatial configuration of habitats (Saunders and Smith 1962; Chisholm et al. 1987; Northcote 1992; Riley et al. 1992) are among the factors expected to influence brook trout motivation for dispersal. Riley et al. (1992) found that summer increases in brook trout densities in reaches with "improved" habitat resulted from decreased emigration rather than increased immigration. Thus the fish were apparently sampling stream habitat rather than responding to an attractant. Such a behavior is consistent with the pattern of immigrants moving in from distant, rather than adjacent, locations. The immigration into removal reaches in this study may have resulted from similar habitat "sampling" behavior by fish seeking better conditions for foraging, hiding, or reproducing (e.g. Gowan et al. 1994).

Dispersal ability should be assessed separately from motivation, as much as possible. In Hillbilly Creek (12% slope), a greater percentage of homing fish (captured in removal reach and released in section 3) than of fish that were originally captured in section 3 moved upstream into the removal reach during 1996. Except for lower Sand Creek (<1% slope), no other site had a greater percentage of marked fish from section 3 later move upstream into the removal reach. The behavior of translocated salmonids can be strongly influenced by a tendency to home (but see Saunders and Smith 1962; Armstrong and Herbert 1997). Since motivation was not accounted for in this study, I cannot conclude that brook trout were incapable of ascending the steepest slopes, where I did not observe immigration from downstream. However, in Hillbilly Creek, the translocated fish would presumably have returned all the way to their site of capture if they were capable. Future studies aimed at determining upstream movement abilities could capitalize on the motivation of brook trout to home, by releasing marked fish downstream of their capture sites in steep streams or downstream of potential dispersal barriers. Learning more about factors motivating dispersal could greatly advance our understanding of relationships between abiotic and biotic ecosystem changes and brook trout invasion of streams.

While steep channels do not inherently form barriers to brook trout dispersal, they may slow the rate of invasion. The combination of conditions necessary to motivate and allow brook trout to ascend steps typical of steep streams may occur infrequently. Numerous factors, including potentially highly variable environmental conditions, can influence the likelihood of a population becoming established (Crowl et al. 1992). Slopes greater than 6 to 8 % can apparently decrease both upstream movement rates and the number of fish moving. When the number of dispersers is small, demographic factors become increasingly important to the probability of successful invasion (Lewis and Kareiva 1993; Kot et al. 1996). For example, given two dispersers, two males cannot become founding fathers, but a male and a female meeting at an appropriate time and place could establish a population. 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 channels do not necessarily prevent brook trout invasion indefinitely.

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. I 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, I have shown that steep reaches can be important dispersal corridors. A better understanding of fish production and dispersal in steep channels will provide insight into invasion processes. Gradually-sloped 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 area invaded (Chapter IV). Biological surveys of steep reaches could help identify and track incipient invasions. Better understanding of the mechanisms, rates, and patterns, of invasions can help us to better manage human activities in such a way that we can avoid facilitating or accelerating future invasions, and can perhaps reverse them where feasible.

Table 1. Stream characteristics and thalweg lengths at the six experimental sites, Valley County, Idaho. Average (avg.) width refers to wetted channel widths. Slope is the channel slope over the entire site. See Methods section for details.

Stream site	Slope (%)	Channel pattern	Stream order	Avg. width (m)	Low flow discharge m <sup>3</sup> /s	Conductivity (S/cm)	Elevation (m)	Site length (m)
Sand lower	<1	tortuous	2	4.0	0.096	54.8	2089	606
Sand upper								
Rock	1	meandering	2	3.3	0.035	40.4	2060	603
Landmark lower	2	meandering	2	2.6	0.015	30.9	2039	622
Rock upper	6	straight	2	3.1	0.031	39.8	2033	455
Sand	9	straight	1	2.9	0.038	60.6	2213	602
Hillbilly	12	straight	1	2.5	0.012	37.7	1981	403

Table 2. For each experiment site, the number of brook trout 95 mm that were marked and released in the downstream (3) and upstream (7) sections, respectively, that were adjacent to the removal reach. The range (percent) of those fish later observed in the removal reaches on any given night is shown. For Hillbilly Creek, I distinguish between fish originally captured in section 3 versus sections 4-6, although all were released in section 3. Streams are listed in order of decreasing channel slope. In Hillbilly and upper Sand creeks, I observed no marked fish that had moved upstream through the entire removal reach.

Site	Originating downstream		Originating upstream	
	Number of marked fish released in section 3	Percent observed in removal reach	Number of marked fish released in section 7	Percent observed in removal reach
Hillbilly (fish from removal reach)	25	20 - 52	---	---
Hillbilly (fish from section 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

Table 3. Summary of chi-square tests comparing length frequencies of marked brook trout immigrants into removal sections (observed frequencies) to length frequencies expected based on lengths of all brook trout marked in each site (expected). Tests were conducted with data pooled across the three gradual and across the three steep sites (1) and repeated without the smallest size class (2). Sizes were based on total lengths. Asterisks indicate that the chi-square is significant at  $p < 0.005$ .

MECHANISMS LIMITING A VERTEBRATE INVASION:

Size class	Observed	Test 1	2	Observed	Test 2	2
		Expected			Expected	
<b>Gradually-sloped sites (&lt;=2%)</b>						
<95mm	1	11.9		---	---	
95-134mm	15	10.1		15	17.9	
>134mm	10	4.0	21.25*	10	7.1	1.64
<b>Steeply-sloped sites (&gt;=6%)</b>						
<95mm	1	22.4		---	---	
95-134mm	10	7.2		10	21.7	
>134mm	22	3.4	122.7*	22	10.3	19.6*

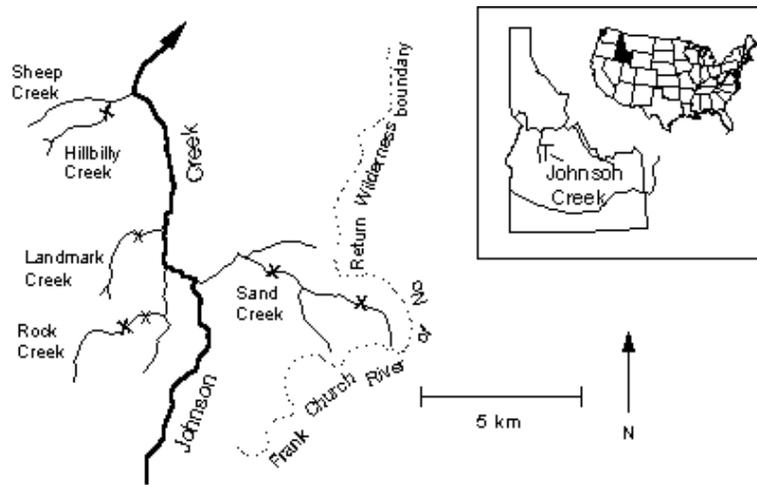


Figure 1. Experimental sites (X) in Johnson Creek, Idaho. Hillbilly Creek was previously unnamed.

Following page:

Figure 2. Schematic profiles of experimental sites drawn approximately to scale in order of decreasing average channel slope. Large vertical steps are shown, however, small steps are obscured by channel slopes measured over longer distances. Numbers along stream profiles refer to potential dispersal barriers (see text). Asterisks indicate the uppermost locations where I saw marked fish originating downstream. The Landmark Creek profile (C) includes section numbers. Note: vertical axes are all on the same scale but are exaggerated relative to the horizontal axes.

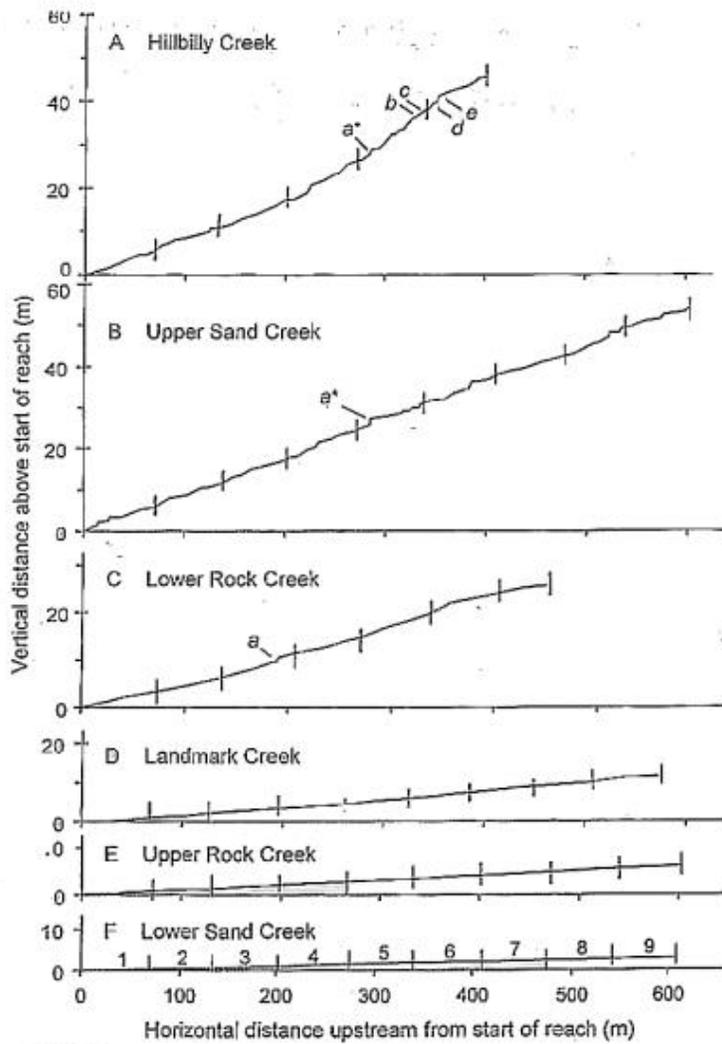


Figure 2.

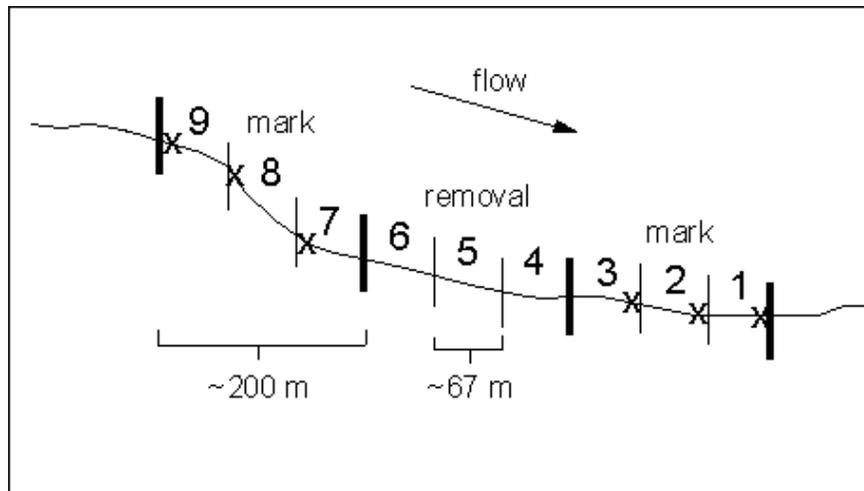


Figure 3. Schematic diagram of an experiment site showing section numbers and locations where I released marked fish (X). Vertical lines delineate sections, with bold lines representing locations where block nets remained in place until all electrofishing in the site was complete. Sections 4-6 were

"removal sections", and sections 1-3 and 7-9 were "marking sections".

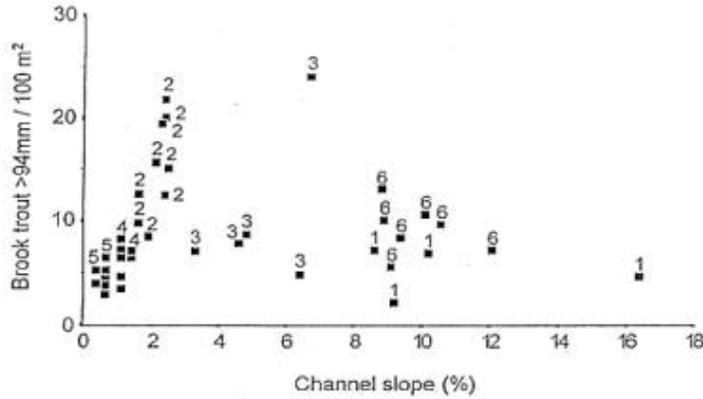


Figure 4. Estimated pre-experimental densities (fish/100 m<sup>2</sup>) of brook trout 95 mm total length in each experimental section versus channel slope of the section. Densities were calculated using actual numbers of fish caught. I calculated a combined density estimate for the three removal sections in every site except Landmark Creek, for which the density of each section is shown. Labels indicate sites: 1 = Hillbilly Creek; 2 = Landmark Creek; 3 = lower Rock Creek; 4 = upper Rock Creek; 5 = lower Sand Creek; and 6 = upper Sand Creek. Two points each from sites 4 and 5 were shifted to the right and left, respectively, for clarity. All points under labels "4" and "5" correspond with the label above the column.

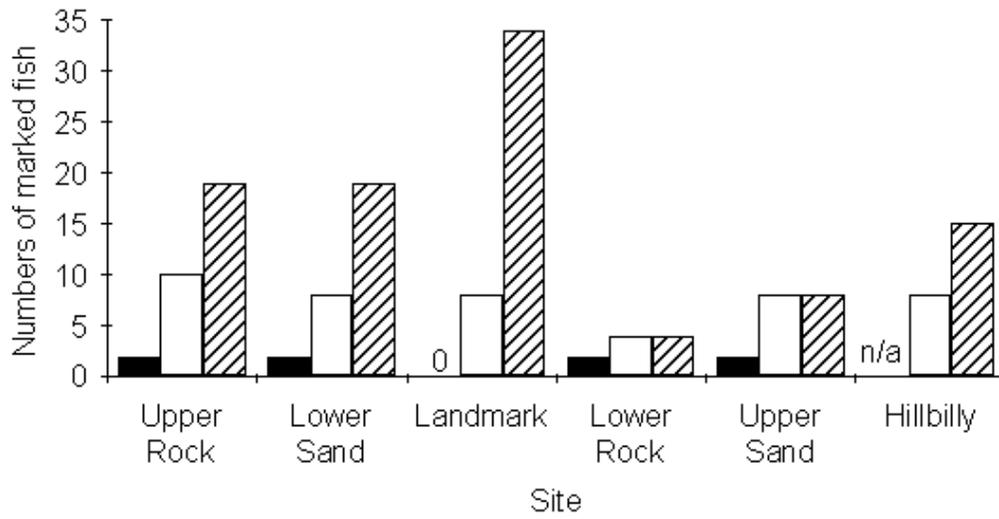


Figure 5. Number of marked fish of all sizes observed in removal sections of each site during 1996 that had moved downstream (closed bars) and minimum (open bars) and maximum (shaded bars) estimates of numbers of marked individuals observed that had moved upstream. See text for explanation of estimates.

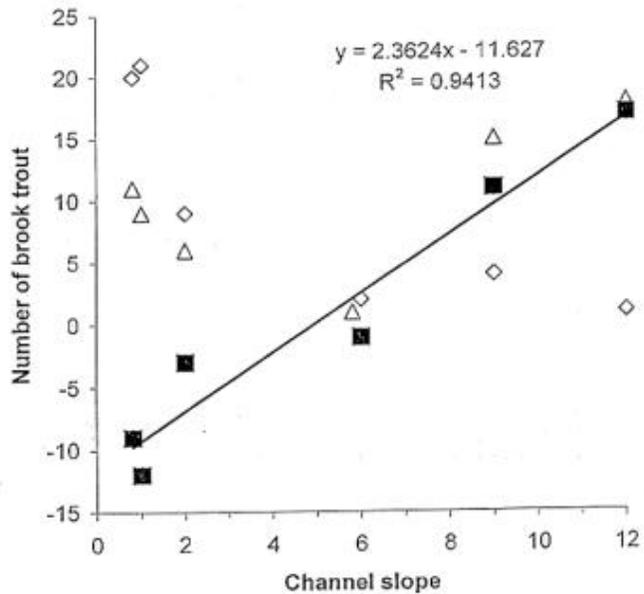


Figure 6. Differences between peak numbers of brook trout immigrants to lower (open triangles) minus upper (open diamonds) removal sections are indicated by closed squares. The linear regression line of the difference in number of immigrants between the sections on channel slope of the site is shown. Only fish 95 mm total length observed in 1996 were considered. The Hillbilly Creek point includes fish originally captured in the removal sections, but the regression was similar with the "homing" fish excluded from the Hillbilly Creek data.

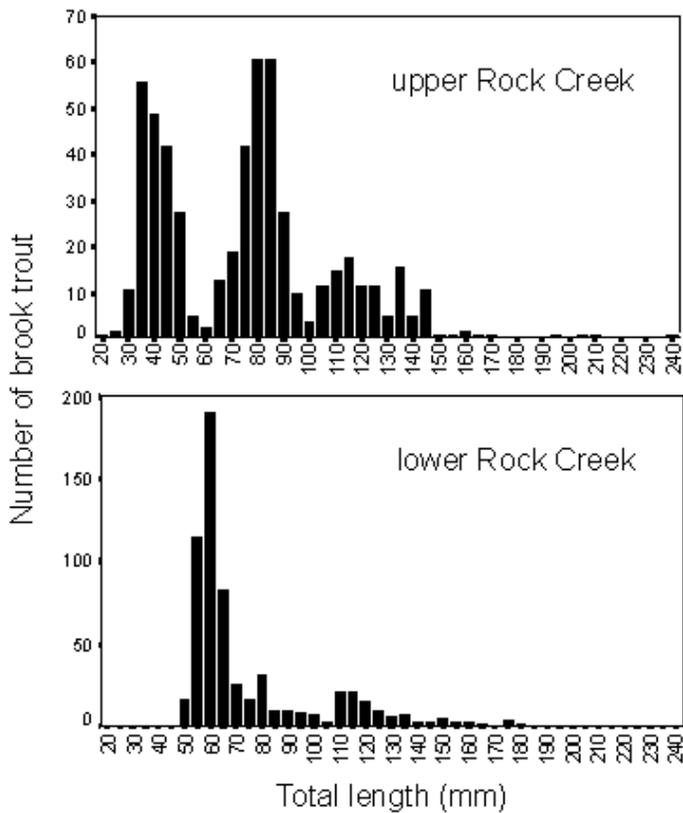


Figure 7. Length frequencies of fish captured during electrofishing in the upper and lower Rock Creek sites, Idaho, in July and August, 1996. The sites were contiguous with a 0.72 m-high step separating the areas where most juvenile fish occurred in each. Note that vertical axes have different scales.

Appendix A. Fish mark and "recapture" data

Table on following three pages:

Table A1. Matrices of the number (#) of brook trout 95 mm marked in each marking section of each experimental site and the numbers of marked and unmarked fish subsequently observed during each snorkel session in the removal sections. Section numbers are indicated in the left column, with the most downstream section always given number 1 (Figure 3). The heavier dashed horizontal lines represent the locations of the removal reaches. The remaining columns show the numbers of brook trout 95 mm observed in each removal section on each snorkel night and show the section where the fish were initially captured. "Day" indicates the number of days since the removal and marking were completed in the site. The number of marked, unmarked, and total brook trout observed in each removal section and night are summarized in the bottom three rows. Matrices are arranged in order of increasing channel slope of the sites.

Question marks indicate marked fish that I observed (usually identified by a fin clip) but on which I could not identify the mark. In the upper Rock Creek site, section numbers followed by "lower" refer to sites from the adjacent downstream site, and in the lower site, section numbers followed by "upper" refer to sites from the adjacent site upstream. In Hillbilly Creek, section numbers (4) and (5) refer to fish that were captured in those removal sections, uniquely marked, and released at the downstream end of section 3. Marked fish observed and totals are given both with (w/) and without (w/o) fish from sections 4 and 5 for Hillbilly Creek. Several of the fish indicated as marked in sections 3 and 7 were actually marked in other sections, but were given the same marks as fish in sections 3 and 7 (generally because of small size) and so were indistinguishable from those fish. Thus, the estimates of the number of fish moving longer distances are conservative.



Table A1 continued.

Landmark Cr.	# marked	Day 1			Day 2			Day 5			Day 8			Day 15			Day 36			Day 63			Day 388		
		4	5	6	4	5	6	4	5	6	4	5	6	4	5	6	4	5	6	4	5	6	4	5	6
1	24																								
2	15																								
3	34	2	1	3	1	3		2	1	2	2	2		3	2	1	2	2		2	2		2	2	
7	33																								
8	37																								
9	29																								
?								1																	
# marked	172	2	1	3	0	1	3	3	1	2	2	0	2	3	2	1	2	2	2	2	2	2	2	2	1
# unmarked		6	3	3	8	7	4	7	4	8	8	7	9	9	7	6	8	8	10	8	2	6	8	2	6
Total		8	4	6	8	8	7	10	5	10	10	7	11	12	9	7	10	10	12	10	4	7	10	4	7

Lower Rock Cr.	# marked	Day 3			Day 6			Day 11			Day 18			Day 54			Day 371		
		4	5	6	4	5	6	4	5	6	4	5	6	4	5	6	4	5	6
1	18																		
2	19	1	2																
3	56	1			1			1			1			1					
7	8																		
1, upper	16																		
2, upper	16																		
3, upper	13																		
7, upper	14																		
8, upper	20																		
9, upper	9																		
# marked*	133	1	1	2	0	1	2	0	0	3	0	0	2	0	0	2	0	0	0
# unmarked**		7	10	6	8	12	5	7	12	5	8	13	4	2	11	5	9	29	16
Total		8	11	8	8	13	7	7	12	8	8	13	6	2	11	7	9	29	16

\* # marked includes only those from within 200 m  
 \*\* # unmarked includes marked fish from further than 200 m.

Table A1 continued.

Upper Sand Cr.		Day 3			Day 5			Day 10			Day 15			Day 34			Day 60			Day 384		
		4	5	6	4	5	6	4	5	6	4	5	6	4	5	6	4	5	6	4	5	6
Section	# marked																					
1	26																					
2	22																					
3	14	2			1	1		1	1		3	1		2	1		2	1				
7	20																					
8	12				1			1														
9	13																					
?																						
# marked	107	2	0	0	2	1	0	2	1	0	3	2	0	3	0	0	3	2	0	3	2	0
# unmarked		2	2	1	2	2	5	3	1	4	5	2	3	14	3	2	9	2	3	17	11	6
Total		4	2	1	4	3	5	5	2	4	8	4	3	17	3	2	12	4	3	19	12	7

Habitat Cr.		Day 2			Day 6			Day 14			Day 30			Day 62			Day 378		
		4	5	6	4	5	6	4	5	6	4	5	6	4	5	6	4	5	6
Section	# marked																		
1	4																		
2	11																		
3	13	2			1			2	3		3	2		1	1		2	1	
(4)*	2	2			2			1	1		1	1		1			2		
(5)*	23	3			3			9	2		8	3		7			1		
(4 or 5)*																			
# marked w/ (4,5)	53	7	0	0	6	0	0	13	6	0	12	6	0	9	2	0	5	2	0
# marked w/o (4,5)	28	2	0	0	1	0	0	3	3	0	3	2	0	1	1	0	2	1	0
# unmarked**		1	5	0	2	4	0	6	4	1	4	1	0	5	3	0	8	2	1
Total w/ (4,5)		3	5	0	3	4	0	9	7	1	7	3	0	6	4	0	10	3	1
Total w/o (4,5)		8	5	0	6	4	0	19	10	1	16	7	0	14	5	0	13	4	1

\* Number in parentheses indicates removal section where fish were caught. All fish in parentheses were released at the downstream end of section 3.  
 \*\* does not include fish captured in sections 4 or 5

# Chapter III: Temporal Changes in Distribution of Nonnative Brook Trout in Central Idaho Streams: An Invasion in Limbo

## Abstract

Limited dispersal ability, insufficient time, and poor reproductive success are potential factors limiting upstream invasion by nonnative brook trout (*Salvelinus fontinalis*) in headwater streams of western North America. Minimal invasion occurred over 25 years in tributary streams in the upper South Fork Salmon River drainage, Idaho. I measured the extent of invasion in 17 streams by comparing fish distributions in 1996 to those as early as 1971. In four streams, invasion beyond the 1971 upstream distribution limit was prevented by steep (>15%) slopes and/or waterfalls. Of

eight streams lacking established brook trout populations when previously surveyed, one had been invaded. Brook trout invaded up to 2.4 km upstream in 3 streams but less than 0.5 km in the remaining 10 streams with accessible habitat. In four other streams, barriers apparently prevented upstream dispersal beyond previous distribution limits. In two streams where invasion did occur, not all accessible habitat was invaded. Where substantial invasion had occurred, the average invasion rate was 5 to 11 m per year, much slower than potential dispersal based on movement rates in other locations. Dispersal ability, alone, did not prevent invasion in most of these streams. Previous experiments I conducted indicated that brook trout can ascend much steeper channel slopes than commonly supposed. However, the limited change in distribution that I observed indicates that invasion of accessible habitat is not inevitable, at least within about eight fish generations. The results confirm that invasion can be an exceedingly slow process and suggest that it may often occur in pulses. Invasion pulses may be promoted by changes in habitat conditions, in demographics of source populations, or in populations of other fishes. Extrapolating patterns of invasion to recolonization by remnant native taxa, I find that native species recovery is likely to be a slow process limited by a complex, spatially variable array of factors.

## Introduction

Invasions by exotic species are a frequent and increasing cause of species extinctions and local extirpations. Freshwater fish introductions have occurred on a global scale, and introduced fishes have contributed substantially to the high endangerment of aquatic fauna relative to other communities (Allan and Flecker 1993). Ross (1991) found that 77% of 31 fish introductions into streams were accompanied by a decline in the native fishes. Better understanding of limitations to invasions and of how physical and biotic characteristics of streams influence their invasibility, is particularly important to aquatic conservation in regions where nonnative species pose a considerable threat to the persistence of native species.

In many instances, even for species invading over large areas, we lack the most fundamental understanding of the invasion process. A sample of typically unanswered questions relating to invasion rates by stream fishes includes the following: 1) Is range expansion by the species ongoing or stalled? 2) Does range expansion occur rapidly after introduction or is it a long, slow process? 3) Does invasion occur sporadically or constantly? 4) Is range expansion inhibited by limitations of habitat and/or by biotic interactions? 5) Which demographic features limit the invasion process (e.g. limited dispersal or low reproductive success)? While the questions seem straightforward, most will have complex answers that will likely vary spatially and temporally.

Brook trout (*Salvelinus fontinalis*), native to eastern North America, have invaded cold water streams and lakes throughout the western U.S. and Canada (MacCrimmon and Campbell 1969). Introductions of the char began in the late 1800's, and the state of Oregon still stocks brook trout extensively in mountain lakes (personal communication, Terry Farrell, Oregon Department of Fish and Wildlife). Brook trout have often been implicated in the demise of native salmonids, particularly bull trout (*S. confluentus*) (papers in Howell and Buchanan 1992; Leary et al. 1993; Rieman and McIntyre 1993) and cutthroat trout (*Oncorhynchus clarki*) (Fausch 1988; Griffith 1988; 1989; papers in Young 1995a). Bull trout are listed as a "threatened" species under the U.S. Endangered Species Act (ESA) (USFWS 1998) and several cutthroat trout subspecies are either listed (papers in Young 1995a) or petitioned for listing under the ESA. An improved ability to predict brook trout invasions could facilitate efficient allocation of limited resources to preserving and/or restoring native salmonids in the western U.S. and may prove important in prioritizing populations of native species for conservation (Baltz and Moyle 1993). Furthermore, insights gained from studying expanding brook trout populations in the West may be useful in conservation of the species in its native range, where its persistence is threatened by numerous factors (Power 1980; Larson and Moore 1985; Meisner 1990)

Fausch (1989) suggested several mechanisms to explain why, in the presence of cutthroat trout, brook trout are typically more abundant in gently sloping, downstream segments of mountain streams than in the steeper (>7% slope) headwater segments. He hypothesized that brook trout invasions of steep segments may be limited by insufficient time to disperse into the headwaters of streams, by poor swimming ability, or by low reproduction or fry survival. Recent experimental work revealed that brook trout will ascend channel slopes as steep as 16 % (Chapter II), so swimming ability probably does not prevent invasion in many stream reaches where cutthroat trout are presently the dominant species. Fausch discounted time as a limiting factor since most brook trout were stocked 50 to 100 years ago, but the hypothesis has not been rigorously tested. Most accounts of ongoing invasions by brook trout exist as unpublished narratives, although two papers describing invasions in individual streams indicate that episodes of invasion occur long after the species was first introduced to a drainage (Griffith 1972; Leary et al. 1993). However, the prevalence of continued invasion over larger areas has not previously been addressed in the scientific literature to our knowledge.

By assessing changes in brook trout distributions over more than 20 years in tributary streams in the upper South Fork Salmon River (SFSR) drainage, Idaho, I investigated the hypothesis that insufficient time has passed for brook trout to invade steep, headwater streams. I compared channel slopes brook trout are capable of ascending to those where invasions had stalled or halted. I also compared potential short-term movement rates, as estimated from other studies, to observed net invasion rates in the SFSR drainage.

Following are definitions of some terms used. Distribution refers to the longitudinal range of occurrence of brook trout in a stream. Defining what constitutes a limit is an important, but often neglected, step in describing processes related to it (Strange and Habera 1998). Population boundaries drawn to include "strays" may have different locations and dynamics than those incorporating only a reproducing population (Janzen 1986). Here I define the distribution limit as the most upstream location where I observed any brook trout. Since only adults (which are apparently the primary dispersers, Chapter II) were usually present near the upper distribution limits, expansion of a distribution does not necessarily imply invasion (the latter requiring establishment).

# Review of studies on brook trout movements

In order to determine whether dispersal is a limiting process in invasion, I must first determine the rate and ability of brook trout to disperse. The following review provides a basis for my estimation of potential dispersal ability by brook trout in the SFSR drainage, Idaho.

The majority of salmonid movement studies using mark-recapture techniques have been biased toward finding short, or no, movements, while nearly all radio telemetry studies of stream salmonids indicate that some individuals moved long distances (Gowan et al. 1994; Gowan and Fausch 1996b). Large proportions of unmarked immigrants, low recapture rates in marking reaches, changes in standing stocks, and captures of fish in weirs, all indicate that movement was an important demographic process in most brook trout populations studied. Gowan et al. (1994) reviewed most of the studies cited here, but focused on what they considered biased conclusions of limited movements. I emphasize the observations of movements longer than several hundred meters contained in most of the papers, while recognizing that long-distance movements were probably more common and longer than actually observed in many studies.

In each of seven published mark-recapture studies of brook trout movements in "low" to "moderate" gradient streams, at least one fish was located farther than 1.6 km from the tagging location, and in most, fish were found farther than 3.2 km away (Stefanich 1952; Saunders and Smith 1955; Smith and Saunders 1958; McFadden 1961; Hunt and Brynildson 1964; Hunt 1965; Shetter 1968). Shetter (1968) reported recaptured brook trout up to 17.7 km upstream and 4.8 km downstream from the tagging site. Smith and Saunders (1958), studying movements between fresh and salt water, recovered over 200 fish beyond the "home" estuary (3.5 km long). The farthest ranging fish recaptured had moved at least 320 km through salt water in 15 months.

Studies involving habitat or fish community manipulations revealed similar amounts of long distance movements to the studies above. In streams with "low" to "moderate" channel slopes, all studies in this category found some fish moving distances between 500 m and 2 km over one or more years. In the most informative studies, fish were recaptured in weirs (Smith and Saunders 1958; Flick and Webster 1975; Riley et al. 1992; Gowan and Fausch 1996b). In a low gradient New York stream, up to 33 % of brook trout marked at one location each year were recaptured in a weir 6.6 km upstream (Flick and Webster 1975). Forty percent of the recoveries were made within one week of marking, indicating rapid, directed movements. In steep (8 - 18% slope) streams in Tennessee, some brook trout moved more than 900 m up- or downstream during a four year study, and several moved between tributaries (Moore et al. 1985). In an experiment conducted in the SFSR drainage, Idaho, I found that some nonnative brook trout moved upstream 130 m in two weeks in channel slopes of 10 to 12 %, and 67 m through slopes of 13 % during two months (Chapter II). Upstream movement occurred in slopes as steep as 22 % (Chapter II).

Since many studies were biased against finding long-distance movements (Gowan et al. 1994), the proportion of fish moving long distances and how far they actually moved is unclear. However, long-distance movements by even a small percentage of the population may be important for predicting invasions since long-distance dispersers can potentially drive invasion rates (Goldwasser et al. 1994; Clark and 12 others 1998). If dispersal ability were the only limitation to invasion, I would expect invasion rates of 130 to >1600 m per year. However, dispersal acts in concert with the net reproductive rate to determine invasion rates. Moreover, movement and dispersal are not synonymous, and no studies I am aware of have tracked spawning locations, let alone reproductive success, of brook trout that moved relatively long distances. Also, the importance of an Allee effect on the net reproductive rate of dispersing brook trout in habitats sparsely occupied by conspecifics is unknown, but is theoretically substantial (Lewis and Kareiva 1993; Kot et al. 1996).

## Methods

The majority of the study occurred in the upper South Fork Salmon River (SFSR) drainage, Valley County, Idaho, upstream of (and including one tributary of) the Secesh River (Figure 1). The SFSR lies in the Idaho batholith where streams tend to have high levels of sand substrate and low fertility (Platts 1979a). Forests are dominated by lodgepole pine (*Pinus contorta*) at higher elevations and Ponderosa pine (*P. ponderosa*) at lower elevations. Stocking records indicate that brook trout were stocked in the drainage from 1932 to 1972 (unpublished data, Idaho Department of Fish and Game (IDFG), Boise), although unrecorded stocking likely occurred earlier and/or later.

I assessed changes in brook trout distributions in 17 tributaries of the SFSR. In this paper, I consider only streams where invasions were assumed to be upstream-directed, with source populations in the mainstem SFSR or in downstream reaches of the tributaries. Headwater lakes within the study drainages were reported not to contain brook trout (unpublished data, Krassel Ranger District, McCall, Idaho, and personal communication, D. Anderson, IDFG, McCall). At the confluence with the SFSR, tributaries ranged from second to fourth order. Stream reaches studied ranged from first to fourth order (Strahler) and wetted stream widths in summer were between 1.6 and 12.9 m (Appendix, Table A1). Channel slopes varied from < 1 % to > 26 %.

Extensive fish surveys were conducted in 14 of the study streams from 1971 to 1974 (Platts 1974; 1979b and unpublished data)(Table 1). In 1971 sampling, Platts installed block nets and detonated primacord in 8 to 27, 15.2 m-long sites per stream (median = 16 sites per stream). Sites were spaced evenly within each land type throughout the streams. In 1974, additional transects in some streams were sampled via electrofishing and/or snorkeling. During the 1980's, several smaller-scale investigations of fish distributions in various tributaries were conducted (Table 1). Also, in 1996 biologists from the Forest Service Rocky Mountain Research Station (RMRS) snorkeled 25 to 30 short (5.6 to 31.1 m long) transects in Lodgepole and Trail creeks. In 1997, they sampled similar reaches in those streams by electrofishing.

From 19 August to 1 October 1996, I revisited the 14 SFSR tributary streams sampled by Platts (in 1971 and 1974) and three tributaries surveyed by other investigators, to determine if brook trout distributions had changed since previous surveys (Table 1). In all streams, I used day snorkeling to define the brook trout distribution limits within 0.5 km of the actual limit. Our sampling design was intended to determine presence or absence of brook trout, not to estimate densities or to determine all year classes present in a stream segment. However, I deliberately searched for juvenile fish in all sites. Our criteria for invasion was the presence of juvenile brook trout (<100 mm total length) beyond the previously reported

distribution limit. The presence of only larger fish (>100 mm) beyond the previous limit was considered expansion of the distribution. The sequence of streams snorkeled was essentially random. The majority of effort was focused on pools since brook trout tend occupy low velocity habitat units even within steep stream reaches (Moore et al. 1985; Cavallo 1997). I attempted to limit snorkeling to times when stream temperatures exceeded 9 °C (Thurrow 1994), however this was not always possible (Appendix, Table A1). I used underwater lights while searching for fish hiding in substrate, woody debris and undercut banks.

I began snorkeling near the uppermost site where brook trout were found previously, or if none were found, I began at the stream mouth. Working my way upstream, I snorkeled three pools. If juvenile and adult brook trout were not abundant, I snorkeled at least three more pools and one run. If they were abundant, I moved upstream 0.5 to 1.0 km, depending on fish densities and habitat changes, and repeated the process. I continued sampling until no brook trout were observed in six pools and one run. In downstream reaches of the larger tributaries, I snorkeled side channels and lateral habitats in addition to main-channel pools (Moore et al. 1985; Cavallo 1997). I snorkeled at least two sites in each stream and snorkeled at least one site upstream of our last brook trout sighting. I did not snorkel pools that were subjectively judged to be of low quality (based on size, depth, cover, and velocity) relative to other pools in the stream. I ended the survey at the uppermost site snorkeled if: 1) no brook trout were observed in the entire stream; 2) the brook trout distribution ended at an obvious barrier such as a large falls (i.e. > 6 m) and no brook trout were previously found above the falls; or 3) other recent fish distribution surveys had been conducted in the stream. Otherwise, I returned downstream and snorkeled a 100 m-long reach approximately 0.25 to 0.50 km upstream of the uppermost brook trout sighting. Channel slope was measured with a clinometer over the entire 100 m. I walked 1 km upstream of the upper distribution limit looking for potential dispersal barriers.

While I undoubtedly missed a few adult brook trout scattered upstream of our survey reaches in some streams, I likely found the entire extent of reproducing populations. In our surveys, brook trout presence was not patchy among sites within streams (Appendix A). More detailed surveys conducted in other brook trout populations indicated that where distributions did not end at barriers to dispersal, adult brook trout were commonly found upstream of the upper limits of juveniles. Since my main goal was to document invasion, defined by the presence of juveniles, my survey methods were appropriate.

I also assessed changes in brook trout distributions over a shorter time interval in two streams, the Little Weiser River and Dewey Creek, in the Weiser River drainage, Adams County, Idaho. In 1993, fish distributions were determined by day and night snorkeling (Adams and Bjornn 1997). In 1997, distributions were reassessed by electrofishing as described above for Trail and Lodgepole creeks (unpublished data, D. Myers, U.S. Forest Service, RMRS, Boise, Idaho).

## Results

At the tributary basin scale, I documented one invasion and no population extirpations in the SFSR tributaries over more than 20 years. Brook trout were observed in 13 of the 17 tributaries snorkeled (Table 1) and in 24 of the 66 sites (Appendix A, Table A1). I found brook trout in two streams where they were absent in 1971 (Table 2). However, I do not consider one of those streams (Six-bit Creek) invaded since only one brook trout was observed, and it was less than 1 km from the creek mouth (Table 1). The other stream (Tyndall Creek) contained multiple age-classes, including juveniles. I found no brook trout in Phoebe Creek, where age 0 brook trout were captured only at the mouth in 1985 (Thurrow 1987), but because I have no firm indication that there was ever a reproducing brook trout population in the creek, I do not consider this an extirpation. In Fourmile Creek, I saw one bull trout x brook trout hybrid, although no brook trout were observed during any surveys of the creek.

At the within-tributary scale, range expansion and invasion were also not extensive. In 7 of 11 streams where I observed brook trout, the upstream limit of their distribution was within 0.5 km of their distribution during previous surveys (Table 3). In four streams, the brook trout distribution had expanded 1.9 to 3.1 km upstream of Platts' uppermost sighting of them (Table 3). However, invasion was more limited than expansion in each stream, with no invasion evident in Curtis Creek, in spite of a 2.2 km increase in distribution (Table 3). In Curtis Creek, Platts had no sample sites between the upper brook trout limit that I observed and 0.8 km downstream, so I may have overestimated the expansion.

Upstream dispersal barriers in the form of very steep channel slopes or waterfalls explained a lack of further upstream invasion in some, but not all, of the tributaries. Of the 11 tributaries containing brook trout in 1996, 4 had barriers to upstream dispersal beyond the earlier distribution limits. Of the seven brook trout streams in which there was no obvious dispersal barrier, brook trout distributions expanded upstream more than 1.9 km in four and remained essentially unchanged in three. In addition, none of the tributary drainages lacking brook trout had barriers to dispersal near their confluences with the SFSR.

The upstream limit of the self-sustaining brook trout population in Lodgepole Creek in 1996 occurred just downstream of an apparently passable culvert. Other workers found one brook trout upstream of the culvert in 1996 and one in 1997 (D. Myers, U.S. Forest Service, RMRS, unpublished data), providing evidence that the culvert was passable to at least some individuals. Although brook trout were abundant in and downstream of a large pool at the base of the culvert both in 1974 and 1996, the upstream distribution limit was unchanged after 22 years. A bull trout population resided upstream of the culvert.

The presence of adult brook trout in a stream does not necessarily mean that invasion is imminent. Mature brook trout have dispersed to several SFSR tributaries, but have not established populations in them. In Camp Creek, two brook trout were observed during two of three surveys in the 1980's, and I observed one in 1996 (Table 1). Although adult brook trout were observed in the stream over a 14 year period, no evidence of an established population has been documented in the creek. In Six-Bit Creek, one mature brook trout was observed, and in Fourmile Creek, a bull x brook hybrid was observed, even though no brook trout have been documented in the creek.

On a shorter time scale, brook trout distributions were also virtually unchanged in the Little Weiser River and Dewey Creek four years after an initial survey. The upper limit of brook trout distributions in 1997 had not expanded beyond the 1993 limit. No waterfalls or steep channel slopes appeared to prevent upstream dispersal of brook trout beyond the 1993 distribution limit in either stream.

## Discussion

Brook trout invasion was minimal over a period of 25 years in the upper SFSR drainage and over 4 years in the Weiser River drainage. Any bias due to comparing results of different methods, was likely to lead to overestimation of the extent of invasion (Appendix B). In most of the streams where little or no invasion occurred, lack of further invasion cannot be explained by poor dispersal ability as Fausch (1989) hypothesized. In two of the three SFSR tributaries where invasion did occur, apparently accessible habitat upstream was still not invaded as of 1996. However, our results are equivocal as to whether brook trout have had ample time to invade headwater streams. The results indicate that invasion of headwater streams can be an exceedingly slow process, and suggest that invasions may stall at some point, only to restart if conditions change (e.g. habitat change or declines in other species). The lower distribution limits of native brook trout in the Great Smoky Mountains National Park retracted from about 600 m elevation at the turn of the century to 900 m in the 1940's to 1200 m in the 1970's (Power 1980), a rate of roughly 8 m of elevation per year, illustrating that changes in the species' distribution can occur gradually over extended periods, even when the changes are apparently the result of multiple anthropogenic alterations of the ecosystem. Since the 1970's, however, the elevations of downstream brook trout limits and upstream rainbow trout limits have fluctuated in many Tennessee streams with no net change among all streams studied (Strange and Habera 1998).

Slow invasion rates and instances of repeated movements to streams without subsequent colonization support the hypothesis that dispersal is not the limiting factor to invasion of many SFSR tributaries at this time. I occasionally found several mature brook trout in streams or stream sections where no evidence of reproducing populations was found. In a steep (average 12 % slope) segment of Hillbilly Creek, Idaho, adult brook trout were abundant but I saw no indication of successful reproduction (Chapter II). Together, the results support previous research indicating that some brook trout will move long distances and that movements in a population fit a leptokurtic better than a normal distribution (Gowan et al. 1994; Gowan and Fausch 1996b). If dispersal limited invasion, the longer dispersal distances, on the long, right limb of the distribution would be expected to drive the invasion rate (Hengeveld 1994; Kot et al. 1996; Clark and others 1998). However, invasion rates were much slower than might be expected based on even low estimates of movement rates. If I assume a constant invasion rate, brook trout would have invaded 5 to 11 m per year over 25 years in the three SFSR tributaries where invasion occurred, and the upper distribution limits of adult fish would have increased at a rate of 40 to 90 m per year. If invasion/expansion was a steady process, it occurred much more slowly than my review of movement rates suggests is possible. I observed that movement rates were somewhat lower in very steep (e.g. > 10 %) than in gentle channel slopes, but even in steep slopes (10 to 12%) I found brook trout moving more than 130 m upstream in two weeks (Chapter II). Furthermore, channel slopes near where distributions ended in five study streams (including the two in the Weiser River drainage) ranged from 1.5 to 8.5 %. Therefore, brook trout were probably capable of dispersing between 1 and > 30 orders of magnitude faster than the observed net invasion rate in these streams.

Alternative explanations for the slow invasion rate are 1) that invasion occurred during one, or several, short interval(s) sometime between sampling dates, or 2) that the distribution changes were merely a snapshot of a fluctuating edge of the distribution (as in Seegrist and Gard 1972; Erman 1986; Larson et al. 1995; Strange and Habera 1998). Since I found no evidence of shrinking distributions in any tributaries, the latter explanation is unlikely. However, sampling at a finer scale may have revealed some fluctuation in the locations of edges (Strange and Habera 1998). If invasion occurred in one pulse, limited dispersal ability still cannot adequately explain why invasions stalled where they did. Limitations on dispersal ability could explain a variable rate of invasion if stream reaches or features were passable only under infrequent, extreme conditions, such as very high flows. However, habitat characteristics of the SFSR streams where invasion proceeded do not support that explanation. Grosholz (1996) found that marine, but not terrestrial, invasions have generally occurred more slowly than predicted, indicating that for organisms with extremely high dispersal rates, much long range movement may fail to result in establishment. Likewise, as Fausch's (1989) remaining hypothesis suggests, successful reproduction (i.e. establishment) may be more limiting than dispersal for brook trout invasion in some stream types.

Our findings present a paradox for managers. Invasion is not inevitable, at least over a period of several decades, wherever brook trout have access to a stream or a reach. However, their ability to disperse upstream through steep slopes means that they potentially have access to much more stream habitat than commonly assumed. It is not surprising that different factors can limit invasion in different places (D'Antonio 1993), but I found that dispersal ability, alone, does not prevent invasion in instances where it was previously suspected to have done so (Fausch 1989). What other factors, then, may be important inhibitors of brook trout invasion?

If invasion is controlled by stochastic processes then time may, indeed, have been insufficient for brook trout to invade all accessible habitat. In Camp Creek, in spite of repeated dispersal to the creek for at least 14 years, no persistent population had been established. In two other SFSR tributaries I found one brook trout or bull x brook hybrid, implying that brook trout and perhaps hybrids moved among tributaries. While there were likely more brook trout in the streams than the one or two observed, densities were extremely low. Demographic stochasticity (e.g. all males in the stream) or Allee effects (Lewis and Kareiva 1993) could prolong the time required to establish a population when relatively few individuals are present.

Abiotic stream characteristics, via their effects on processes other than dispersal, are potentially extremely important in determining the invasibility of streams (Moyle and Light 1996). Steep channel slopes may inhibit invasion by reducing survival at early life history stages, as suggested by Fausch (1989). I hypothesize that within a stream, limited areas, predictable based on physical features, serve as nodes for brook trout reproduction. Pulses of invasion may occur as either physical obstacles to dispersal between nodes or demographic limitations to establishment in the nodes are overcome. Knowledge of the size and dispersion of potential nodal areas within a stream and the difficulty of dispersing between them may assist in predicting the invasibility of a stream. In some stream systems, hydrologic regime (particularly flood timing and intensity) may inhibit invasion by limiting reproductive success and/or survival of older fish (Meffe 1984; Larson et al. 1995; Moyle and Light 1996). Physiological limitations (e.g. on individual growth) imposed by stream temperatures may inhibit invasion via effects on population growth or carrying capacity (e.g. Shuter and Post 1990). Interactions between channel slope and other abiotic factors (e.g. stream size or temperature) and/or biotic factors (e.g. interspecific competition or food availability) may also influence the invasion process (Magoulick and Wilzbach 1998b).

Habitat change may facilitate pulses of invasion. Griffith (1988) assessed brook trout distributions over ten years in two streams where brook and cutthroat trout were sympatric. In one stream where the habitat was degraded over the interval, he observed brook trout invasion. In the other,

with no habitat degradation, no invasion occurred during the same period. Similarly, increases in the ratio of brook to bull trout in a Montana stream over eight years (Leary et al. 1993) occurred during a period of extensive anthropogenic disturbance of the watershed. Due to a moratorium on logging in the SFSR drainage during the interval of our study, few land-use disturbances occurred in the drainage. However, the legacy of past human activities was still evident. Insufficient data were available to evaluate whether stream habitat changes resulting from processes such as landslides, wildfires, floods, or changing rates of sedimentation and recruitment of large woody debris may have differentially influenced invasion among tributaries.

The number of individuals dispersing may influence invasion rate differentially in stream segments with different channel morphologies. Dispersal can influence the direction (Carey 1996) and rate of invasion but it does so in concert with the net reproductive rate (Kot et al. 1996). The importance of immigration versus reproduction in determining population growth rates near the edges of distributions probably varies along a continuum of habitat types. In steep, confined stream channels where reproductive success is low, immigration may contribute more than reproduction to brook trout population growth (particularly where a source of immigrants exists upstream, Chapter IV). However, both reproduction and upstream dispersal are likely to be limited and highly variable in very steep stream reaches, resulting in minimal and/or sporadic population growth. In a marine system, high inter-annual variability in dispersal and recruitment apparently contributed to the three-fold variation in the rate of range expansion by the European green crab (*Carcinus maenas*) in three disjunct locations (Grosholz 1996).

Biotic and abiotic characteristics of source, receiving, and intervening matrix areas can all exert control over dispersal and invasion processes. Conditions in the source area can influence dispersal rate, seasonal timing, and the age, size and health of emigrants. Lidicker and Stenseth (1992) classified the proximate motivations for dispersal of small mammals according to three axes: intrinsic factors, extrinsic factors, and enforced or voluntary dispersal. Conditions in the source area can stimulate enforced dispersal. Extrinsic factors in the source area that influence dispersal may include abiotic and economic conditions, and social and interspecific interactions (Lidicker and Stenseth 1992). Habitat quality and biotic factors in the matrix surrounding the source population can influence the tendency of individuals to disperse, as well as the distance and success of dispersal (Hansson 1991). Conditions in the receiving area can influence an individual's decision to remain in the new area (Riley et al. 1992) as well as affecting growth, fecundity or survival of those remaining (Meffe 1991). Characteristics of mainstem rivers, particularly channel confinement, and perhaps predation pressure, are likely to influence the number of brook trout dispersing among tributaries. The distribution of suitable habitat on the landscape likely influences dispersal since, generally, the further apart the source and receiving habitats are, the lower the immigration rate into the latter will be (Sjögren 1991; Hanski et al. 1995; Sheldon and Meffe 1995; however, see Ruhr 1956).

A better understanding of the motivations for dispersal in salmonids is important to improving our understanding of the invasion process and of the role of human activity in it. If poor habitat quality stimulates dispersal, habitat degradation in streams containing nonnative fishes may accelerate invasion upstream or into neighboring streams. For example, food limitation resulting in lowered condition factor motivated dispersal by salmonids in laboratory settings (Wilzbach 1985; McMahon and Tash 1988; Mesick 1988) and possibly in the wild (Gowan and Fausch 1996b). On the other hand, high quality habitat for an exotic species may result in larger source populations that support higher rates of dispersal and, thus, invasion. Distant source populations can have substantial influences on upstream community structure, as indicated by dramatic changes in species composition, relative abundances, and production of both native and nonnative fishes have been demonstrated in unaltered tributaries of newly formed reservoirs (Ruhr 1956; Crisp et al. 1984; Penczak et al. 1984; Pringle 1997). Finally, we need to better understand the possible role of biotic resistance by other fish populations in inhibiting brook trout dispersal and invasion (Griffith 1988). This knowledge is necessary to determine whether invasion-prevention efforts are best directed toward maintaining the strongest possible populations of native fishes or to depleting, and preventing dispersal by, the invading species.

In addition to informing efforts to prevent or reverse invasions, aspects of invasion theory are relevant to conservation of native species because recovery of remnant, native salmonid taxa will often depend on fish successfully recolonizing formerly occupied habitats, a process strikingly similar to invasion. Similar to the plight of brook trout in the eastern USA, most taxa of salmonids in the western USA have suffered dramatic and widespread range contractions, resulting from multiple ecosystem alterations (Frissell et al. 1993; Young 1995b). Lessons from brook trout invasions suggest that recolonization is likely to be a slow and discontinuous process and that limiting factors will often be multi-faceted and spatially variable. Therefore, treatments of single factors will probably seldom lead to widespread recolonization by native species. Rather, treatment of multiple abiotic and biotic factors, and attention to subtle demographic features of sometimes distant source populations may be required to successfully assist the recovery of native salmonids.

Table 1. Presence (+) or absence (-) of brook trout in tributaries of the upper South Fork Salmon River, Idaho, in various surveys. Uncertainty regarding species identification is indicated by "(?)". Number of fish observed is given when few were found. Thurow (1987) snorkeled and electrofished only habitats where steelhead trout were expected to occur. Cascade Environmental Services (CES)(1989) personnel subsampled one to three 200 m sites per stream by snorkeling and electrofishing. Krassel Ranger District personnel snorkeled a subset of each habitat type in the Buckhorn and Lick Creek drainages (methods in Overton 1997).

Tributary	Platts	(Heagy 1982)	Thurow	CES	Krassel	This	Comments
	1971		1984-1985		1993-1994		
	(1974)a			1989		study	
Bear	+		+				+
Blackmare	1		-	+			+
Buckhorn	-		-	-	+(?)		-
Little							
Buckhorn					-		-
W Fork	-		-	-	-		-
Cabin	+			+			+

MECHANISMS LIMITING A VERTEBRATE INVASION:

Camp		2	2	-	1	Heagy e-fished 0.6 km at mouth and at SFSR bridge
Cougar	+	+	+		+	Heagy e-fish 0.8 km at mouth
Curtis	- (+)		+		+	
Trail	1				+	
Dollar	+		+	+	+	
Fitsum	-		-		-	
Fourmile	-		-	-	-	1 bull x brook hybrid
Lodgepole	+ (+)				+	
Phoebe		-	+b		-	Heagy e-fish 200 m at mouth
Six-Bit	-				1	
Tyndall	-				+	

- a. Symbols in parentheses are from the later year.
- b. Only brook trout observed were age 0 individuals at mouth of stream

Table 2. Presence or absence of brook trout observed by Platts in 1971 or 1974 versus by me in 1996 in tributary drainages and in individual streams in the South Fork Salmon River, Idaho.

Brook trout in early 1970's	Brook trout in 1996			
	# of Drainages		# of Streams	
+	7	0	8	0
-	2	3	2a	4b

- a. Only one brook trout was observed in one of these streams. See text.
- b. One hybrid was seen in one of these streams.

Table 3. Changes in upper limits of brook trout distributions since Platts' survey (1971, 1974). The upstream expansion of the upper distribution limit refers to changes in the occurrences of brook trout, even if represented by only a single large fish. Upstream invasion indicates the uppermost location where I found evidence of reproduction (see text) relative to Platts' uppermost sighting of brook trout of any size. Falls or steep gradients that may have hindered dispersal beyond upper distribution limits in 1971 and 1996 are noted.

Stream	Extension of upstream distribution limit (km)	Upstream invasion (km)	Barrier within 1 km of earlier upstream limit?	Description of potential barriers inhibiting upstream dispersal beyond 1996 distribution limits
Bear	2.6	2.1	no	8 m long falls- not vertical
Blackmarea	0.2	0	no	
Cabin	0	0	yes	15% slope; 7 falls >0.6 m;
Campb	0.5	0	no	
Cougar	0	0	yes	2 falls >6 m
Curtis	2.2c	0	no	
Trail	1.9	1.2	no	
Dollar	0.5	0	yes	falls 8 m
Lodgepole	0(0.6)d	0	no	
Six-Bit	0.5	0	yes	21% slope; 4 falls 0.6-1.0 m
Tyndall	3.1	2.4	no	

- a. Much of the stream was invisable from a lake at the head of tributary, but no upstream invasion above the tributary confluence occurred.
- b. Comparison to distribution in 1980's.
- c. Possibly overestimated (see text).
- d. Other workers found one brook trout 0.6 km upstream of previous limit (see text).

Figure on following page:

Figure 1. Study streams and other major tributaries of the upper South Fork Salmon River, Idaho. Italicized stream names indicate that no brook trout were observed in those streams. Small arrows on two tributaries indicate that invasions were downstream-directed and are shown here only to illustrate brook trout distributions.

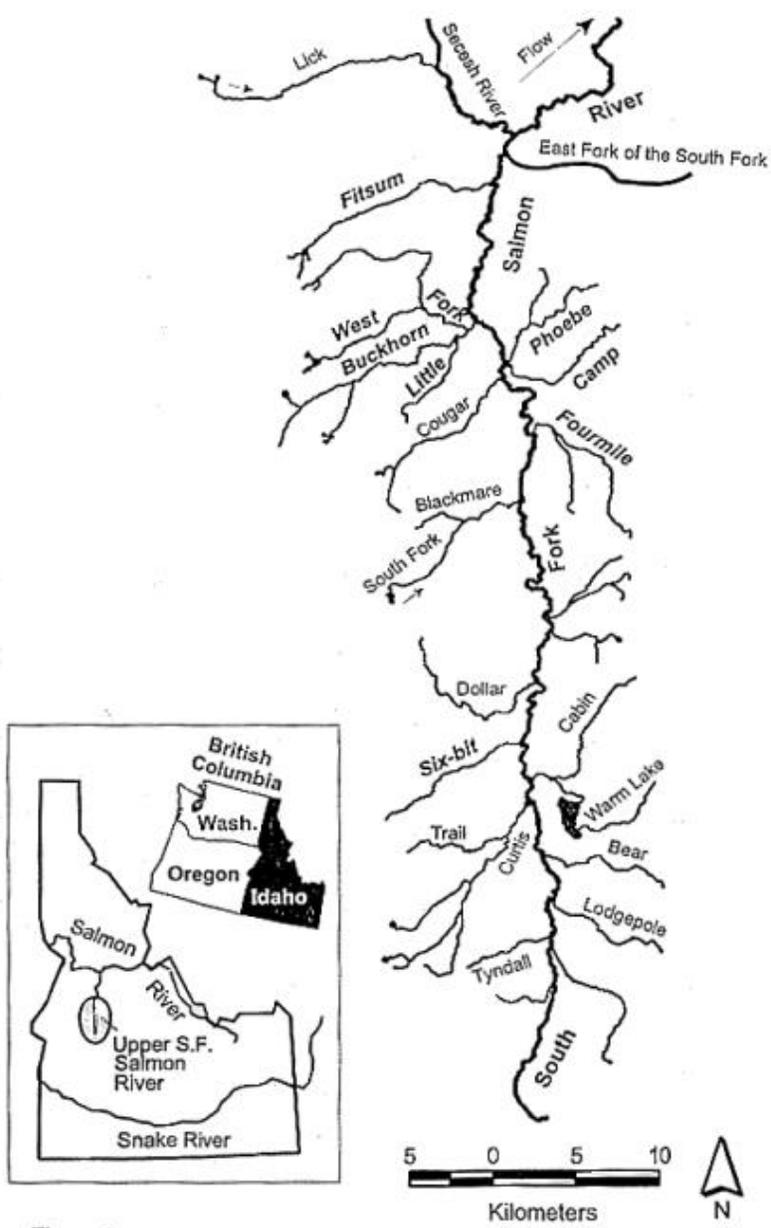


Figure 1.

## Appendix A: Site descriptions and brook trout observations

Table A1. Location and physical descriptions of South Fork Salmon River, Idaho, snorkel sites. Numbers of brook trout are reported in total length categories. Temperature and wetted stream width were measured at the time of snorkeling. Elevations and locations were taken from U.S.G.S. 1:24,000 scale topographic maps. Locations reported as township, range, section, 1/4 section, 1/4 1/4 section.

Brook trout		Date	Start	Temp.	Stream	Width	Elev.
<100	100	(m/d)					

MECHANISMS LIMITING A VERTEBRATE INVASION:

Stream	Site	mm	mm	1996	time	(oC)	order	(m)	(m)	Location				
Bear	A	7	3	8/26	1125	9.3	2	3.5	1679	15N	7E	19	SW	NW
Bear	B	1	2	8/26			2		1701	15N	7E	19	NW	SE
Bear	C	3	2	8/26	1425	13.2	2	2.5	1740	15N	7E	19	SE	NE
Bear	D	1	2	8/26	1525	12.1	2	2.6	1762	15N	7E	20	SW	SW
Bear	U	--	2	8/27	1325	11.3	2	3.5	1792	15N	7E	20	SW	SE
Bear	E	--	2	8/26	1623	11.2	2	4.1	1841	15N	7E	20	SW	SE
Blackmare	A	3	--	9/19	1638	8.0	3	7.5	1277	17N	6E	10	SE	SE
Blackmare	B	1	2	9/17	1741	8.0	3	8.4	1347	17N	6E	10	SW	SE
Blackmare	C	--	2	9/16	1602	8.0	3	6.2	1579	17N	6E	16	NW	SW
Blackmare	D	--	--	9/16	1753	8.0	1	4.2	1600	17N	6E	17	SE	NE
Buckhorn	A	--	--	9/7	1634	10.9	4	12.9	1180	18N	6E	4	SW	SW
Buckhorn	B	--	--	9/5	1500	10.9	3	9.5	1219	18N	6E	8	NW	SE
Little Buckhorn	A	--	--	9/5	1411	8.3	3	4.1	1222	18N	6E	8	SE	NW
Little Buckhorn	B	--	--	9/4	1709	10.2	3	3.6	1283	18N	6E	8,17		
Little Buckhorn	C	--	--	9/4	1500	9.2	2	2.7	1323	18N	6E	17	NW	SW
Little Buckhorn	D	--	--	9/4	1605	9.5	2	3.0	1341	18N	6E	17	NW	SW
W.F. Buckhorn	A	--	--	9/5	1053		3	6.7	1204	18N	6E	8	NE	NE
W.F. Buckhorn	B	--	--	9/6	1204	9.3	3	9.3	1237	18N	6E	5	SW	SE
Cabin	A	--	11	8/20	1515	9.0	2	3.8	1710	16N	7E	30	NE	NW
Cabin	U	--	--	8/21	1625	9.2	2	4.1	1719	16N	7E	30	NE	NE
Cabin	B	--	--	8/20	1258	8.0	2	3.0	1743	16N	7E	19	SE	SE
Camp	A	--	--	9/30	1330	7.5	3	1.7	1201	18N	6E	15	SW	NW
Camp	B	--	1	9/30	1500	9.0	3	2.4	1216	18N	6E	15	SW	SE
Camp	C	--	--	9/30	1600	8.0	3	4.0	1244	18N	6E	22	NE	NW
Camp	D	--	--	10/1	1350	7.0	3	2.0	1280	18N	6E	22	NE	NE
Cougar	A	--	1	9/18	1345	7.5	3	5.5	1204	18N	6E	21,22		
Cougar	B	5	--	9/18	1500	7.5	3	5.7	1219	18N	6E	21	NE	SE
Cougar	C	1	2	9/18	1622	8.0	3	5.8	1247	18N	6E	21	SE	NW
Cougar	D	--	6	9/19	1207	7.0	3	8.0	1311	18N	6E	21,28		
Cougar	E	--		9/19	1307	7.5	3	5.0	1317	18N	6E	28	NW	NW
Curtis	A	--	1	8/19	1245	8.2	3	7.3	1585	15N	6E	15	SW	NE
Curtis	B	--	1	8/19	1440	9.3	3	7.3	1609	15N	6E	15	SW	SE
Curtis	U	--	--	8/19	1745	10.7	3	6.9	1618	15N	6E	15,22		
Curtis	C	--	--	8/19	1642	10.7	3	5.0	1628	15N	6E	22	NW	NW
Dollar	A	--	3	8/22	1302	7.9	3	6.3	1615	16N	6E	21	SE	SE
Dollar	B	--	3	8/22	1411	8.8	3	5.0	1643	16N	6E	28	NE	NW
Dollar	U	--	--	9/14	1500	8.9	3		1676	16N	6E	21,28		
Dollar	C	--	--	8/22	1624	9.4	3	4.4	1713	16N	6E	21	SW	SE
Fitsum	A	--	--	9/6	1104	6.2	4	10.3	1143	19N	6E	9	SE	NE
Fitsum	B	--	--	9/6	1217	7.1	4	10.7	1189	19N	6E	8,9		
Fitsum	C	--	--	9/6	1416	8.3	4	9.7	1244	19N	6E	8	SW	SE

Table A1continued.

Stream	Site	Brook trout		Date	Start	Temp.	Stream	Width	Elev.	Location				
		<100	>=100	(m/d)						1996	time	(oC)	order	(m)
Fourmile	A	--	--	8/21	1600	11.2	3	5.0	1253	18N	6E	35	NW	NW
Fourmile	B	--	--	8/21	1653	10.7	3	5.3	1265	18N	6E	26	SW	SW
Fourmile	C	--	--	10/1	1650	8.0	3	6.7	1305	18N	6E	26	SE	SW
Lodgepole	A	--	3	9/9	1630		3	3.0	1652	15N	6E	36	SE	NW
Lodgepole	B	--	4	9/9	1713	9.2	3	4.5	1664	15N	6E	36	SE	NE
Lodgepole	C	--	--	9/9	1400		3	4.5	1686	15N	7E	31	SW	NW
Phoebe	A	--	--	9/6	1700	10.1	4	3.1	1201	18N	6E	15	NW	SW
Phoebe	B	--	--	9/6	1745	9.5	4	1.8	1225	18N	6E	15	NW	SE
Six Bit	A	--	--	8/28	1110	10.3	4	5.5	1539	16N	6E	34	NE	NE
Six Bit	U	--	1	8/28	1430	11.1	4	7.4	1567	16N	6E	34	NE	NW
Six Bit	B	--	--	8/28	1230	10.3	4	6.7	1640	16N	6E	34	NW	NE
Six Bit	C	--	--	8/28	1715	11.9	4	4.2	1686	16N	6E	33	NE	SE
Trail	A	--	1	9/25	1150	5.0	3	5.0	1585	15N	6E	15	SW	NW
Trail	B	9	6	9/25	1545	9.5	2	5.2	1695	15N	6E	20	NE	NE
Trail	C	--	2	9/23	1620	5.0	2	2.8	1704	15N	6E	20	NE	NE

## MECHANISMS LIMITING A VERTEBRATE INVASION:

Trail	D	--	--	9/24	1612	6.0	2	4.0	1737	15N	6E	17	SW	SE
Trail	E	--	--	9/24	1358	5.0	2	3.0	1780	15N	6E	17	SW	SW
Trail	F	--	--	9/24	1451	5.0	2	2.1	1811	15N	6E	18	SE	SE
Tyndall	A	--	--	8/29	1315	9.4	2	3.4	1637	14N	6E	2	NE	SE
Tyndall	B	--	--	8/29	1404	9.4	2	2.7	1643	14N	6E	2	SE	NW
Tyndall	C	--	--	8/29	1530	9.1	2	2.9	1655	14N	6E	2	SW	NE
Tyndall	D	3	--	8/29	1630	9.4	2	3.3	1676	14N	6E	2,3		
Tyndall	U	1	1	9/3		9.4	2	2.6	1695	14N	6E	3	SE	MID
Tyndall	E	--	--	9/3	1305	7.5	2	2.3	1710	14N	6E	3	SE	SW
Tyndall	F	--	--	9/3	1453	8.1	2	3.4	1750	14N	6E	10	NE	NE

## Appendix B: Potential for Bias in Analysis

Even though I found evidence for relatively little brook trout invasion in the study streams, my estimates of invasion are potentially liberal due to differences in sampling methods over time. At a stream reach scale, my snorkel observations suggested a continuous, rather than patchy, brook trout distribution (Appendix A, Table A1). However, in Platts' 1971 prima-cord sampling, brook trout observations were patchy, and brook trout smaller than 100 mm were particularly uncommon. Although such patchiness could reflect an incipient invasion, I suggest that it is a reflection more of methods than of actual distributions. In 1974, Platts electrofished the lower 1.6 km of Curtis and Lodgepole creeks and found abundant brook trout where none had been found during 1971 sampling with prima-cord (W.S. Platts, unpublished data on file at U.S. Forest Service, RMRS, Boise, Idaho). The differences were due either to rapid invasion or to ineffectiveness of prima-cord samples in short stream reaches at capturing brook trout. Based on catch data and comments on Platts' data forms, it appears that prima-cord sampling for brook trout may have been less effective in larger stream reaches where the fish were more frequently associated with side channels, lateral habitats, and large woody debris. If prima-cord was less effective than snorkeling for detecting brook trout, our estimates are likely to overestimate the actual incidence or rates of invasion.

## Chapter IV: Downstream Dispersal and Invasion Following Fish Introductions to Mountain Lakes ... It's All Downhill From Here

### Abstract

The majority of high mountain lakes in the western United States contain introduced salmonid fishes, even though most were historically fishless. Brook trout (*Salvelinus fontinalis*), native to eastern North America, have been widely introduced in lakes and streams of the western USA and Canada and have adversely impacted native fauna. I used data on brook trout distributions in 17 lake-outlet streams to assess the channel slopes and waterfall heights through which the fish dispersed downstream. I also compared channel slopes occupied in upstream- versus downstream-directed invasions. Brook trout dispersed downstream through 80 % slopes, over 18-m-high waterfalls, and further than 15 km downstream from source lakes. The steepest slopes they occupied were in streams invaded from headwater sources. Upstream-directed invasions in slopes steeper than about 17 % were apparently limited by swimming ability rather than by an inability to occupy steep stream reaches. Due to asymmetry in upstream versus downstream dispersal ability, substantially more stream area is potentially invadable by fish from headwater populations than from downstream populations. The magnitude of the difference depends, in part, on the geography of the stream network, particularly the density and distribution of headwater lakes and their locations relative to barriers inhibiting upstream dispersal. For example, introductions in all headwater lakes would allow brook trout access to an additional 33 % of the total tributary stream length in the South Fork Salmon River drainage, Idaho, but only to an additional 4 % in the upper Big Hole River drainage, Montana. Rapid growth, even at high elevations, in some lakes and lake-outlet streams likely confers demographic, behavioral, and foraging advantages on individuals invading downstream in lake-outlet streams versus upstream in high-elevation streams without lakes. Largely because they allow access to more stream habitat and can create demographic and behavioral advantages, fish introductions to headwater lakes potentially pose more extensive threats to native stream fauna than do introductions lower in the watersheds.

# Introduction

Interactions with nonnative species are one of the leading causes of species extirpations and declines in freshwater ecosystems (Miller et al. 1989; Allan and Flecker 1993). Salmonids, including salmon and trout (*Oncorhynchus* spp. and *Salmo* spp.) and char (*Salvelinus* spp.), have been widely introduced to freshwater ecosystems worldwide. 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, a mountainous region of the Pacific Northwest (USA) (Thurow et al. 1997). Nonnative fish invasions originating in relatively low elevation habitats have impacted native aquatic fauna in large portions of many drainages. In this paper, I address the additional invasion of headwater refugia resulting from fish stocking in headwater lakes and explore some implications for native stream fauna.

Fisheries managers have stocked fish (including species native to the region) in naturally fishless lakes throughout the western USA since the late 1800's, primarily to provide sport fishing. Similar practices have occurred in Scandinavia since the 12th century or earlier (Nilsson 1972) and continue in headwater lakes world-wide. 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 are repeatedly stocked whether or not self-sustaining populations of fish were established after earlier introductions (personal communication, R. Knapp, Sierra Nevada Aquatic Research Laboratory, University of California). Brook trout are particularly easily established in lakes, probably because they will spawn in either inlet or outlet streams or over spring seeps within lakes (Reimers 1958). In most western states brook trout stocking is now uncommon, but it continues in mountain lakes in Oregon (personal communication, Terry Farrell, Oregon Department of Fish and Wildlife).

Fishless lakes and lake-outlet streams above barriers to upstream fish dispersal historically provided native stream fauna with refuges from native fishes (Figure 1). In addition, remnant populations of some native fishes have persisted upstream of barriers in drainages where nonnative fishes have invaded lower stream segments (Power 1980; Townsend and Crowl 1991; Closs and Lake 1996). Even where dispersal barriers are not present, headwater streams are frequently strongholds for native salmonids (Larson and Moore 1985; Fausch 1989; Larson et al. 1995; Dunham et al. 1997). Historical records are often inadequate for distinguishing between historically fishless stream segments and ones historically containing native fishes, so I will not do so in this analysis. Because of the importance of headwater stream refuges 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 attention.

Many populations of native vertebrates in small, high elevation streams may be relatively unstable due to slow growth, late maturity, low fecundity, and low survival during long, harsh winter conditions. Such populations may be ill-equipped to withstand additional stresses imposed by an introduced species. Lakes deep enough to sustain fish (but fishless, nonetheless) are often demographically important, if not essential, to many high elevation amphibian populations, and possibly metapopulations (Bradford 1989; Liss and others 1995; Tyler et al. 1998). Populations of some organisms that appear to coexist with fish predators/competitors in streams may actually represent sink populations that are dependent on source populations in upstream refuges to provide immigrants (Resetarits 1995). Therefore, fish introductions that functionally eliminate headwater refuges could potentially cause local extirpations of a native species that appeared to coexist with the introduced fish when an upstream refuge for the native still existed.

Nonnative fishes potentially influence native fauna via predation, competition, spread of diseases or parasites, inducement of behavioral changes, and hybridization, among other mechanisms (Nilsson 1972; Miller et al. 1989; Krueger and May 1991; Stewart 1991; Bradford et al. 1993; Blaustein et al. 1994; Tyler et al. 1998). Fish introductions into mountain lakes have caused dramatic changes in both community composition and population structures of native fauna, including zooplankton (Johnson 1980; Chess et al. 1993), insects and other invertebrates (Nilsson 1972; Reimers 1979), amphibians (Bradford 1989), and in some cases, native fishes (Nilsson 1972; Crowl et al. 1992). The impacts of fish introductions on biota in lake-outlet streams are poorly understood, but are potentially substantial. In headwater streams within their native range, young brook trout reduced survival and growth of the salamander *Gyrinophilus porphyriticus* (Resetarits 1991; Resetarits 1995). Tailed frog (*Ascaphus truei*) larvae increased refuge use in water chemically conditioned by brook or cutthroat trout, a behavior that may reduce growth rate in the presence of the predator (Feminella and Hawkins 1994). Bechara et al. (1992) demonstrated that brook trout can have a top-down influence on benthic invertebrates and periphyton in small streams. Brook trout have contributed to declines in native bull trout (*Salvelinus confluentus*) populations via hybridization, and possibly competition or other mechanisms (papers in Howell and Buchanan 1992; Leary et al. 1993). In some regions, brook trout have displaced or replaced native cutthroat trout in streams, although the mechanisms are unknown (Griffith 1988; Fausch 1989; De Staso and Rahel 1994; Dunham et al. In Press). For these reasons, some scientists have recommended against introducing fish where they could contact native fishes downstream (Krueger and May 1991; Lee and others 1997).

Downstream-directed invasions (with lake source populations) may result in greater overlapping distributions and potential for adverse interactions between brook trout and native bull and cutthroat trout than would low-elevation introductions. Unlike most other native fishes in the S.F. Salmon River basin, native bull and cutthroat trout numbers per stream length were positively correlated with elevation (Platts 1979b). In other locations, both species frequently occur upstream of brook trout (Fausch 1989; Adams and Bjornn 1997). In the Bitterroot River basin, Montana, brook trout typically occupied smaller streams at lower elevations than those occupied by bull trout, possibly due to different habitat preferences (Rich 1996). One might expect, then, that downstream-directed invasions with high-elevation source populations, would result in greater overlapping distributions and potential for adverse interactions between brook trout and native bull and cutthroat trout than would low-elevation introductions.

In typically steep, mountain streams, limited dispersal ability is the most obvious mechanism potentially restricting upstream dispersal and invasion by fishes. Most mathematical models used for predicting invasions (e.g. diffusion models) assume equal dispersal by organisms in all directions and locations (Hastings 1996; Kot et al. 1996). However, for lotic (flowing water) organisms, as well as some terrestrial ones (Carey 1996), dispersal is primarily linear and is often different, both in rate and frequency, in each direction and at different locations along the dispersal route (Johnson and Carlton 1996). In mountain streams, upstream fish movement is frequently blocked by barriers, such as waterfalls, but

downstream movements may be less inhibited. We can improve our ability to predict fish invasions in streams by understanding dispersal abilities and tendencies in each direction throughout stream networks.

In this paper, my first goal is to establish the relative implications of headwater versus downstream introductions for salmonid dispersal and invasion in stream-lake networks. Secondly, I discuss conservation implications of headwater lake fish stocking for fauna using downstream habitats. Finally, I make inferences about dispersal limitations in upstream-directed invasions by making comparisons to downstream-directed invasions. Brook trout are well-suited for my analysis for several reasons: 1) they were widely introduced to, and have readily established populations in, both lakes and streams, 2) they appear to have detrimental effects on numerous native species, and 3) they are easily distinguishable from all native species in the Rocky Mountains. I investigated the first question both through inference from present-day distributions relative to known or supposed stocking locations in headwater lakes and through hypothetical projections of potential invisable area resulting from upstream versus downstream introductions.

## Methods

I collected data both in the field and from other biologists to assess downstream dispersal of brook trout in lake-outlet streams. I assembled and evaluated various surveys of fish distributions for which I could infer downstream dispersal from lakes. Sites and dates of fish introductions were well-documented in some drainages, but in others, I assumed where introductions had occurred based on present fish distributions and stream morphologies. Because I was interested in dispersal through steep channel slopes, I only analyzed downstream-directed invasions in lake-outlet streams containing slopes greater than 10%. I included streams in the data set only if they met at least one of the following criteria: 1) brook trout were documented as previously stocked or recently present in a headwater lake feeding the stream, 2) 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 3) brook trout occurred upstream of an impassable falls (greater than 3 m high) or of a stream reach with channel slope exceeding 17 %.

I conducted fish distribution surveys in Blackmare and Lick creeks, Valley County, Idaho in 1996 and in the South Fork (S.F.) Little Joe River, its tributary Moore Creek, and Twelvemile Creek, Mineral County, Montana, in 1997 (Appendix A). In the Idaho streams, I determined brook trout presence/ absence 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. I restricted sampling mostly to pools because within steep stream reaches, brook trout use primarily pool habitat (Moore et al. 1985). Channel slope was measured with a clinometer in a portion of each snorkeling reach. In the S.F. Little Joe River and Moore Creek, I collected fish by multiple-pass electrofishing without block nets in 100 m-long reaches. Channel slopes were measured throughout each reach with a rod and level. I sampled seven, roughly evenly spaced, 100 m reaches in Moore Creek and two additional reaches in the S.F. Little Joe River, downstream of the confluence with Moore Creek. In Twelvemile Creek, I electrofished one pass through four reaches, each longer than 300 m.

I obtained data for other streams with downstream-directed invasions from U.S. Forest Service biologists. The methods used for fish sampling are noted 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 based on changes in channel morphology, stream confluences, etc. (e.g. defined as "reaches" in Overton 1997).

The maximum channel slope that brook trout dispersed downstream through was determined either from on-site channel slope measurements or from U.S.G.S. 1:24,000 topographic maps, whichever was steepest. Map-derived slopes were calculated over 100 to 200 m of stream. I report the heights of the highest *known* waterfalls over which brook trout dispersed downstream (Appendix A). Since 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 through which brook trout dispersed in each stream.

I made conservative estimates of the distances that brook trout from lake-origin populations had dispersed or invaded downstream. I only included distances to the mouths of lake-outlet streams or to reaches where I was confident that the brook trout were descendants of fish in the lake of interest. I estimated minimum distances that individual fish probably dispersed from the spatial distribution of fish locations relative to reproductive areas. For eight streams where I had adequate data, I estimated distances between the most downstream location with evidence of successful reproduction (detection of age 0 brook trout) and the most downstream observation of older brook trout in the stream and inferred that individual fish had likely traveled the entire distance.

The maximum channel slope where brook trout occurred was determined from field measurements at fish sampling reaches over distances of 30 to 150 m (Table 1). Most data sets included channel slopes and fish occurrences on stream segment scales (up to several km long), and I could not determine whether brook trout actually occurred in the steepest reaches within the segment. Therefore, data from only a subset of streams were used to assess the occurrence of brook trout in steep reaches. However, in many streams, the reaches containing the steepest slopes were not sampled for fish.

I collected data on streams with upstream invasion vectors in 13 tributary drainages of the upper South Fork (S.F.) Salmon River, Valley County, Idaho, in 1996. I used the same methods as those described above for the two Idaho streams with downstream-directed invasions. 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 <1 to 23 %.

I compared length at age of brook trout in a lake-outlet stream system (Moore Creek/S.F. Little Joe River) and a nearby, stream lacking a headwater lake (Twelvemile Creek). I electrofished multiple reaches in each stream to collect all size classes of fish present (Appendix B). I aged fish using sagittal otoliths (Chapter V)

To explore the larger drainage-scale significance of headwater lakes as colonization sources, I used some simple landscape rules to classify potentially invisable stream lengths for brook trout originating from mainstem versus headwater sources in the upper portions of two drainages with contrasting morphologies: the upper S.F. Salmon River, Idaho, and the upper Big Hole River, Montana. The landscape rules were that 1) brook trout

would disperse downstream through any slope and over any waterfalls, 2) channel slopes steeper than 17 % and waterfalls higher than 2.5 m were barriers to upstream dispersal, 3) invasions could originate from all headwater lakes and from all tributary confluences with the mainstem rivers, and 4) intermittent streams could be used as dispersal corridors. The first two assumptions are illustrated in Figure 1. The characteristics of barriers to upstream dispersal were based on mark-recapture experiments conducted in various channel slopes (Chapter II and unpublished data). Channel slopes limiting invasions are probably closer to 13 % over distances measurable on the topographic maps. However, I chose 17 % so that estimates of the area potentially invadable from upstream, but not downstream, would be conservative. All areas accessible to fish were considered potentially invadable in the model, although other factors clearly influence the invadability of a stream. I identified the most downstream location where either channel slope exceeded 17 % over distances of 100 to 200 m on U.S.G.S. 1:24,000-scale topographic maps or a known barrier occurred. I also identified dispersal barriers upstream of headwater lakes. After digitizing barrier locations in a GIS, I classified stream segments into three categories: potentially invadable from 1) headwater lakes 2) mainstem sources, or 3) neither. I tallied stream segment lengths by category within each basin

## Results

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

Brook trout distributions extended as far as 22 km downstream of lakes in stream systems where no apparent downstream source populations existed (Figure 3; Appendix A). I 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 I report in some drainages. In contrast, brook trout were abundant and reproducing in Elizabeth Creek 0.5 km downstream of Ice Lake, but were not found in any of the nine reaches sampled further downstream.

Adult brook trout occupied very steep reaches in some streams with downstream-directed invasions. I observed brook trout in reaches with 19 % channel slopes in Blackmare and Moore creeks and 23 % slope in Gedney Creek (Table 1). In 4 of 7 streams, brook trout were observed in the steepest reaches sampled. However, in a Lick Creek reach where channel slopes ranged from 17 to 24 % and numerous falls occurred, no fish were observed even though apparently suitable habitat (large pools) was present and brook trout occurred both up- and downstream of the reach. No age 0 or yearling-size fish were observed in such steep reaches, indicating that local reproduction did not occur there.

Preliminary analysis indicates that the relationship between brook trout invasion, distribution, and channel slope may be confounded by stream size. Where channel slopes exceeded 9 %, brook trout occurred in reaches with wetted stream widths up to 3.8 m where invasions were upstream-directed, but up to 8.1 m where invasions were downstream-directed (Table 1). Of the reaches included in Table 1, the proportion with wetted widths > 4 m was significantly greater for streams with downstream- than upstream-directed invasions (Fisher's exact test,  $p$ -value = 0.045). A more thorough analysis will require random sampling for brook trout in a range of stream widths and channel slopes in streams invaded from each direction.

In most cases, I could not determine whether fish in the steepest reaches were transient or resident for some time. However, in Moore Creek, an individual brook trout occupied the same pool in a reach with 19 % slope for at least four days. In Hillbilly Creek (upstream-directed invasion), fish apparently maintained residency throughout a year (July 1996 to August 1997) in pools within reaches characterized by 13 to 20% channel slopes (Chapter II).

The relative amounts of potentially invadable stream habitat from headwater versus mainstem sources were highly dependent on the drainage basin morphology, specifically the locations of barriers to upstream dispersal and the distribution of headwater lakes. The landscape analysis predicted that 33 % of tributary stream length was invadable only from headwater sources in the upper S.F. Salmon River drainage versus 4 % in the upper Big Hole River drainage (Figure 4). Moreover, in the S.F. Salmon River drainage, only one lake (Warm Lake) was invadable from the mainstem, and three entire tributary drainages were inaccessible to brook trout moving upstream. However, in the Big Hole River drainage, numerous lakes were invadable from downstream and primarily short, headwater reaches of streams were inaccessible to brook trout from downstream sources. Exceptions in the Big Hole were several streams with no surface-water connection to the mainstem (personal communication, Bruce Roberts, U.S. Forest Service, Wisdom, Montana).

Age 0 brook trout in the uppermost reach of Moore Creek (100 m below the outlet of Moore Lake) grew significantly faster than those in any other reach sampled in Moore Creek, the S.F. Little Joe, and Twelvemile Creek (ANOVA,  $d.f.$  = 12,  $P$  < 0.000, LSD post-hoc comparisons  $P$  < 0.000) (Figure 5 and Chapter V). In Twelvemile Creek, the trend in size was decreasing with increasing elevation (line fit to mean age 0 fish length in each reach: slope = - 0.04,  $P$  = 0.03). In the S.F. Little Joe / Moore Creek, the relationship between size and elevation was quadratic, with size decreasing with increasing elevation up to about 1.6 km downstream of Moore Lake and then increasing steeply with elevation up to the lake. Accompanying the faster growth, brook trout in the two reaches nearest the outlet of Moore Lake matured at least one year earlier (males at age 1, females at age 2) than individuals in the lower half of Moore Creek and in the upper half of Twelvemile Creek (Chapter V).

## Discussion

The rate of stream invasion may be driven by many factors, including dispersal ability, dispersal options, and demographic pressures in potential source populations. I found evidence that each of these three factors may facilitate greater stream area being invaded from upstream than from downstream sources of initial introduction. Although my discussion is based on brook trout distributions and behaviors, the patterns discussed are likely applicable to invasions by other salmonids as well.

Upstream dispersal ability or inclination, rather than inability to occupy a steep reach, apparently inhibits upstream invasions where slopes exceed about 17%. Brook trout in most of the study streams dispersed downstream through the steepest slopes they encountered. In downstream-directed invasions, where dispersal ability was not limiting, brook trout sometimes occupied steeper slopes than those they dispersed through in upstream-directed invasions. Because of differences in methods among studies, my data probably included the steepest stream reaches containing brook trout in streams with upstream-directed, but not downstream-directed, invasions. Thus, brook trout may inhabit even steeper reaches than I report where invasion vectors were downstream.

When a fish moves upstream, it usually retains the option of returning "home" if it encounters unsatisfactory conditions; however, downstream movement in mountain streams involves greater risk since the option of returning "home" may be lost. Other organisms, including some mammals and birds, make forays into multiple new habitats before dispersing (Woolfenden and Fitzpatrick 1984; Holekamp and Sherman 1989). Fish leaving a lake and moving down through extreme channel slopes or over a large waterfall would be unable to return to the lake, so downstream exploratory movements or passive displacement would automatically become dispersal.

Fish unable to return home and not encountering ideal habitat have two options: continue moving in search of better conditions or remain in sub-optimal habitat. I suggest that brook trout dispersing downstream through steep slopes are more likely to colonize distant or less suitable habitats than are fish originating in suitable habitat lower in a drainage. In a variety of animals, movements through hostile matrices tend to be longer and/or faster than those through benign matrices (Hansson 1991; Schultz 1998). In the Great Smoky Mountains National Park (GSMNP) some of the longest recorded distances moved by tagged brook trout were by individuals that had moved downstream over waterfalls. Our data indicate that some brook trout moved relatively long distances, at least 15 km, down lake-outlet streams and the larger streams they joined, and I assume that some fish dispersed downstream over longer distances than I report (see Gowan and Fausch 1996b). Assuming that brook trout in the West prefer small streams (Kozel and Hubert 1989; Bozek and Hubert 1992; Rich 1996), forced occupation of less suitable habitat may be one possible explanation for the occurrence of brook trout in larger, steep streams in downstream- than upstream-directed invasions.

I hypothesize that larger source pools of fish are generally available for downstream-directed than upstream-directed invasions at high elevations. Downstream emigration of brook trout from lakes varies depending on many factors including fish stock, stocking frequency, quality and availability of lake or inlet spawning habitat, age at maturity, survival, and possibly density of fish in the lake relative to food resources (Cone and Krueger 1988; Van Offelen et al. 1993; Josephson and Youngs 1996). Brook trout frequently "overpopulate" lakes, becoming stunted when food is limited, particularly where reproduction or repeated stocking occur (Reimers 1979; Donald et al. 1980). Such high population densities relative to available resources may encourage brook trout to emigrate from lakes, as has been demonstrated experimentally with other species and habitats (Wilzbach 1985; McMahon and Tash 1988). However, high population densities that retard growth also prevent the demographic advantages associated with rapid growth (see below). If spawning habitat is not available, brook trout tend to emigrate when mature (an issue where repeated stocking occurs). In four Adirondack lakes, 33 to 69 % of the total lake population emigrated during the fall spawning period, apparently seeking suitable spawning habitat (Josephson and Youngs 1996). When densities are not excessively high, faster salmonid growth in mountain lakes or outlet streams, such as upper Moore Creek, than in high-elevation streams is common (Domrose 1963; Haraldstad et al. 1987; Hayes 1995). Faster growth may typically result in larger, earlier maturing, more fecund colonists in downstream- than upstream-directed invasions, as observed in fish in Moore versus Twelvemile creeks (Chapter V). Such demographic shifts may increase the rate and/or likelihood of successful invasion in small, high-elevation stream reaches.

Our results confirm that emigration from high elevation lakes in the West is common, though emigration rate may not be constant within or between years. I operated a two way fish weir in the outlet of Moore Lake, Montana from late July to early October, 1997, and observed virtually no downstream emigration from the lake (S. Adams, unpublished data). However, based on the distribution and population structure of brook trout in the outlet stream and on annuli spacing in otoliths (S. Adams, unpublished data), I infer that at least some fish still emigrate from the lake. Most emigration from the lake presumably occurs either primarily during the spring runoff, or only occasionally, perhaps when condition factors of the fish become low.

Higher emigration rates may occur within the first several generations after fish are initially introduced to a lake. Both the tendency for and the direction of emigration appears to have a genetic component in fish (Northcote 1981; 1992; Van Offelen et al. 1993). Selection may act against downstream emigration from lakes to which there can be no return migration (Northcote 1992; Elliott 1994). Therefore, local adaptation could reduce the incidence of downstream emigration over time. In some cases, local adaptation of various salmonid life history traits has apparently occurred in less than 20 generations after introductions, although concomitant differentiation of allozymes has not been detected (Snowdon and Adam 1992; Quinn and Unwin 1993; Quinn et al. 1996). Repeated introductions of fish to a lake could conceivably disrupt the selection process, thereby increasing rates of downstream emigration.

If early emigrants from a lake establish a self-sustaining population in the outlet stream, continued emigration from the lake may not be necessary to sustain the stream population. However, if dispersing individuals do not successfully colonize the outlet stream, invasion, *per se*, does not occur and the stream is a sink habitat, sustainable only via continued immigration (Pulliam 1988; Schlosser and Angermeier 1995). An outlet stream community may be impacted by immigrating fish even if a self-sustaining population is not established within the stream (McFadden 1961; Hawkins and Sedell 1990).

Clearly, processes other than just dispersal limit invasibility of streams by brook trout. Several S.F. Salmon River tributaries with substantial distances predicted as invulnerable from mainstem sources did not contain brook trout (S. Adams, unpublished data). In some systems where brook trout were distributed for several kilometers downstream of a lake, there was little evidence of reproduction in the stream. The variation among drainages in dispersal and invasion distances indicates that invasion is not inevitable everywhere that brook trout have access to a stream. The reasons for minimal dispersal and lack of invasion in some streams (e.g. Elizabeth Creek, Appendix A) were not evident from my data, but understanding the sources of variation in these processes may be important for understanding the mechanisms of both downstream- and upstream-directed invasions. I suspect that the size and dispersion of relatively gradually-sloping, alluvial stream segments that may serve as nodal areas of reproduction are important in determining the invasibility of a stream.

## Conservation Implications

In drainages where significantly more stream length is invadable from headwater compared to downstream introductions (e.g. the S.F. Salmon River), headwater introductions of nonnative fish potentially decrease the available refuge area for native fauna and, thus, increase opportunities for displacement of native species. For species threatened by introduced fish, the probability of maintaining strong headwater populations that can sustain or refound other populations diminishes as more stream area is invaded by fish.

Repeated stocking of headwater lakes may increase risks to downstream fauna for several reasons. If the species does not reproduce in the system, repeated stocking obviously perpetuates its presence, increasing the duration of interactions with native species. Increased fish densities in lakes after stocking may result in reduced condition factors, and thus increased emigration, if food is limited. In lakes with self-sustaining populations, repeated stocking may disrupt selection for reduced emigration from the lakes, thereby tending to increase emigration for generations to come.

Faster growth of brook trout emigrating downstream from lakes or from lake-outlet streams has several implications beyond the demographic considerations discussed above. First, the outcomes of behavioral interactions among salmonids are frequently size-dependent with the larger fish obtaining the best foraging locations or territories, regardless of species (but see Rose 1986; Nakano et al. 1998). In Moore Creek near the lake outlet, age 0 brook trout are as large as age 1 brook trout further downstream, and thus, emigrants from the upper reaches would be expected to have a strong advantage in interspecific interactions downstream. Second, since salmonids are gape-limited predators, faster growth would allow them to consume larger prey (e.g. amphibian or fish) at an earlier age.

The simple exercise of classifying potentially invadable area from lake versus mainstem sources can provide useful guidance for resource managers. If a percentage of headwater lakes in a basin are to be stocked with a fish species also present at lower elevations, stocking lakes that are a short distance upstream of barriers may have the least potential for negative impacts on downstream biota. Stocking multiple lakes in one tributary basin, rather than one lake in multiple basins, may have may also reduce downstream effects. Landscape-scale analyses may also enlighten choices of potential lake-stream networks to target for eradication of nonnative fishes (see Knapp and Matthews 1998). Systems where nonnative fish emigrate from headwater lakes and occupy, but do not colonize, the outlet streams are also good candidates for fish removals from lakes. For example, Ice Lake (Appendix A) is the only lake known to contain brook trout within a large area, and as of 1996, the species had invaded little of the outlet stream. Brook trout eradication from that lake would remove the one population with potential for invading a large drainage area. More detailed examination of streams or stream segments that are predicted to be invadable but have not yet been invaded may improve our understanding of the mechanisms limiting invasion.

Table 1. Channel slope and wetted stream width of the steepest reach where brook trout were found and the slope of the steepest reach sampled, for streams in which brook trout occupied reaches with slopes > 9%. Some streams with downstream-directed invasions were excluded because the resolution of channel slope data was inadequate or stream width data were unavailable. Streams with upstream-directed invasions are a subset of 12 brook trout streams studied in the South Fork Salmon River drainage, Idaho (Chapters II, III).

Stream	Maximum slope with brook trout (%)	Maximum slope sampled (%)	Average wetted width (m) in reach with brook trout
<b>Downstream-directed invasions</b>			
Gedney Creek	23a	28	4.2
Moore Creek	19b	19	1.8
S.F. Blackmare Creek	~19c	~19	7.1
Lizard Creek	16a	16	5.0
Running Creek	15a	15	6.6
Rainbow Creek	12	14	2.0
Lick Creek	10c	24	8.1
<b>Upstream-directed invasions</b>			
Hillbilly Creek	17d	17	2.8
Bear Creek	13b	13	3.5
Upper Sand Creek	12e	12	2.3
Cabin Creek	12c	12	3.8

a. slope measured over stream distance of 150 m

b. slope measured over stream distance of 100 m

c. slope measured over stream distance of approximately 30 m

d. slope measured over stream distance of 70 m (includes 34 m of 20 % slope with brook trout)

e. slope measured over stream distance of 60 m

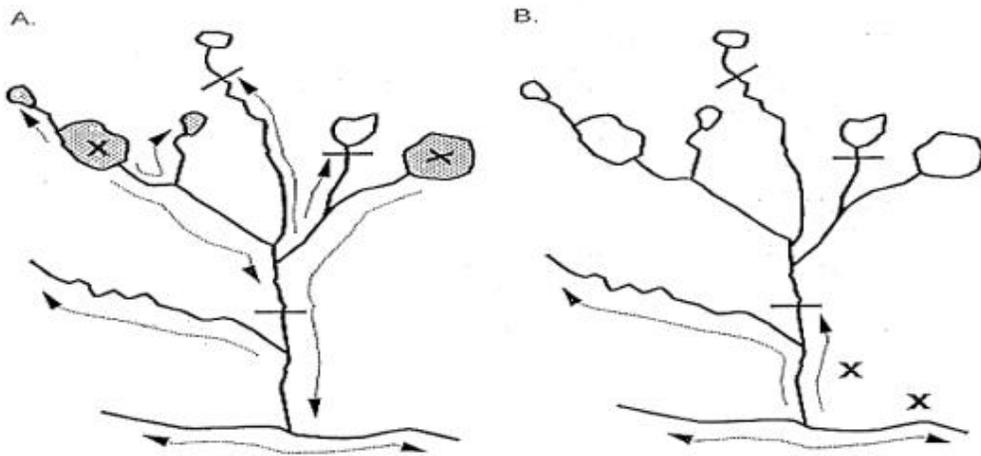


Figure 1. Schematic diagram of a hypothetical drainage with brook trout introductions in headwater lakes (A) versus downstream (B). Arrows and dashed lines indicate the direction and extent of invasions from locations of introductions (X's). Bars bisecting the streams indicate physical barriers to upstream dispersal. Lakes containing brook trout are stippled.

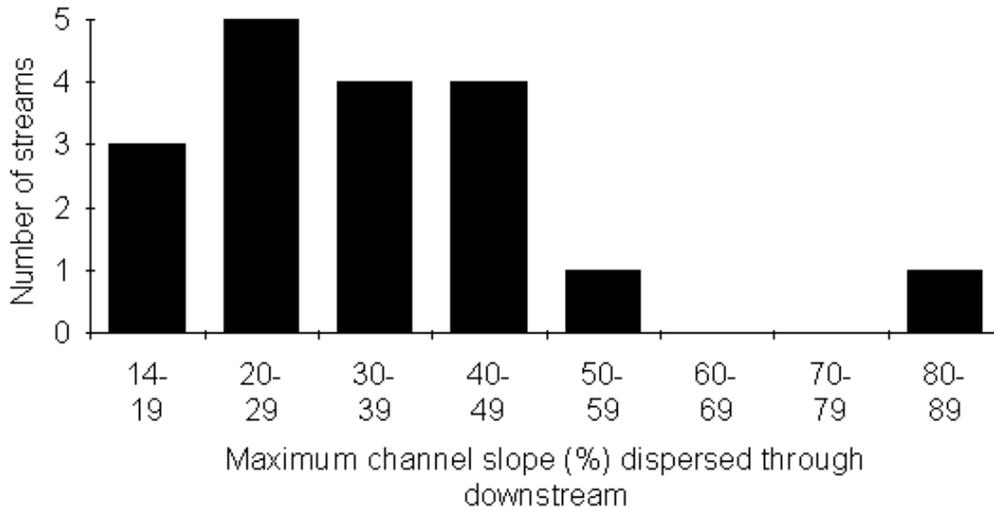


Figure 2. Estimated maximum channel slopes through which lake-origin brook trout or their progeny dispersed downstream.

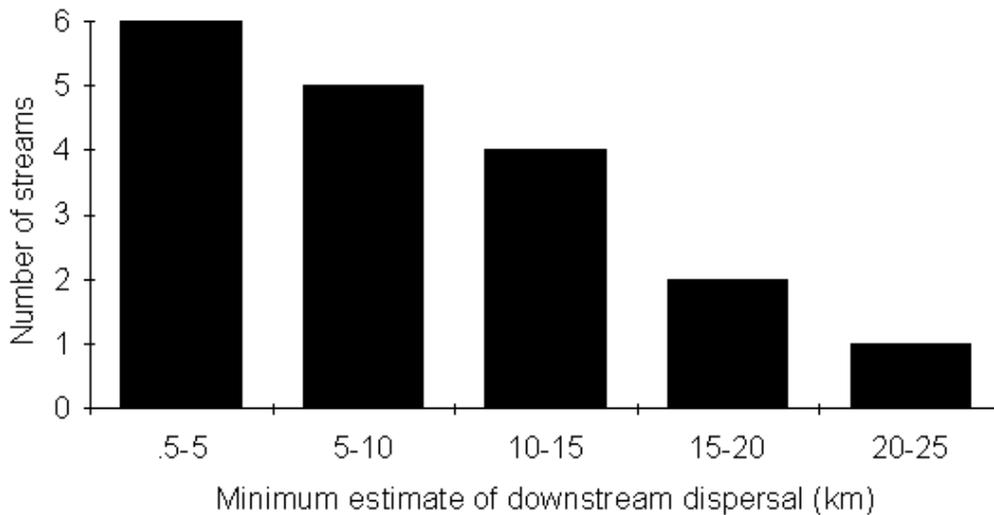


Figure 3. Minimum estimates of distances downstream from lakes that brook trout in lake-origin populations occurred in Idaho and Montana streams. This does not imply that individual fish moved the distances shown; both dispersal and colonization may be reflected.

Figure on following page:

Figure 4. Areas potentially invisable from brook trout source populations in mainstem locations (light gray shading) and additional areas invisable from *only* from source populations in headwater lakes (dark shading). Areas classified as not invisable are not shaded. See text for explanation of assumptions and methods. Most named streams and all lake-outlet streams were analyzed. In the upper Big Hole River drainage (A), Montana, 946 km of stream were invisable from downstream and 46 km from upstream with 53 km not invisable. The star indicates Wisdom, Montana. In the upper South Fork Salmon River drainage (B), Idaho, 199 km of stream were potentially invisable from mainstem and 151 km from headwater lake sources, and 101 km were accessible from neither source.

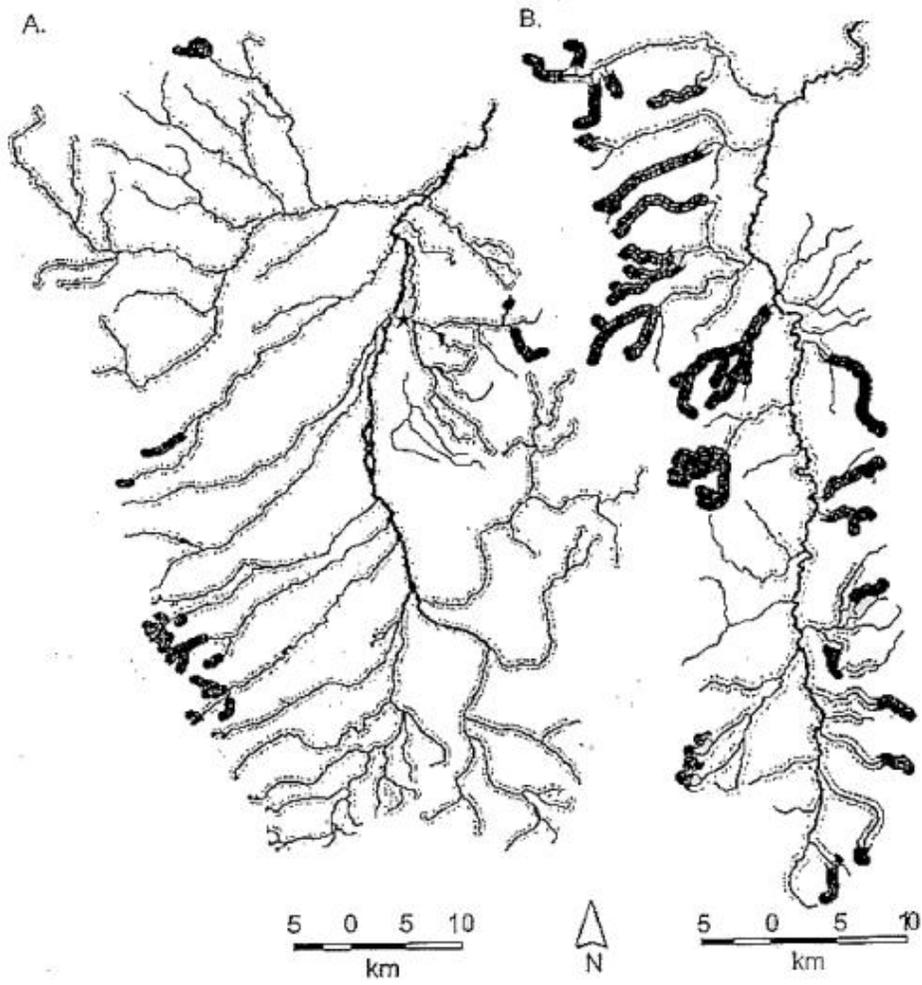


Figure 4.

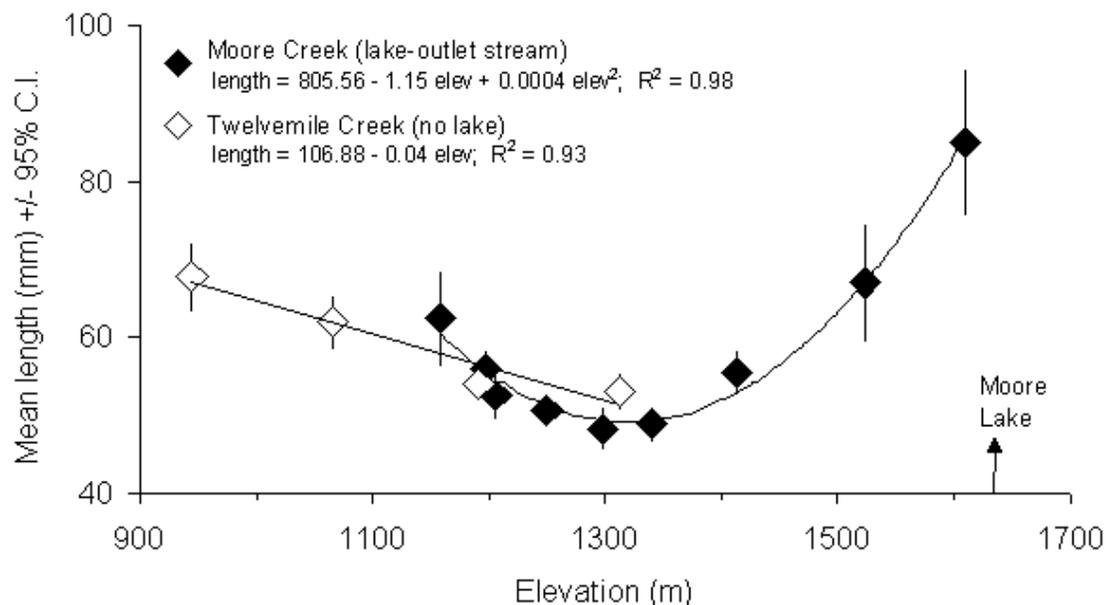


Figure 5. Mean total lengths (with the caudal fin compressed) of age 0 brook trout versus elevation in Twelvemile Creek (open symbols), Montana, a stream with no lake, and in Moore Creek / South Fork Little Joe River (closed symbols), Montana, a lake-outlet stream system. The two lowest-elevation closed symbols represent the South Fork Little Joe River below its confluence with Moore Creek. Fish were collected between 11 September and 6 October, 1997.

## 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. 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).

Stream	Drainage	Max. slope (%)	Height of falls (m)	Km down-stream	Brook trout in lake	Stocking date(s)	Fish sample method	Source of data unless otherwise indicated
SF Blackmare Cr.	S.F. Salmon R, ID	26 - site	n/a	11.7 - m	yesa	1937b	DS	this study
Lick Cr.	S.F. Salmon R, ID	24 - site	12	17.0 - m	yesa	1935-72b	DS	this study
Moore Cr.	St. Regis R, MT	19 - site	3.5	3.2 - m	yes	ND	E/ NS	this study
Warm Springs Cr.	M.F. Salmon R, ID	14 - map	n/a	22.4 - m	yes	ND	E / DS	unpublished data, C. Zurstadtc
Slate Cr.	Salmon R, ID	22 - site	n/a	13.4	yese	ND	DS	unpublished data, K. Munsond
Lizard Cr.	Selway R, ID	30 - map	n/a	8.5	yese	1947e	DS	unpublished data, P. Greenf
Rhoda Cr.	Selway R, ID	50 - map	3	18.8 min.	yesf, noe	ND	DS	unpublished data, P. Greenf
Running Cr.	Selway R, ID	30 - map	10	9.3 min.	yes,	ND	DS	unpublished data, P. Greenf
Buck Lake Cr.	Selway R, ID	40 - map	18	10.8 min.	yese	1940-47	DS	unpublished data, P. Greenf
W.F. Gedney Cr.	Selway R, ID	40 - map	n/a	5.8 min.	yese	1948	DS	unpublished data, P. Greenf
Surprise Cr.	Lochsa R, ID	38 - site	n/a	10.7 - m	ND	ND	DS	(Clearwater BioStudies Inc. 1995b)
Stanley Cr.	Lochsa R, ID	48 - site	n/a	7.5	yese	ND	DS	(Clearwater BioStudies Inc. 1995a)
Old Man Cr.	Lochsa R, ID	24 - map	n/a	4.0 - min.	yese	1940e	DS	(Clearwater BioStudies Inc. 1997b)
Old Man Lake Cr.	Lochsa R, ID	37 - map	n/a	2.7 - m	yese	1940e	DS	(Clearwater BioStudies Inc. 1997a)

MECHANISMS LIMITING A VERTEBRATE INVASION:

Chimney Cr.	Lochsa R, ID	48 - map	n/a	4.9 - m	yese	1940e	DS	(Clearwater BioStudies Inc. 1997a)
Elizabeth Cr.	N.F. Clearwater, ID	80 - site	n/a	0.5	yese	ND	DS	(Clearwater BioStudies Inc. 1993)
Meadow Cr.	N.F. Clearwater, ID	24 - map	n/a	8.2 - min.	yese	ND	DS	(Clearwater BioStudies Inc. 1993)
Rainbow Cr.	S.F. Clearwater, ID	14 - site	n/a	3.4 - m	yes	1937-46	E	Unpublished data, D. Maysm

- a Personal communication, Don Anderson, Idaho Department of Fish and Game, McCall
- b Unpublished data, S. Clark, Idaho Department of Fish and Game, Boise.
- c Lowman Ranger District, Boise National Forest, Lowman, Idaho.
- d Slate Creek Ranger District, Nez Perce National Forest, Idaho.
- e Unpublished data, E. Shriever and P. Murphy, Idaho Department of Fish and Game, Lewiston.
- f Nez Perce National Forest, Grangeville, Idaho.
- m Crooked River Ranger District, Nez Perce National Forest, Idaho.

## Appendix B. Fish collection and temperature data

Table B1. Location and stream size at reaches in Montana streams where fish were collected (between 10 September and 7 October 1998). Moore Creek flows into the South Fork Little Joe River. Thermal units are sums of average daily water temperatures over the interval. Temperature is reported for the fish sampling reach nearest the actual temperature measurement location. A subset of brook trout were aged by their otoliths and the data used to estimate ages of remaining fish based on total length.

Reach	Elevation (m)	Stream width (m)	Distance from head-waters (km)	Thermal units (oC) 8/1/97 to 9/30/97	Number brook trout collected	Number brook trout aged by otoliths	Number age 0 brook trout
<b>South Fork Little Joe River</b>							
1	1158	8.0	4.4		11	--	4
2	1198	6.1	3.5	524	32	--	7
<b>Moore Creek</b>							
1	1207	3.2	3.2	554a	34	21	13
2	1250	3.1	2.8		67	16	20
3	1298	2.9	2.3		68	0	13
4	1341	2.0	1.6	526	94	40	40
5	1414	2.1	1.1		44	9	20
6	1524	2.7	0.5		28	22	8
7	1609	1.8	0.1	929a	21	18	6
Moore	1620		0		--	--	--
<b>Lake</b>							
<b>12 Mile Creek</b>							
1	945	5.5	18.8	639	47	35	12
2	1067	5.6	12.1	574	46	34	10
3	1192	5.5	7.6		61	51	3
4	1314	3.1	4.6	444	56	34	18
water-	1469	1.8	2.7		--	--	--

fall

- a. Annual thermal units, from 7/31/97 to 7/30/98 (with temperatures for 6/11/98 to 7/28/98 interpolated because of missing data) were 1544 for reach 1 and 2340 for reach 7.

# Chapter V. Within and Between Stream Variation in Demographics of Nonnative Brook Trout

## Abstract

I documented longitudinal trends in first year growth, length at age, age at maturity, and fecundity of nonnative brook trout (*Salvelinus fontinalis*) along two contrasting streams in western Montana. Densities and abundances of both brook and westslope cutthroat trout (*Oncorhynchus clarki lewisi*) were highly variable among reaches. The observed patterns in population structures and demographic processes are consistent with Schlosser and Angermeier's (1995) hybrid model of population dynamics, which integrates patchy and source-sink population processes. I estimated fish densities by snorkeling or electrofishing and dissected brook trout to determine sex and maturity, and fecundity. I used otoliths to determine brook trout age and to qualitatively assess first year growth. In Twelvemile Creek, which is not lake-fed, growth and fecundity were greater and age at maturity lower in downstream than in upstream reaches. The gradual reduction in reproductive output upstream supports the idea that extreme or lethal conditions are not necessary to create a distribution boundary. Complex suites of factors can influence fish growth rate and are, thus, also expected to limit invasion. In Moore Creek, a lake-fed stream, fish growth and related reproductive parameters were greater upstream. Among all reaches, lengths of age 0 and 1, but not age 2, fish were positively correlated with mean August stream temperatures, although factors other than temperature also influenced growth. Among reaches of one stream, age at length varied by up to three years, and age at maturity by as much as two years. Population demographic studies should account for the possibility of intrapopulation trends in vital rates. The extreme variation in demographic rates and fish densities suggest that both source-sink and patchy population processes may be important in determining the extent of stream invasions, and probably influence interspecific population dynamics as well. If my assessment is correct, human activities with the potential to influence demographics in a source area should be of great interest to those concerned with invasion of connected habitats.

## Introduction

The study of within-population variation in the demographics of stream fishes should provide biologists with better understanding of the dynamics of entire populations and of mechanisms causing some distribution and demographic patterns. The variation in demographics among areas within stream networks can provide clues about the importance of source and sink areas to maintenance of the overall population distribution structure (Schlosser and Angermeier 1995). Understanding the interrelationships among parts of the population improves one's ability to predict how alterations of one part of the system are likely to affect other parts or the whole. Increased attention to within population demographic variation should also allow more accurate extrapolation and generalization of demographic processes to other stream systems or parts of the same system. Intrapopulation variability in demographic rates is likely of particular importance in mountain stream systems where large gradients in environmental parameters such as stream temperature, channel slope, and stream size tend to occur over relatively short distances.

Although the vast majority of salmonid demographic studies have considered the population as a unit, several have examined demographic variation at lower levels of organization. Hutchings (1993; 1994) considered intrapopulation demographic variation of brook trout (*Salvelinus fontinalis*), but looked only at individual-level variation. He found that individual growth rate influenced age at maturity of brook trout within one stream reach. Several studies that have examined stream segment or reach level variation in demographic parameters have had contrasting results. Magoulick and Wilzbach (1998a) found that instantaneous growth rates of unconfined brook trout were higher in upstream than downstream reaches, but that the opposite was true for caged fish (all rates were negative). Newman and Waters (1989) found temporal, but not consistent spatial, variation in brown trout growth within a Minnesota stream. They suggested that behavioral size segregation best explained differences in fish sizes among sections and that factors influencing growth rate and recruitment operated at a scale of the entire stream. In contrast, Lobón-Cerviá and Rincón (1998) found that relative differences in brown trout growth rates among stream sections were constant over nine years, despite temporal variations in growth at all sites. Other studies have found dramatic within-stream differences in fish growth (Heggberget et al. 1986) or recruitment (Schlosser 1995; Schlosser and Angermeier 1995). Increased fish growth in reaches immediately downstream of lakes is documented for several species and locations (Heggberget et al. 1986; Haraldstad et al. 1987; Hayes 1995; Degerman et al. 1996).

A common within-stream trend is for fish size to be larger in downstream than upstream reaches (Purkett 1951; Heggberget et al. 1986; Schlosser 1991; Bachman, 1984 #1065, but see Hughes and Reynolds 1994). Determining the relationship between the gradient in fish size and population demographics requires elucidation of the mechanisms creating the gradient. Possible mechanisms responsible for the variation in mean size include: 1) variations in fish growth among areas (Bachman 1984), 2) size-dependent movement of fish (Smith and Saunders 1958; Hughes and Reynolds 1994), 3) differences in the size-dependence of survival among areas (Smith and Griffith 1994), or 4) a combination of these causes. Variable fish growth among reaches may result from differences in stream temperature, food availability, and/or energy expenditure, among other causes (Bachman 1984; Elliott 1994; Lobón-Cerviá and Rincón 1998). Size-dependence of movements may arise from size-dependent changes in habitat preference (Smith and Saunders 1958; Hughes and Reynolds 1994), from intercohort competition for preferred positions (Bohlin 1977; Hughes and Reynolds 1994), or from size-dependent swimming ability. The latter is primarily relevant to upstream movements, however, so is not expected to create a size gradient with larger fish downstream. Also, an inability to meet their greater energetic requirements (Bachman 1984; Gowan and Fausch 1996b) or a lack of adequate cover (see below) may induce larger fish to move downstream to larger stream reaches (Smith and Saunders 1958). In Idaho streams, I observed that larger brook trout tended to move more than smaller fish, at least during summer and fall (Chapter

II). Size-dependent mortality can result from energetic deficiencies (Cunjak et al. 1987; Hutchings 1994), predation (Schlosser 1988; Harvey and Stewart 1991), or fishing, and can influence the patterns of abundance and the size distribution of fishes within a stream.

Schlosser and Angermeier's (1995) hybrid model of spatial variation in demographic processes (hybrid model, hereafter) proposes that many stream fish populations are characterized by both source-sink and patchy population processes. The source-sink model predicts that a "source" population augments "sink" populations via dispersal and/or supplies migrants that recolonize the sink populations after local extinctions. Higher reproductive output and/or survival as well as greater temporal stability characterize source relative to sink populations. Patchy population processes result from spatial habitat heterogeneity and high rates of dispersal among habitats, typical of species that require different habitats depending on life stage and/or season. In the hybrid model, patchy processes operate at a fine scale whereas source-sink processes function at a coarser scale. Intrapopulation variation in demographic processes and population structure at multiple scales is predicted under the hybrid model.

If the hybrid model applies to stream populations of brook trout, then reduction or loss of brook trout "source" areas are predicted to result in contraction of distributions, whereas increases in source populations may result in distribution expansion (Pulliam 1988; Schlosser and Angermeier 1995). Within the native range of brook trout, where emphasis is on restoration of the species, expansion of distributions is desirable. However, in the western USA, where nonnative brook trout are considered a threat to many native salmonids, managers often attempt to reduce distributions and to predict and limit invasions.

While the potential importance of metapopulation dynamics and spatial variation in demographics is receiving increasing attention in relation to conservation of stream fishes (e.g. Young 1995a; Dunham and Rieman In press), the concepts remain frequently overlooked in the context of stream fish invasions. Temporal fluctuations in upstream distribution limits of invading salmonids is one indication that source-sink dynamics may be important in determining and maintaining upstream distribution limits of the invaders (Seegrist and Gard 1972; Larson et al. 1995; Closs and Lake 1996). Ignoring intrapopulation spatial variability and the potential for source-sink dynamics may lead to an inability to determine causal relationships between ecosystem features and population abundance at a local scale, erroneous or irrelevant estimates of population growth rates, and misunderstanding of conditions influencing interspecific competition and coexistence. Attempts to define the factors limiting invasions may ultimately fail if conditions at invasion fronts are considered while relationships with distant source populations are ignored (Carter and Prince 1981; Lennon et al. 1997). Lack of attention to spatial differences in demographics and to movements among subpopulations has allowed biologists and managers to commonly ignore the offsite, and especially upstream, effects of ecosystem alterations on community and population structures and demographic processes (Ruhr 1956; Crisp et al. 1984; Penczak et al. 1984; Winston et al. 1991; Pringle 1997).

Identifying factors limiting invasions is an important step in predicting and preventing or reversing invasions. Abrupt ecotones or barriers to dispersal can create sharp distribution limits and may be relatively easy to identify. However, distribution limits need not be created by extreme gradients in the ecosystem (Caughley et al. 1988; Hengeveld 1990; Lennon et al. 1997). Gradual changes in population or metapopulation dynamics can result in relatively sharp distributional edges in some circumstances (Lennon et al. 1997). Many factors, both abiotic and biotic, determine demographic rates in stream fishes (e.g. Elliott 1994). Furthermore, if source-sink dynamics are important, demographic rates in both the source and sink areas are predicted to influence a population's distribution (Pulliam 1988). To complicate matters further, I found that the factors and mechanisms limiting the distribution of brook trout varied among streams within a drainage (Chapter III), a result that is likely applicable to many stream fishes.

I investigated intrapopulation trends in demographics of nonnative brook trout along two contrasting streams. In a stream with no physical barriers to upstream movement, I examined demographic changes throughout the brook trout population to determine whether subtle demographic changes were sufficient to limit the upstream distribution of the species. To provide a contrast, I also studied a lake-outlet stream, where the longitudinal gradient in stream temperature, and probably in food availability, was reversed over part of the stream length. I examined the relationship between longitudinal changes in brook trout size along the stream and differences in growth (as measured by size at age). I then determined the association of different growth rates with fecundity (number of eggs per mature female) and female age at maturity. I discuss the potential roles of stream temperature and other factors in creating within-stream variability in growth. I also assessed within-stream variability in abundance and density of age 0 and older brook and westslope cutthroat trout (*Oncorhynchus clarki lewisi*, a native species thought to interact with brook trout) and discuss potential causes and implications of the observed patterns in brook trout populations.

## Study Areas

The two study streams were in the St. Regis River drainage (Mineral County) of western Montana (Figure 1). The study areas on both streams were in the Lolo National Forest. Moore Creek is a small, short (3.2 km), steeply-sloping stream originating from Moore Lake (Appendix A, Table A1). The thermal regime of the upper stream reach was strongly influenced by the lake. Shading and groundwater upwelling contributed to downstream cooling. Old growth cedar forest with minimal understory dominated the riparian area along the lower 3/4 of the stream. Clearcuts existed in upland portions of the drainage. A dirt road parallels the creek along much of its length and allows vehicle access to Moore Lake. Although the stream is easily accessible in places, little fishing apparently occurred, probably due to the small size of the creek and its proximity to better fishing. I saw no anglers, and found no evidence of fishing in the stream during 1997. Moore Creek joins the South Fork of the Little Joe (SFLJ) Creek about 14 km upstream of the St. Regis River.

Twelvemile Creek is larger, longer (22.6 km), and more moderately sloped than Moore Creek (Appendix A, Table A1). Human activities, including logging and road construction, have apparently influenced channel characteristics, and fishing has probably had a considerable effect on the trout populations. Some logging has occurred in riparian zones along the lower 2/3 of the creek, and in upland areas throughout the drainage. Downstream of the study area, the creek flowed through private land for 3.6 km before joining the St. Regis River. On private land, the creek was channelized and aggraded, becoming nearly intermittent at times during the summer of 1997. Rock Creek, a tributary to the downstream end of Twelvemile Creek, flowed through meadows and a pond at its lower end, providing a potential source area of brook trout that could move upstream into Twelvemile Creek. Angler access was easy throughout much of Twelvemile Creek; in several places, I saw people fishing from the roadbed.

Although I saw fewer than 20 individuals fishing the creek in 1997, several local residents fished frequently, particularly in the downstream half of the study area.

Historical records of fish stocking and road construction in the study area are incomplete. The Montana Fish Wildlife and Parks fish stocking database records do not indicate any brook trout stocking in Moore Lake, Moore Creek, or Twelvemile Creek. Brook trout could not have invaded Moore Lake from downstream (Chapter IV), so I infer that the lake was stocked with brook trout, some of which invaded downstream. Long-time local residents told me that brook trout were stocked in Twelvemile Creek. The stocking probably occurred along the downstream end of the creek, and subsequent upstream invasion created the present distribution. All recorded brook trout stocking in the St. Regis River drainage occurred between 1933 and 1942. The latest records of brook trout stocking in Mineral County were two records from 1950. The road to Moore Lake was probably not constructed until the early 1960's, but a trail to the lake had probably existed since before 1950 (personal communication, Dick Wilkenson, engineer, Superior District, Lolo National Forest). Thus, brook trout have probably maintained self-sustaining populations in the waters at least since 1950. Cutthroat trout were stocked in Moore lake from 1949-53, but are now absent from the lake (according to all anglers queried) and from the upper reaches of Moore Creek. Cutthroat trout were stocked in Twelvemile Creek in all but three years from 1937 to 1952.

## Methods

### Stream temperatures

I recorded stream temperatures throughout the summer and fall of 1997 in seven sites and during the winter of 1997-1998 in three sites. In Twelvemile Creek, I recorded summer temperatures at four sites (Figure 2) and winter temperatures at the most upstream site. I recorded temperatures at three sites in Moore Creek during the summers of 1997 and 1998. The most upstream site was 50 m downstream of the lake outlet (Figure 3). Winter temperatures were recorded at the upstream and downstream sites. Hobo-temp temperature loggers, placed under rocks on pool bottoms, recorded the instantaneous stream temperatures at intervals of 1 hour to 3 hours 12 minutes, the longer intervals occurring in the winter. In several instances, one to two week gaps in temperature data were filled by interpolation.

### Population indices

I sampled fish in multiple reaches within each stream. All reaches sampled are numbered or lettered beginning at the downstream end of the stream. Numbers of Twelvemile Creek snorkel reaches very roughly approximate the miles (along the road) upstream of the confluence of Twelvemile and East Fork Twelvemile creeks.

I indexed fish densities and abundances by different methods in Twelvemile and Moore creeks because of differences in the efficiencies of snorkeling versus electrofishing in the two streams. Before sampling fish abundance, I compared day and night snorkeling with electrofishing in Twelvemile Creek and compared night snorkeling with electrofishing in Moore Creek.

In Twelvemile Creek, I indexed trout population size by night snorkeling in 24, 100 m-long reaches at intervals of approximately 0.8 km (measured along the road)(Figure 2). Reaches were located as far from the road as possible, and each included at least two pools. I conducted all snorkeling at night between 26 Aug and 17 September, 1997. In order to minimize bias due to timing of snorkeling, I first randomly selected snorkel reaches at 1.6 km intervals (reaches 1, 2, ..., 10; Figure 2) to snorkel. When the first 10 reaches were completed, I then randomly selected reaches interspersed with those already snorkeled (reaches 1.5, 2.5, ..., 9.5). Reaches numbered 10.5 through 11.75 were snorkeled last. Fish numbers in the "Results" section are actual numbers observed. I did not adjust the number of fish observed because I had little information about sampling efficiency.

I collected fish by electrofishing to obtain information about age, sex, maturity, and fecundity. Between 11 and 25 September 1997, I electrofished four reaches of Twelvemile Creek (reaches A-D; Figure 2). I concentrated electrofishing effort in habitats where I expected brook trout to occur. I also made more effort to capture larger brook trout because I wanted to maximize the sample size for fecundity estimates. Therefore, electrofishing data from Twelvemile Creek cannot be used for estimating densities or relative year class abundances.

In Moore Creek, I conducted three electrofishing passes without block nets in two reaches and two passes in the remaining five reaches between 30 September and 6 October, 1997. Reaches were 100 m-long and were located every  $0.54 \pm 0.10$  km (mean  $\pm$  1 standard deviation)(Figure 3). Reach 7, the uppermost reach, ended about 50 m downstream of the outlet of Moore Lake. One person operated a battery powered, backpack electrofisher (Smith-Root type VII POW), while one or two others netted fish. The electrofisher was usually operated at 600V and 50 Hz with a pulse width of 1 ms (Smith-Root setting I-3). Intervals between passes were about 1 hour. Fish from each pass were held in separate live-buckets until all electrofishing in the reach was complete.

I conducted single electrofishing passes in two, 100 m reaches of the South Fork of Little Joe Creek, downstream of the confluence with Moore Creek, in October 1997. The creek was too large for effective population sampling with one electrofisher. My objective in sampling the reaches was to estimate brook trout growth, not to estimate densities.

### Age determination

I used sagittal otoliths to age a subset of the brook trout collected. Previous authors have validated the use of otoliths for aging brook trout (Grande 1965; Dutil and Power 1977; Power 1980), including old fish from stunted populations (Reimers 1979; Hall 1991). I used two slightly different methods for aging the fish. For both methods, I mounted otoliths on microscope slides with Crystal Bond adhesive, ground them on wet 1500 grit sandpaper and counted annuli under a dissecting microscope with transmitted light. I considered the dark rings observed under reflected light to be annuli ("winter bands", Dutil and Power 1977; Reimers 1979). I report fish age as the number of annuli counted, so fish in their first year

of life were age 0. In the first method, otoliths were ground to the core and polished with 0.05 Alumina 3 micropolish on both sides then viewed with an Optimas image analysis system (at the laboratory of Dr. Douglas Markle, Oregon State University, Corvallis). The Optimas system allowed me to mark the locations of the core, annuli (if any), and otolith edge on a computer image of each otolith (Figure 4). Knowing the distances was useful both for some validation of annuli and for comparing first year growth of fish among reaches, but did not improve my ability to age fish once I determined what constituted an annulus. For use in the Optimas imaging system, otoliths had to be ground until extremely thin, but not ground through the core, which was very time consuming. However, most otoliths could be aged through a binocular microscope with minimal grinding in a fraction of the time required for the previous method. So, for the second method, I ground only the sulcus side of the otolith (Hall 1991), wetted the ground surface with water, and counted annuli under a dissecting microscope with reflected light. Occasionally, I had to grind the opposite side and/or polish the otolith for better clarity. Viewing otoliths under a compound microscope with transmitted light clarified annuli patterns in several instances.

As a check on my assignment of ages to otoliths, 24 otoliths from Twelvemile Creek (reach B) were aged independently by a second person (G. Castillo) who had extensive experience aging otoliths. Due to time constraints, G.C. aged eight of the otoliths only before they were ground. I aged some otoliths before, and all after, grinding.

I distinguished between age 0, age 1, and older cutthroat trout based on length-frequency distributions and references to earlier age-length data from westslope cutthroat trout in Montana (Liknes 1984; Downs 1995). However, the ages in those studies are not entirely reliable because they used scales to age fish, and westslope cutthroat trout often fail to form a scale annulus their first year (Downs 1995). Moreover, age 0 cutthroat in the present study may have a bi-modal length-frequency distribution. Since growth was different in the two streams, I indicate the sizes of cutthroat trout considered age 0 for each stream.

## Brook trout size and reproductive status

All salmonids collected during September and October were identified, measured for total length, and weighed to the nearest 0.1 g. Species other than brook trout were released. Brook trout were killed in an overdose of MS-222 (except those from Moore Creek reach 3 due to an adequate sample size from the stream) and stored in ice for up to 15 hours before processing (most were processed within six hours). In Moore Creek I measured fork lengths of a subset of fish for comparison to total length. For most fish older than age 0, I visually examined the gonads to determine maturity and sex, when possible, and weighed the gonads of mature fish. After determining the minimum size-at-maturity, I examined gonads only from fish expected to be mature and from a subset of fish expected to be immature. I preserved ovaries in a dilute formalin solution, later transferred them to 70% ethanol, and made a complete count of eggs within three months.

In many reaches, some brook trout began spawning before I collected fish. Ovaries with loosely attached, easily dislodged eggs and/or incomplete ovarian tissue surrounding the eggs indicated that the female may have released some of her eggs. Firmly attached eggs, intact tissue surrounding the ovary, and dull fish coloration were all indications that spawning had not begun (Reimers 1958). Since there was a continuum in the condition of the ovary, I was unsure of the spawning status of some fish. Therefore, I discarded any low outliers in the fish weight to fecundity relationship, possibly resulting in fecundity estimates biased toward higher fecundities.

## Results

### Stream temperatures

Longitudinal patterns in stream temperatures were different in the two streams. The inverse relationship between stream temperature and elevation in Twelvemile Creek was typical of mountain streams (Figure 5). In Moore Creek, the relationship was partially reversed and more complex. Summer temperatures were warmest upstream, cooled with distance downstream from the lake, and then slightly warmed again further downstream. Dense shade, groundwater upwelling, and tributary inputs counteracted the warming effect of the lake on the stream within about one kilometer, and the more typical trend of downstream warming resumed part way down the stream. Although winter cooling and spring warming at the upstream site lagged behind that at the downstream sites, the cumulative annual thermal units upstream greatly exceeded those downstream (Table 1). The mean August temperature in the upper Moore Creek site was 16.89 oC in 1997 and 18.36 oC in 1998. Despite being 665 m higher in elevation and north facing, the upper Moore Creek site had a mean August temperature that was 6.6 oC warmer than the downstream site in Twelvemile Creek in 1997. All sites in Moore Creek accumulated more thermal units in 10.5 months than did the upstream site in Twelvemile Creek (Table 1).

### Population indices and fish collection

The efficiency of fish sampling techniques varied between Twelvemile and Moore creeks. While snorkeling undoubtedly underestimated the number of fish present in Twelvemile Creek, it was more efficient than single-pass electrofishing in the two reaches where comparisons were made (Table 2). In order to conduct multiple-pass electrofishing, I would have had to drastically reduce the number of reaches sampled. Moreover, the downstream-most reaches were clearly too wide to be sampled effectively with the one electrofisher available. Night snorkeling was more efficient than day snorkeling for detecting trout > 60mm in most instances (Table 2). Also, at night I was able to approach fish more closely and, thus, estimate lengths more accurately. In Moore Creek, two-pass electrofishing was more efficient than night snorkeling (Table 3). The small size of Moore Creek made detecting fish by snorkeling difficult, and the difficulty would have increased in the narrower, shallower reaches upstream of reach 4. Density indices between streams are not directly comparable because I used different sampling methods in each.

Fish species diversity increased downstream in both stream systems studied. In the most downstream reaches of Twelvemile Creek, cutthroat trout, brook trout, and sculpin (*Cottus* spp.) were abundant, and brown trout (*Salmo trutta*), rainbow trout (*O. mykiss*), and mountain whitefish

(*Prosopium williamsoni*) were observed or captured occasionally. The specific identity of the sculpins in the St. Regis River drainage has not been resolved among taxonomists. In Moore Creek, brook and cutthroat trout were present in the lowest four reaches, but only brook trout upstream. I observed cutthroat, brook, and bull trout (*Salvelinus confluentus*) in the SFLJ Creek, as well as bull x brook trout hybrids (see Adams 1994 on accuracy of identifying hybrids). I found tailed frogs (*Ascaphus truei*) in both stream systems.

In Twelvemile Creek, the upper distribution limit of brook trout occurred near reach number 10.5 (Figure 2). Near the upper limit of the brook trout distribution limit, the channel became more confined and the channel slope increased up to about 8 %, but the slope remained more gradual than slopes where brook trout occurred in Moore Creek and in some of the streams I studied in Idaho (Chapters II through IV).

I calculated population estimates for 2-pass depletion electrofishing in Moore Creek. However, because of low population sizes (usually less than 30 fish), confidence intervals were frequently extremely wide (Riley and Fausch 1992). For estimates in which the probability of capture was greater than 0.3, the unbiased population estimate was usually about the same as the number of fish caught. In reaches 1 and 4, where I used 3-pass electrofishing, three or fewer additional fish were caught on the third pass in each group analyzed (data split by species, age {0, 1, >1}, and site). Therefore, I chose to use the number of fish actually captured in two passes for all further analyses, understanding that the population indices are slightly smaller than the true fish abundances.

Fish densities were highly variable among reaches in both Twelvemile and Moore Creeks. In Twelvemile Creek, numbers and densities of both age 0 and older brook and cutthroat trout were highly variable among reaches (Figures 6-8; Appendix B, Table B1). Brook trout numbers and densities were also variable in Moore Creek, but cutthroat trout, where present, occurred at consistently low densities (Figures 9-11; Appendix B, Table B2). In Moore Creek, the density of brook trout peaked midway down the stream in reach 4 (Figures 10, 11). Woody debris and gravel substrate were abundant in the reach. When I snorkeled the reach, nearly all adult fish were paired or in groups and the beginnings of numerous redds were visible.

I found the highest densities of age 0 fish of both species in shallow side channel habitats that seldom contained older fish (except, perhaps, small age 1 cutthroat trout). In calculating densities, I included side channel areas in the total reach area for age 0, but not for older fish. However, because age 0 fish primarily used stream margins and side channels, I present linear (number per 100 m) as well as areal (number per 100 m<sup>2</sup>) densities of age 0 fish. In Twelvemile Creek, the linear densities of age 0 brook and cutthroat trout were much greater in one reach than in any other, but the reach containing the peak density was different for each species (Figure 6). The linear densities of age 0 brook trout per reach were not significantly correlated with side channel area or with distance upstream, however the incidence of reaches containing no age 0 brook trout increased toward the upstream distribution limit. Areal densities of age 0 fish and older, conspecific fish were significantly, positively correlated for both brook and cutthroat trout in both streams (Table 4). I found no significant correlation between areal densities of age 0 brook and cutthroat trout (Table 4).

## Age

I determined ages of 280 brook trout (49 % of all brook trout captured by electrofishing - Table 5) by examining otoliths. The distance from the core to the edge of the otolith was highly correlated with fish length (for all reaches/streams combined,  $r = 0.88$ ,  $p = 0.000$ ,  $n = 177$ ), confirming that otoliths continued to grow as fish grew. Annuli were distinct in otoliths from most fish older than age 0. Lengths of age 0 fish from most stream reaches did not overlap with lengths of older fish, so I could independently determine their age by two methods: fish length-frequency analysis and otolith examination. The distance from the core to the edge of the otolith of age 0 brook trout collected in the fall was slightly less than the distance from the core to the first annulus in older fish, suggesting that the first ring was laid down after most of the first year's otolith growth was complete. The number of rings increased with fish size during the early years of relatively rapid growth, as expected if rings were annuli (Figure 12).

Annuli were more distinct on otoliths of slow growing fish from colder reaches than on faster growing fish from warmer reaches. Assigning ages to most otoliths from most reaches was straightforward. In comparing ages assigned to otoliths (from Twelvemile Creek, reach B) by two readers, I found 96% agreement. The one otolith assigned different ages was from a five year old fish that G.C. aged whole, and the first annulus was not visible until the otolith was ground. Conversely, fish from near the outlet of Moore Lake were more difficult to age. Annuli were faint and the spacing between them was large. I collected some brook trout from the lake outlet in July 1998 to help verify the annuli observed in otoliths from fish collected in 1997. All indications were that I correctly aged fish collected in 1997. Some otoliths could not be aged either because the otolith had multiple primordia or annuli were not evident on large otoliths from large fish. Occasionally when one otolith was unreadable, the other otolith in the pair was readable. Most unreadable otoliths were from relatively large fish or fish from the upper reaches of Moore Creek.

Trends in the distance from the core to the first annulus (i.e. a correlate of first year growth) were evident within streams, but the direction of the trend was opposite in the two streams. In Moore Creek, the distance to the first annulus was greater in fish from upstream, whereas in Twelvemile Creek, the distance was greater in fish from downstream (Figure 13). Fish from some reaches were excluded from the analysis because I measured only a subset of otoliths using the Optimas imaging system.

## Brook trout growth and reproductive status

Longitudinal trends in brook trout growth, age-at-maturity, and fecundity were evident in both streams but, consistent with otolith growth patterns, were opposite in direction in the two streams. Conversely, I found no evidence of within-stream differences in length-weight relationships or in fecundity-at-size. Each of these parameters is discussed in greater detail below.

Brook trout length at age showed longitudinal trends similar to those described for the distance to the first annulus in otoliths. In Twelvemile Creek, brook trout were smallest at age in the upstream electrofishing reach and largest in the downstream reach (Figure 14; Appendix B, Table B3). Conversely, in Moore Creek, the brook trout were largest in the upstream reaches closer to the lake outlet and smallest in the middle reaches (Figure 15; Appendix B, Table B4). Age 0 fish again increased in size in the most downstream reaches (including the two SFLJ Creek reaches), resulting in

a quadratic relationship between length of age 0 brook trout and elevation (Figure 16). Lengths at ages 0 and 1, but not age 2, were significantly ( $p < 0.05$ ), positively correlated with stream temperature in both streams (Figure 17).

The differences in lengths-at-age between the upstream and downstream ends of the two streams were equivalent to one or more years of growth at the slowest annual growth rates. For example, the larger age 1 fish from the downstream end of Twelvemile Creek were larger than most of the age 2 and some of the age 3 fish from the upstream end. The mean length of age 2 fish in the downstream reach was larger than all but one fish collected in the upstream reach (Appendix B, Table B3). The disparity in mean length at age among sites increased with age, but the variation in length also increased. In Moore Creek, age 0 fish from the upstream reach were as large or larger than age 1 fish from the downstream reach.

Body weight followed the same patterns as length (Appendix B, Tables B5-B6). Reported body weights for brook trout are weights *without* gonads for mature fish (except Moore Creek reach 3 where I did not dissect fish) because at the time of collection, some fish had spawned but others had not. The relationship between length and weight was consistent among sites and streams as well as between brook and cutthroat trout (Table 6, Figure 18). The log-log relationships of length and weight were linear with excellent fit to the regression line for both species and streams (Table 6, Figure 19)

Female brook trout matured earliest in reaches with the fastest growth (Figure 20). Some estimates of the proportion of females mature at a given age (particularly for age 2 fish) were uncertain for two reasons. First, in the youngest age class containing maturing females there were often immature fish that I was unable to sex, so the total number of females was uncertain. Second, in some instances I was unable to distinguish between immature and post-spawning females. However, the pattern of earlier maturation downstream in Twelvemile Creek and upstream in Moore Creek was evident even with the uncertainty.

Both length and weight were closely correlated with fecundity (Figure 21). As expected, the median number of eggs produced per mature female was highest in reaches where growth rate was highest (Figure 22). I used regression to develop an equation to predict fecundity. The regression equations were used to estimate the number of eggs produced by females that had already begun spawning. Regressions on weight fit better than on length for populations in both creeks (Table 7). In Moore Creek, the linear equation of eggs on weight fit better than the quadratic equation. In Twelvemile Creek, although the linear equation fit the data as well as the quadratic equation statistically, the quadratic appeared to fit the two points for larger fish better (Figure 22A) and was thus used for estimating fecundity. Sample sizes were insufficient to compare size-fecundity relationships among reaches.

## Discussion

Biologically meaningful levels of variation in demographic parameters occurred along the lengths of both the lake-fed and the non-lake-fed stream. Fish densities, particularly among age 0 salmonids, fluctuated greatly, but without statistically significant longitudinal trends, among 100-m-long reaches, suggesting that important nursery areas exist patchily within these streams. Brook trout growth, age-at-maturity, and fecundity, however, varied in a predictable, longitudinal pattern along each stream. In Moore Creek, where at least some environmental gradients (e.g. temperature, channel slope, and perhaps food supply) were steeper, shifts in demographic parameters similar in magnitude to those in Twelvemile Creek occurred in about one-fifth the distance.

The patterns I observed in both population structures and demographic processes are consistent with Schlosser and Angermeier's (1995) hybrid model. The model predicts that some areas within the stream should support higher reproductive output and/or survival than other parts. Growth differences, probably driven largely by temperature but also by other factors, occurred over large spatial scales within the streams. The growth differences were sufficient to create differences in reproductive output that, in turn, could create source and sink areas at the scale of stream segments. However, if increased survival compensated for reduced growth and reproductive output, then source-sink dynamics would not be necessary to maintain the population distribution. The model also predicts variations in fish density, size structure, and possibly recruitment at a smaller scale, resulting largely from fish movements within a spatially heterogeneous habitat. I found that fish abundance and size structure and recruitment of age 0 fish were all highly variable among 100-m-long reaches.

The observed trends in brook trout demographic parameters in Twelvemile Creek may provide a sufficient explanation for the upstream distribution limit of the population. The rates of birth, death, immigration, and emigration combine to determine population growth. The bulk of data I collected addresses birth rates, but some inference about immigration and emigration can be made as well. A gradual decline in growth, and a concomitant decline in fecundity and increase in age at maturity, occurred with distance upstream in Twelvemile Creek. Unless compensated by increased survival, the shift in the suite of parameters is expected to lead to decreases in birth rate and local subpopulation growth rate with distance upstream.

Similar longitudinal trends have been reported in other studies. Cooper et al. (1962) reported slower growth of brook trout upstream than downstream. Coastal cutthroat trout growth between July and May was less upstream than downstream over 3.8 km of stream with an average channel slope of 2.2 % (Harvey 1998). In high elevation Colorado streams, production in several salmonid species was lower upstream than downstream (Scarnecchia and Bergersen 1987). However, Scarnecchia and Bergersen (1987) pointed out that if much lower elevation streams had been included in the study, the relationship between elevation and production would likely have been mound shaped, with production declining in lower, excessively warm streams.

The longitudinal trends in growth, female age-at-maturity, and fecundity, support the idea that extreme conditions, such as lethal temperatures or barriers to dispersal, are not necessary to create a population distribution boundary and limit invasion. Moreover, many features of ecosystems, both biotic and abiotic, influence demographic parameters such as growth. Therefore, complex suites of factors can contribute to creating a demographic boundary. While some factors (e.g. temperature) may have a more widespread or consistent influence on demographic rates than others (e.g. species interactions), alteration of any of a number of factors may influence the location of a distribution boundary. Finally, because of the importance of immigration and emigration among sub-populations, the conditions ultimately determining the location of the boundary may not even

occur at the boundary itself (Pulliam 1988).

## Growth, survival, and movements

Multiple abiotic and biotic factors influence fish growth. Water temperature, level of energy intake, and fish size were apparently the three most important factors influencing brown trout growth (Elliott 1994). Other factors include habitat quality, maturity, individual variation in behavior and physiology, and intra- and interspecific behavioral interactions. Behavioral influences on growth may include energy expended in defense, aggression, and foraging, indirect effects of predators (Lima 1998), and behavioral thermoregulation. Dispersal can also influence the apparent growth rate of fish in a stream segment when growth is evaluated based on length at age, as in this study.

The differences in brook trout growth among reaches were correlated with water temperature. Temperature is commonly considered the most important factor regulating growth rates of salmonids (e.g. Elliott 1994; Lobón-Cerviá and Rincón 1998), including brook trout (Purkett 1951; Baldwin 1956; Haskell et al. 1956; McCormick et al. 1972). Given unlimited food, brook trout growth generally increases with temperature up to an optimum between 12.4 and 15.4 °C, above which growth rate declines (Baldwin 1956; Haskell et al. 1956; McCormick et al. 1972; Magoulick and Wilzbach 1998b). Contrary to the pattern I found in Twelvemile Creek, unconfined brook trout in a Pennsylvania stream had higher instantaneous growth rates in an upstream than a downstream reach during the summer (albeit both were negative). However, temperatures upstream were within the optimal range, whereas those downstream were higher than optimal. Summer temperatures at the upper Moore Creek site exceeded the optimal temperature for brook trout growth in both 1997 and 1998. However, cold spring seeps downstream of the lake outlet may have allowed the fish to thermoregulate behaviorally. Also, a longer growing season in the upper reaches may have compensated for reduced growth during periods of the highest temperatures.

Food and temperature interact strongly in influencing growth. As temperature increases, the importance of food intake as an influence on growth rate increases due to increased metabolic rates (Haskell et al. 1956). Warm temperatures and limited food can lead to decreases in growth rate (Donald et al. 1980; Elliott 1994; Lobón-Cerviá and Rincón 1998). Conversely, growth in cold temperatures can be limited by food intake and absorption, and by slow metabolic rates. Furthermore, at very cold temperatures, food intake is more likely to be limited by digestive rate than by food availability (Cunjak et al. 1987).

I suspect that differences in food availability explain the faster apparent growth rate of fish in Twelvemile Creek than in Moore Creek even at similar temperatures. Twelvemile Creek had greater discharge and a much more open canopy than Moore Creek. The amount of leaf litter and detritus that accumulated on weir fences in Twelvemile Creek was orders of magnitude greater than in Moore Creek. Thus, I suspect that primary productivity and both allochthonous and autochthonous invertebrate production were greater in Twelvemile Creek.

Several processes may be responsible for weaker correlations found between fish size and stream reach temperature in older than in younger fish. First, movement of fish among reaches characterized by growth differences should increase the variance in fish length at age. Older fish captured in a given reach may have undergone most of their growth in a reach with very different temperature regimes. However, Kreuzweiser (1990) found that marked brook trout recaptured in the same section where marked, showed differences in growth rate of 2 to 5 times among individuals, suggesting to him that fish may have had "niche-specific" growth rates. Second, among brook trout aged 1 and 2, large differences apparently existed in energy allocation to reproduction. Because fish in different reaches matured at different ages, their differential allocation of energy to reproduction was probably reflected in their growth rates. Third, as fish grow, their thermal optima for physiological performance parameters generally shift to slightly lower temperatures (Spigarelli and Thommes 1979; Hazel 1993). Thus, the warm temperatures in upper Moore Creek may be more detrimental to older than younger fish. In addition, smaller fish may be more effective than larger fish at foraging on the small seston transported out of the lake. Finally, angling probably removed many of the fastest growing age 2, and perhaps age 1, fish in the lower reaches of Twelvemile Creek. Also, angling in Moore Lake probably influenced the size distribution of age 1 and 2 fish that emigrated to the stream.

While survival was not estimated, the observed age distributions indicated that survival of at least older age classes may be slightly higher upstream than downstream in Twelvemile Creek and the opposite in Moore Creek. However, slight differences in adult survival are expected to have less effect on population growth than would changes of similar magnitude in larval and juvenile survival [e.g. simulation models in Marschall, 1996 #370; Clark, 1997 #417; Chapter VI].

### Survival rates of eggs and of

age 0 fish are expected to vary spatially, as well as temporally. Egg to age 0 and first winter survival may be lower and/or more spatially variable upstream than downstream in Twelvemile Creek. The increased incidence of reaches where no fry were observed upstream indicates that adults do not spawn in many of the reaches, the eggs or fry do not survive, or the fry emigrate. Lateral and side channel habitats are smaller and occur more infrequently upstream, indicating that appropriate nursery areas may be limiting. However, catastrophic losses of eggs and larvae may be more common downstream, where rain-on-snow events and ice flows that scour the stream bottom are likely more prevalent. Overwinter survival of age 0 brook trout could potentially be lower in upstream than downstream reaches of Twelvemile Creek due to higher mortality of smaller fish in harsher environments (Hunt 1969b; Smith and Griffith 1994; Meyer and Griffith 1997). In general, opposite trends would be expected in Moore Creek. However, the middle and lower reaches of Moore Creek apparently have abundant groundwater upwelling that moderates stream temperatures and may increase survival of age 0 fish (Latta 1969). Also, the stream channel appears to be more stable than in Twelvemile Creek. In Moore Creek, lateral habitats for nursery areas were the most prevalent in the middle reaches. Although the only study reaches containing side channels in Moore Creek were the upper three, most of them contained minimal cover and, thus, may not have been suitable for nursery areas.

Documenting movements of age 0 fish is important to estimating survival and understanding population dynamics. However, such documentation is extremely difficult, in part because of inadequate methods for marking very small fish. The distance to the first annulus may be useful for making probability-based estimates of the general areas of origin for fish within stream networks characterized by pronounced spatial differences in growth rates. The assumption is that variation in distance to first annulus is created by fish moving within the stream or stream-lake network after completing at least the majority of first year growth. Analysis of otoliths or scales has been used to determine the age at which fish

entered lakes or oceans, or the age at which they became piscivorous (Hayes 1995). Heggberget et al. (1986) used growth patterns determined from scale analyses to determine the river reach where adult Atlantic salmon had originated. Hayes (1995) used otolith microstructure to distinguish among early life history patterns of adult rainbow trout in a lake.

Alternative explanations also exist for the bimodal distributions of the distance to first annulus that I observed. The bimodal distribution could be an artifact of small sample sizes. Conversely, it could be a real pattern, but one that results from differences in parental spawning times and/or growth differences within a reach. Validating this approach would require larger sample sizes, a time series of samples within and between years, and estimation of the variation in otolith growth among individuals known to have reared in one reach.

Using the assumption that variation in the distance to first annulus is due to movements by age 1 or older fish, I make tentative inferences about movements of fish within the study streams. The fish captured in the downstream end of Twelvemile Creek (Figure 13A, open squares) show a bimodal distribution of distances to the first annulus. The fish with the shorter distances may be fish that originated upstream, where growth of age 0 fish was slower. If such an interpretation of the patterns is correct, it suggests that more fish moved from the upstream to downstream end of the study area than vice versa. However, the sample size was small and the method is tenuous. In Moore Creek, several fish apparently moved from the lake and/or upper reaches of the creek downstream into the lower reaches of Moore Creek (Figure 13B). The majority of fish moving into the downstream reaches may have continued on into SFLJ Creek. The large variation in the distance to first annulus of age 1 fish in reach 6 of Moore Creek is probably due to differences between fish rearing in the reach versus immigrating from the lake or lake outlet. Due to culverts and waterfalls, fish from reach 5 could not have moved upstream into reach 6.

My results from Twelvemile Creek indicate that high levels of dispersal do not occur but that some dispersal from upstream to downstream occurs. If source-sink dynamics maintain the population distribution in Twelvemile Creek, some low level of dispersal from downstream to upstream must occur. However, the dispersal could occur in a leap-frog fashion, in which case it would not be evident by examination of otoliths. Conversely, high rates of dispersal over long distances would presumably overwhelm local variation in demographic rates. The occurrence of upstream dispersal in the stream remains to be more fully investigated. Based on results from other systems, some upstream movements likely occur (Gowan and Fausch 1996b and Chapters II and III). The degree to which those movements represent dispersal is unknown.

## Fish size gradient

Although I found some evidence for downstream movements of larger fish, such dispersal cannot fully explain the observed trends in population structure. In Twelvemile Creek, the gradient in fish sizes was due at least partially to differences in growth. The largest fish downstream were the same age or younger than the largest fish upstream. In Moore Creek, the fastest growth occurred in the two most upstream reaches, the opposite of the pattern expected from downstream movements of faster growing fish.

Size-dependent movements and/or differential survival of large fish throughout the streams may also be partially responsible for the trends in fish size (Newman and Waters 1989). The distances to the first annuli on otoliths indicate that a number of fish captured downstream in Twelvemile Creek had dispersed from upstream. In Moore Creek, although the fastest growth occurred upstream, more large fish were captured downstream, suggesting high mortality and/or high emigration rates of large fish from upstream reaches. Analysis of otoliths suggested that some of the large fish downstream had immigrated from reaches near the lake outlet after their first year of growth (Figure 13B). Because large fish in shallow water are likely to be at the greatest risk of predation by diving or wading predators (Harvey and Stewart 1991), predation could contribute to a distributional pattern of larger fish downstream, both by causing increased mortality of large fish in headwater reaches and by favoring a behavioral response of downstream migration of larger fish. However, fishing is another form of size-selective predation, and fishing pressure was much higher in downstream than upstream reaches of Twelvemile Creek. Thus, I expect that higher fishing mortality downstream would counteract any longitudinal size gradient in the stream created by wading or diving predators. Size-selective overwinter mortality in young fish would likely favor faster growing fish in all reaches, but may be more pronounced upstream in Twelvemile Creek where winter conditions are harsher and persist longer (Cunjak et al. 1987; Smith and Griffith 1994; Quinn and Peterson 1996; Meyer and Griffith 1997).

## Variation in abundance/density

The variation in salmonid densities that I observed is probably typical of mountain streams in which habitat heterogeneity occurs at several spatial and temporal scales. I observed similar variation in brook trout densities among reaches within the Idaho streams discussed in Chapter II (unpublished data). Variation in abundance and density was particularly high for age 0 brook trout. Similarly, in a Wyoming stream, 70% of the age 0 brook trout in the entire stream occurred in one beaver pond (Thompson and Rahel 1996). Understanding causes of the variation in densities of age 0 salmonids may be particularly important for both predicting invasions and restoring salmonid populations. Large brook trout tend to move more extensively and occupy stream reaches not used by smaller, age 0 and perhaps age 1 fish (Chapters II and III), suggesting that older fish are more flexible in their habitat use. Possible sources of variation in density of age 0 fish include, clumped locations of redds, post-emergence aggregation of age 0 fish in certain habitats, and/or variable survival of age 0 fish among habitats. All of these processes probably occur to differing degrees in various streams. Brook trout, as well as other salmonids, concentrate spawning in a small proportion of the apparently-suitable spawning habitat (Essington et al. 1998). Factors that are not often measured, such as groundwater upwelling, help explain the aggregations in some stream systems (Benson 1953; Curry and Noakes 1995a). High densities of age 0 salmonids have been explained by proximity to high density spawning areas in some streams (Beard and Carline 1991). Some movement of fish into appropriate rearing habitats must occur, because high densities of age 0 brook trout occurred in side channels where no redds were observed. Hunt (1965) described fairly extensive movements of age 0 brook trout both up and downstream through gradual channel slopes.

Survival in early life-history stages is still poorly understood but likely contributes to the observed patchiness. Large numbers of age 0 brook trout occurred almost exclusively in side channels. Since side channels provide the habitat apparently preferred by age 0 brook and cutthroat trout (Lentz 1998), survival is likely higher in side channels than in habitats that provide less protection from fish predation (e.g. stream margins and lateral habitats that are well connected to the main channel). Moreover, some of the side channels with high densities of age 0 fish had dense brush

cover, further protecting fish from avian predation. Thus, the distribution of side channels along a stream may play a critical role in the population dynamics and the locations of source areas both at the stream and stream segment scales. However, density of age 0 brook trout was not significantly correlated with side channel area in Twelvemile and Moore creeks. The proximity of a side channel to a high-density spawning area may be a key determinant of its importance as a nursery area.

Interactions between brook and cutthroat trout may also be important in determining densities of age 0 fish. No correlation was detected between densities of age 0 fish of the two species. However, the lack of negative correlation does not imply a lack of interaction between the species. If age 0 fish of both species prefer the same habitats, then in the absence of interspecific interactions, densities should be positively correlated. However, negative interactions that lead to brook trout domination of some reaches/habitats and cutthroat trout domination of others could result, by late summer, in a lack of statistical correlation between densities of the two species.

## Implications for sampling design

The observed variability in demographic parameters within mountain streams has implications for sampling design of studies examining salmonid demographics or fish habitat relations. Demographic parameters in a reach should be considered no more typical of the entire stream than are habitat features in the reach. Many studies of stream fish demographics have compared demographic parameters among multiple streams based on sampling in one reach per stream. Valid comparisons of demographic parameters among streams require either sampling multiple reaches along each stream or carefully selecting a single site per stream, taking into account geomorphic characteristics, thermal regimes, food quality and quantity, and species assemblage. Although my results are based on one sampling period, the trends in relation to stream temperature suggest that the patterns are likely to be generally consistent over time (Lobón-Cerviá and Rincón 1998). Thus, increasing the temporal scale of sampling cannot compensate for limited spatial sampling. Larger gradients of physical parameters along a stream are likely to lead to stronger trends in demographic parameters along a stream (cf. Newman and Waters 1989). One common response to high variability in field studies is to sample larger areas or to combine samples. Heimbuch et al. (1997) suggest a method to combine samples to obtain more reliable depletion estimates of fish population size. However, in some cases, the variability itself is the key to understanding ecological processes. For example, recognizing extreme variability in age 0 brook trout abundance allows one to then focus on the cause of the variability. By understanding the factors contributing to high abundances in some reaches, I may increase our understanding of the invasion process. However, if sample reaches were 300 m rather than 100 m, or if data from multiple reaches were combined for analyses, ecologically important variability may have been lost, particularly near the outlet of Moore Lake where steep environmental gradients existed. My abundance data were probably collected at too large a scale (100 m reaches) to adequately represent the patchiness in age 0 fish abundance.

## Future research

Several avenues of research would help clarify the importance of gradual declines in population growth rate to distribution limits of brook trout in particular, and stream salmonids in general. I suspect that the most fruitful research will focus on processes occurring in early life stages to determine whether increases in survival compensate for decreases in growth. It would be helpful to understand how interspecific interactions influence survival of age 0 fish, particularly during the critical period occurring in the first two to three months after emergence (Latta 1962, 1969; Elliott 1994). One approach would be to study nursery habitats from spring through late summer, with particular attention to changes in abundance and species dominance and to the following questions. Within a stream, are nursery habitats (e.g. side channels) containing the most fish consistent from year to year? Is the dominant species within each nursery habitat consistent among years? If consistent, is the species composition driven by intra- or interspecific factors? An examination of differential survival, particularly of early age classes, in various portions of a stream would fill an important gap in my demographic analysis. How do changes in survival exacerbate or ameliorate the population-level effects of declines in individual growth, age-at-maturity, and fecundity within streams? On what spatial scales do changes in survival occur? I suspect that variations in survival of age 0 fish occur both at a scale paralleling the observed changes in growth and at a within-reach scale dependent on the habitat quality. What are the mechanisms driving changes in survival? Understanding how the presence of other salmonid species influences brook trout demographic parameters (and vice versa), and whether the influence is spatially variable, could potentially provide insight into the regional variation in the prevalence of coexistence of brook trout and native salmonids.

Several approaches would allow one to test the applicability of Schlosser and Angermeier's (1995) hybrid model to stream fish invasions. The explorations of spatial differences in survival mentioned above would facilitate indirect tests of the importance of the hybrid model. Population models could then be used to estimate the importance of immigration to maintenance of peripheral subpopulations. The most direct test would be to either eliminate a source population or prevent dispersal from it and to follow the population dynamics in the fragmented subpopulations afterwards. With proper observations prior to manipulation and control populations, such an approach could provide a powerful test of the hypothesis that subpopulations near distribution limits are supported by distant source populations. Such drastic population manipulations are often feasible when working with nonnative species that managers would like to eliminate anyway. In fact, brook trout removals in headwater lakes are already being conducted (Knapp and Matthews 1998) and provide an ideal situation for testing the model in systems with downstream-directed invasions.

Modelling population growth would allow a quantitative assessment of the importance of the observed variations in demographics to brook trout population growth. Lacking information on fish survival, modelling can provide estimates of the change in population growth rate relative to various magnitudes of change in survival. Also, modelling approaches allow one to explore which vital rates are likely to have the greatest influence on population growth. Ultimately, such approaches could help us understand how human activities can promote or hinder invasions. Chapter 6 presents some modelling approaches to demographic analysis of the brook trout in Twelvemile Creek.

Table 1. Thermal units (sum of average daily temperatures, °C) during two intervals for sites in two streams in the St.Regis River drainage, Montana.

Site

MECHANISMS LIMITING A VERTEBRATE INVASION:

Dates	Upper Moore	Middle Moore	Lower Moore	Upper Twelvemile
7/31/97 to 7/30/98	2340	n/a	1544	n/a
7/31/97 to 6/10/98	1550	1049	1065	879

Table 2. Comparisons of the numbers of fish observed during day and night snorkeling and captured during electrofishing (e-fish) in three, 100 m, reaches in Twelvemile Creek. "Unknown" are salmonids that were not identified to species due to observer inexperience on one night. Water temperatures during day and night snorkeling are shown.

Reach	Brook trout						Cutthroat trout						Unknown	Temperatures	
	<= 60mm			> 60mm			<= 60mm			> 60mm			<= 60mm	(oC)	
	e-fish	day	night	e-fish	day	night	e-fish	day	night	e-fish	day	night	night	Day	Night
1		3	3		2	8		3	10		2	30	12	10.5	13
5	4	12	4	1	9	10	2	7	5	6	22	12	11	12.5	11
10	1	5	2	3	8	12	1	7	2	11	14	23	0	9	9

Table 3. Comparisons of the numbers of fish observed during night snorkeling and two-pass (2P) and three-pass (3P) electrofishing in two 100 m reaches of Moore Creek, Montana. Stream temperatures (temp.) during snorkeling are shown.

Reach	Brook trout						Cutthroat trout						Night snorkel
	<= 60mm			> 60mm			<= 60mm			> 60mm			temp. (oC)
	snorkel	2P	3P	snorkel	2P	3P	snorkel	2P	3P	snorkel	2P	3P	
1	2	9	12	14	19	22	4	6	11	14	12	14	7
4	15	35	38	33	51	56	0	0	0	2	3	3	6.5

Table 4. Pearson's correlation of 1) densities (number per 100 m<sup>2</sup>) of age 0 brook and cutthroat trout with densities of older conspecifics and 2) densities of age 0 brook trout with age 0 cutthroat trout. Cutthroat trout ages were estimated based on fish length (see text).

Species, age	Brook, > 0	Cutthroat, > 0	Cutthroat, 0
<b>Twelvemile Creek</b>			
Brook, 0	r = 0.536 p = 0.010		r = 0.282 p = 0.203
Cutthroat, 0		r = 0.427 p = 0.048	
<b>Moore Creek</b>			
Brook, 0	r = 0.831 p = 0.020		r = -0.324 p = 0.479
Cutthroat, 0		r = 0.889 p = 0.007	

Table 5. Numbers of brook trout from each reach that were aged by otoliths and the percentages of all brook trout collected in each reach that were aged by otoliths. Few age 0 fish were aged by otoliths because, in most reaches, ages of first year fish were clearly evident based on length-frequency analyses.

Reach	Number of fish aged by otoliths (%)	Number of fish age > 0 aged by otoliths (%)	Distances to annuli determined?
<b><i>Twelvemile Creek</i></b>			
A	35 (74)	29 (83)	yes
B	34 (74)	28 (78)	no
C	51 (85)	51 (88)	yes
D	34 (61)	32 (84)	yes
<b>Total</b>	<b>154 (74)</b>	<b>140 (84)</b>	
<b><i>Moore Creek</i></b>			
1	21 (62)	17 (81)	yes
2	16 (24)	16 (34)	yes
3	0 (0)	0 (0)	no
4	40 (43)	39 (72)	no
5	9 (20)	9 (38)	no
6	22 (79)	18 (90)	yes
7	18 (86)	12 (80)	yes
<b>Total</b>	<b>126 (35)</b>	<b>111 (47)</b>	
<b>Grand total</b>	<b>280 (49)</b>	<b>251 (62)</b>	

Table 6. Regression equations of  $\log_{10}$  body weight (g) on  $\log_{10}$  total length (mm) for brook trout captured in late September and early October, 1997. Body weight excludes gonad weight for mature brook trout. All regressions and parameters are significant at  $p < 0.000$ .

Stream	Species	N	Constant	Slope	S.E. of estimate	R <sup>2</sup>
Twelvemile	brook	209	-5.046	2.997	0.048	0.992
Moore	brook	352	-5.182	3.055	0.051	0.993

Table 7. Regression equations for predicting number of eggs per mature female brook trout (Y) at the beginning of the spawning period. Females that may have begun spawning or that had egg numbers that were low outliers were excluded from the analysis (see text), so predictions may be slight overestimates. Body weights (BWT) were whole fish weights (g) minus gonad weights (g) in grams. Lengths (L) were total lengths (mm). Equations in bold were used to estimate egg numbers for females that had already begun spawning.

Regression equation	N	S.E. of estimate	R <sup>2</sup>
<b><i>Twelvemile Creek</i></b>			
$y = -651.824 + 5.432 L$	26	77.70	0.850
$y = 17.951 + 5.358 BWT$	26	65.30	0.894
<b><math>y = 71.4124 + 3.5224 BWT + 0.0112 BWT^2</math></b>	26	64.64	0.900
<b><i>Moore Creek</i></b>			
$y = -279.760 + 3.0179 L$	22	37.08	0.603
<b><math>y = 21.2405 + 5.2551 BWT</math></b>	22	31.86	0.721
$y = 22.7961 + 5.1451 BWT + 0.0018 BWT^2$	22	32.74	0.721

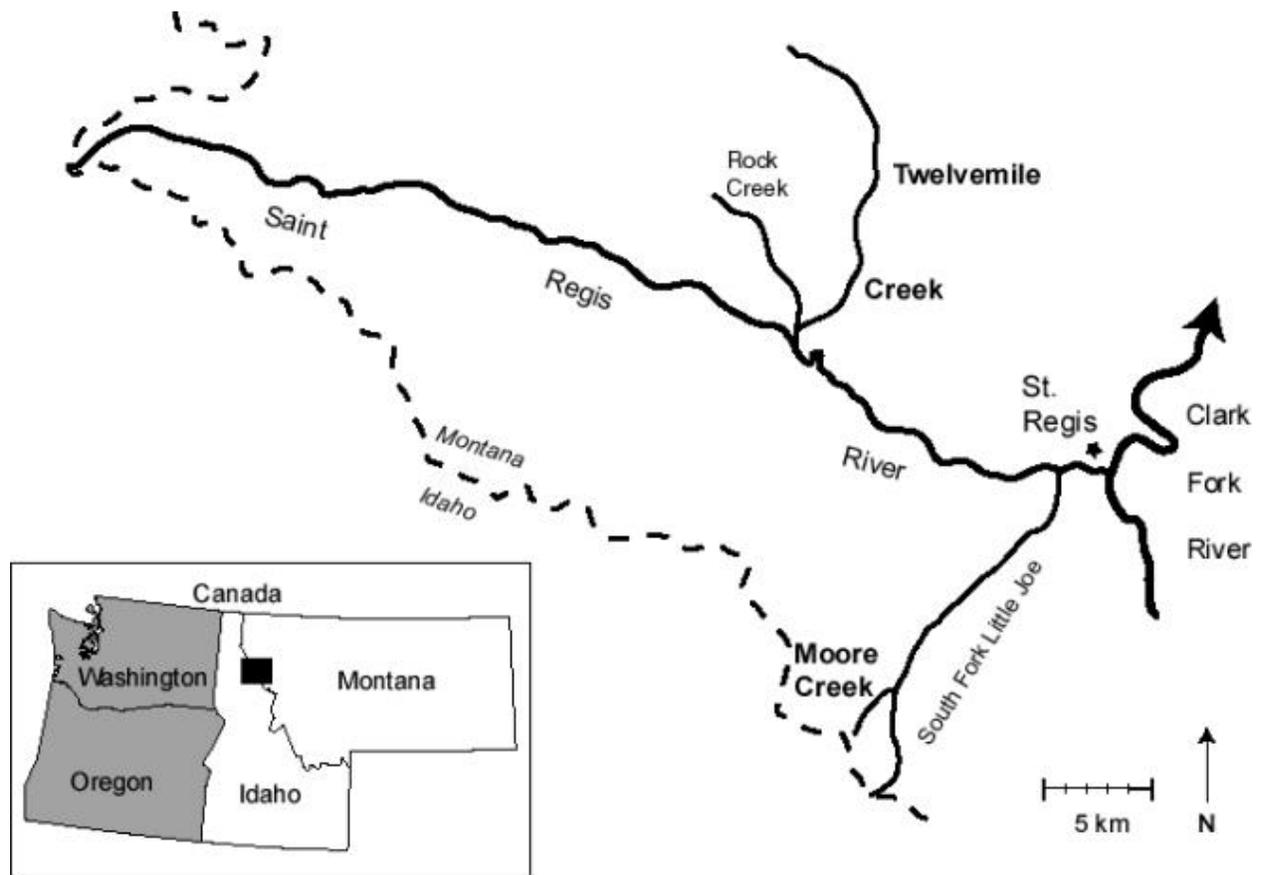


Figure 1. Study streams, Twelvemile and Moore creeks, in the St. Regis River drainage, Mineral County, Montana, U.S.A. The dashed line is the Montana / Idaho border.

Figure on following page:

Figure 2. Twelvemile Creek, Montana, study area. Numbers indicate 100-m-long snorkel reaches. Letters A to D indicate areas of varying length where brook trout were collected by electrofishing. Temperature recording sites are marked by stars.

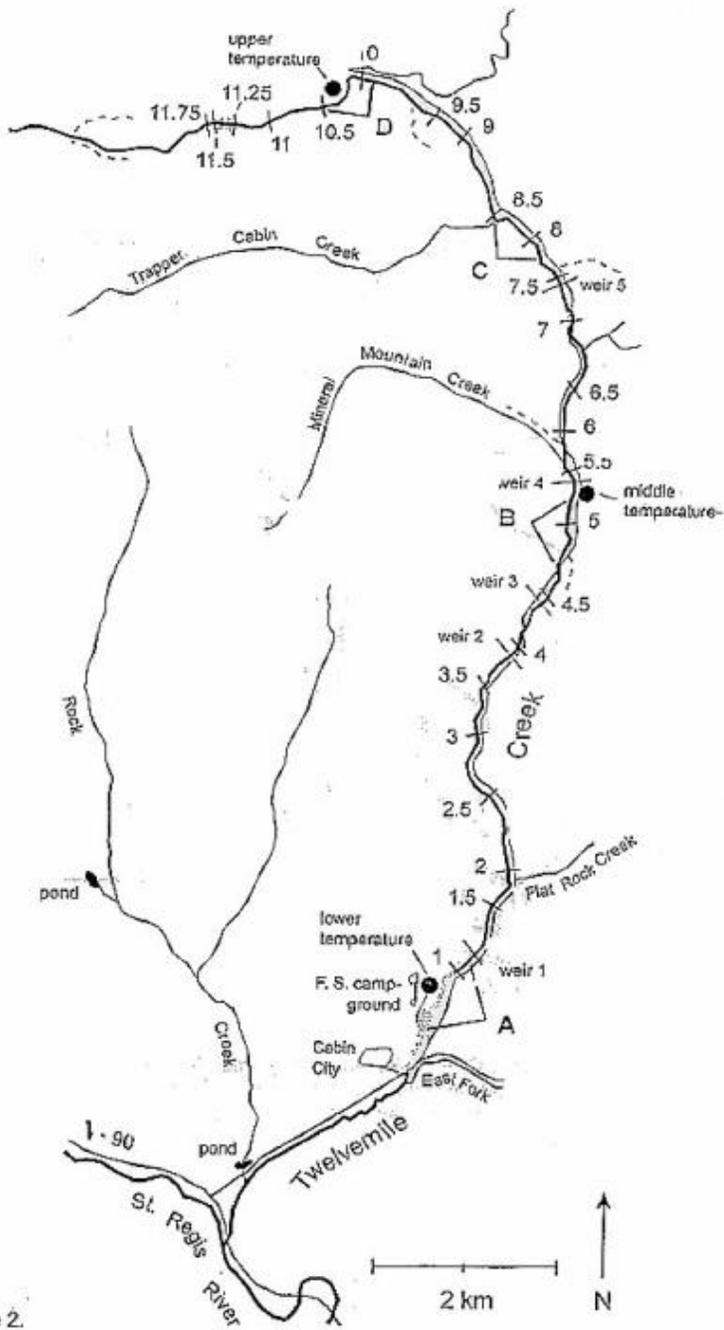


Figure 2.

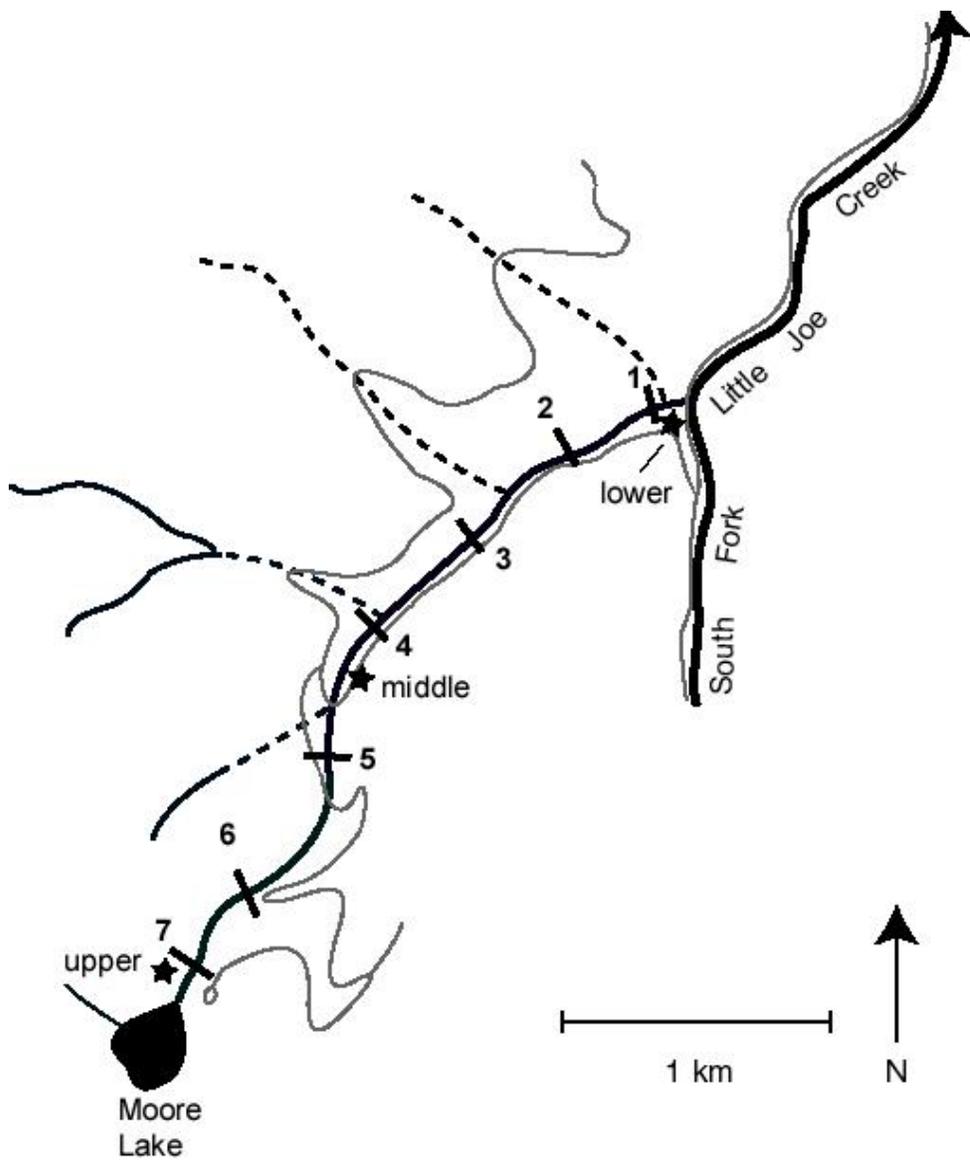


Figure 3. Moore Creek, Montana, study area. Numbers indicate 100-m-long electrofishing reaches. Stars indicate upper, middle, and lower temperature recording sites. Black lines indicate streams (dashed if intermittent), and gray lines represent roads, some of which were closed.

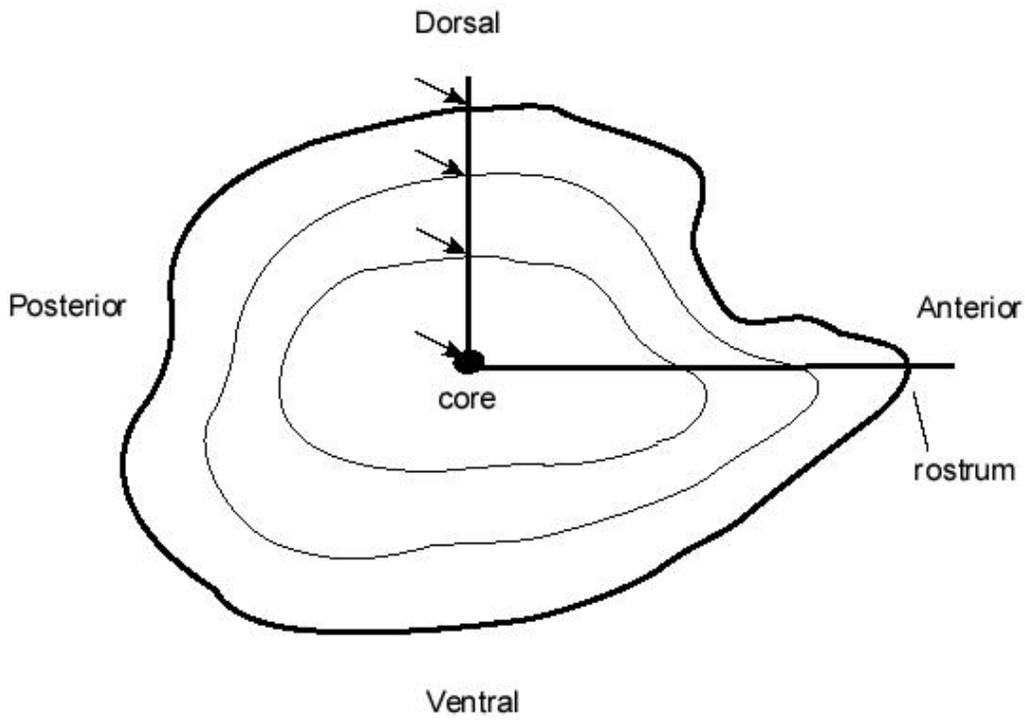
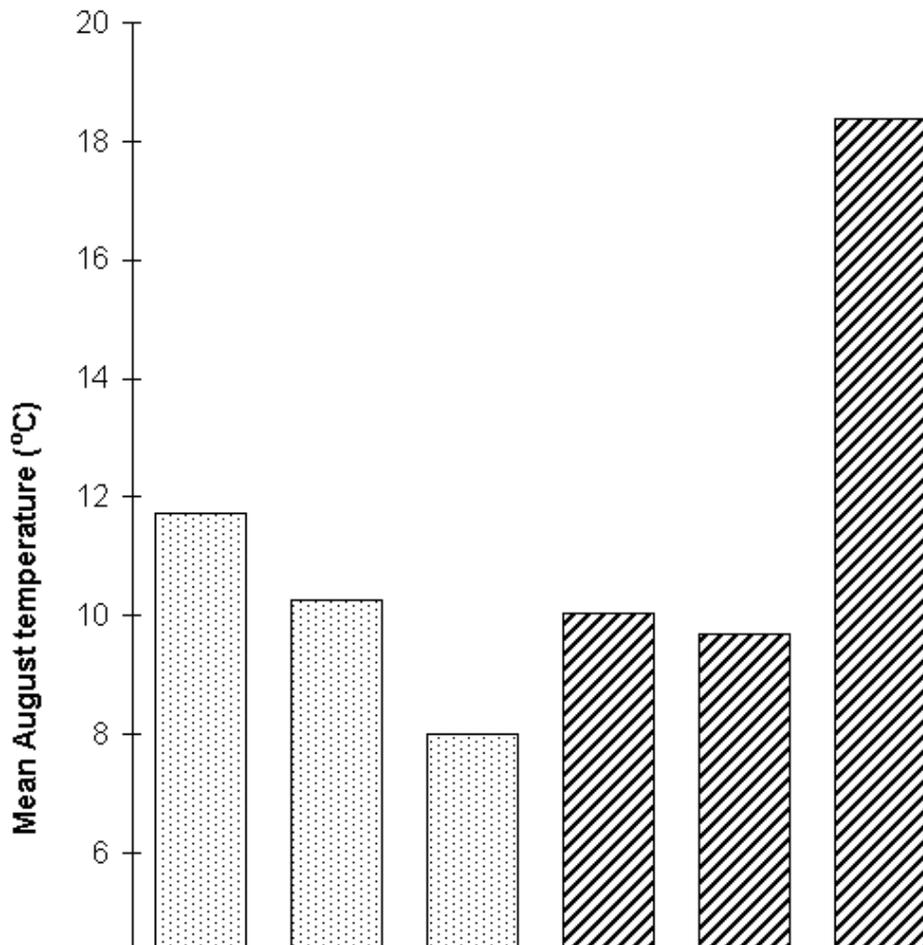


Figure 4. Schematic diagram of a sagittal otolith with 2 annuli (lighter lines). Measurements were made along a dorsal radius (shown as vertical line) perpendicular to a line extending from the core through the rostrum (horizontal line). Arrows indicate locations marked for measurements using the Optimas image analysis system. The program calculated distances between marked points.



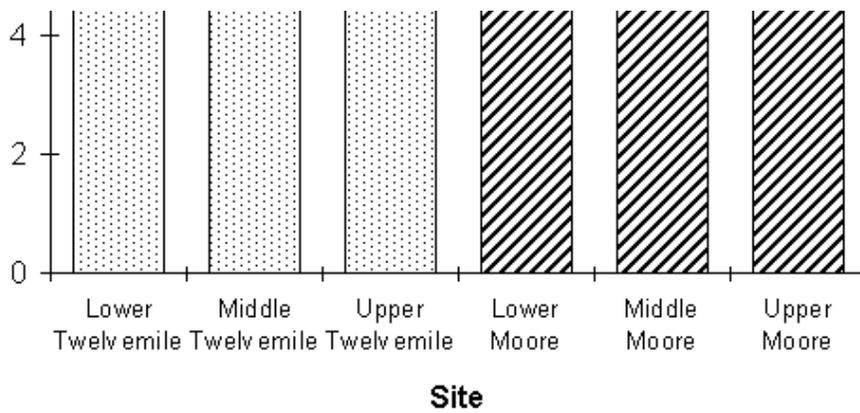


Figure 5. Mean stream temperatures during August 1997 for sites in Twelvemile and Moore creeks, Montana. The upper site in Moore Creek was about 50 m downstream of the outlet of Moore Lake.

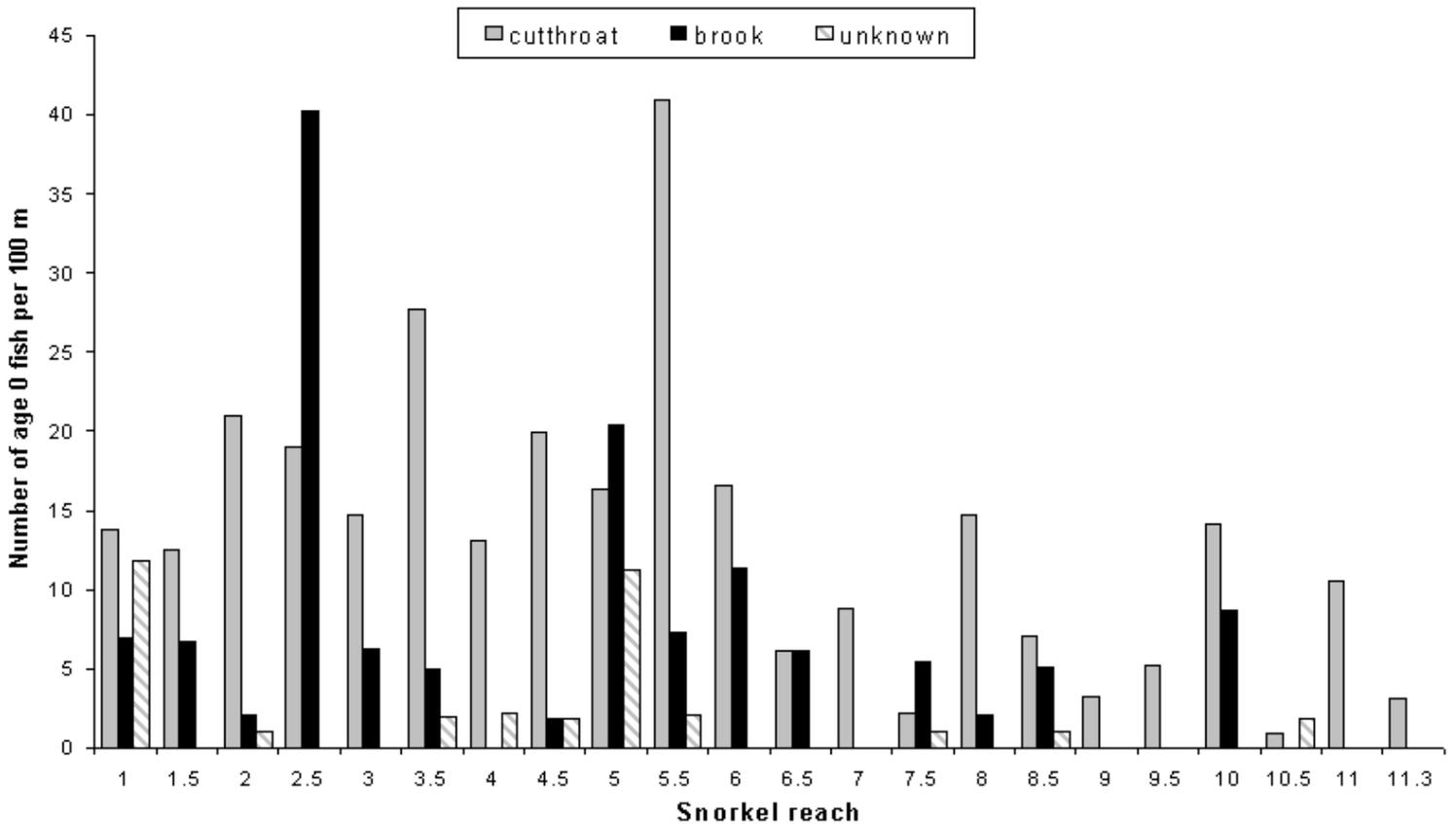


Figure 6. Linear densities (number per 100m) of cutthroat and unidentified trout  $\leq 70$  mm (estimated age 0) and age 0 brook trout in Twelvemile Creek, Montana. Density indices were derived from night snorkel counts in August and September, 1997. Based on lengths, I estimated that at least 60 % of the unidentified fish in reach 1 and 50 % in reach 5 were cutthroat trout.

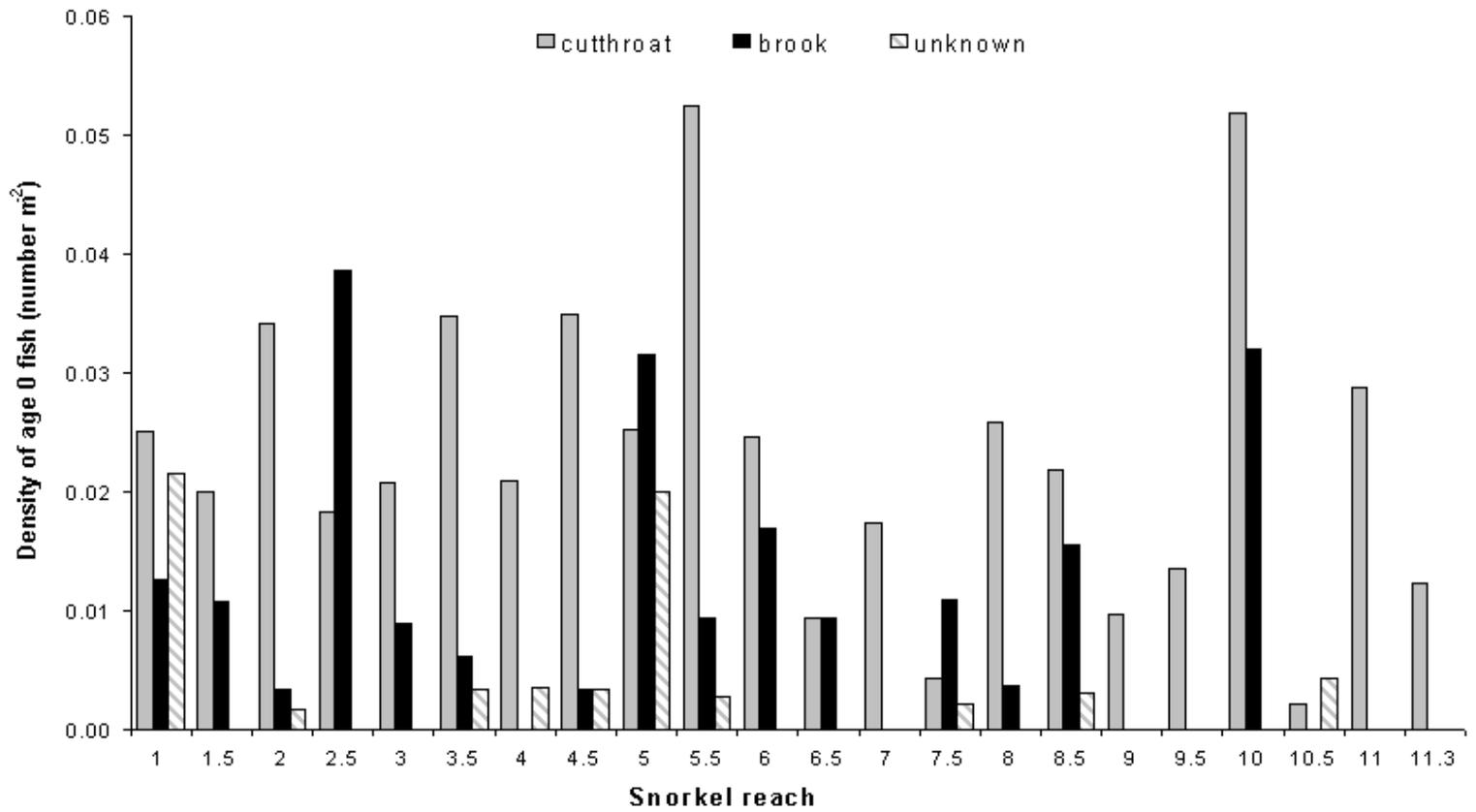


Figure 7. Areal densities (number per [S1] 100 m<sup>2</sup>) of cutthroat and unidentified trout  $\leq$  70 mm (estimated age 0) and age 0 brook trout in Twelvemile Creek, Montana. Density indices were derived from night snorkel counts conducted in August and September, 1997. Based on lengths, I estimated that at least 60 % of the unidentified fish in reach 1 and 50 % in reach 5 were cutthroat trout.

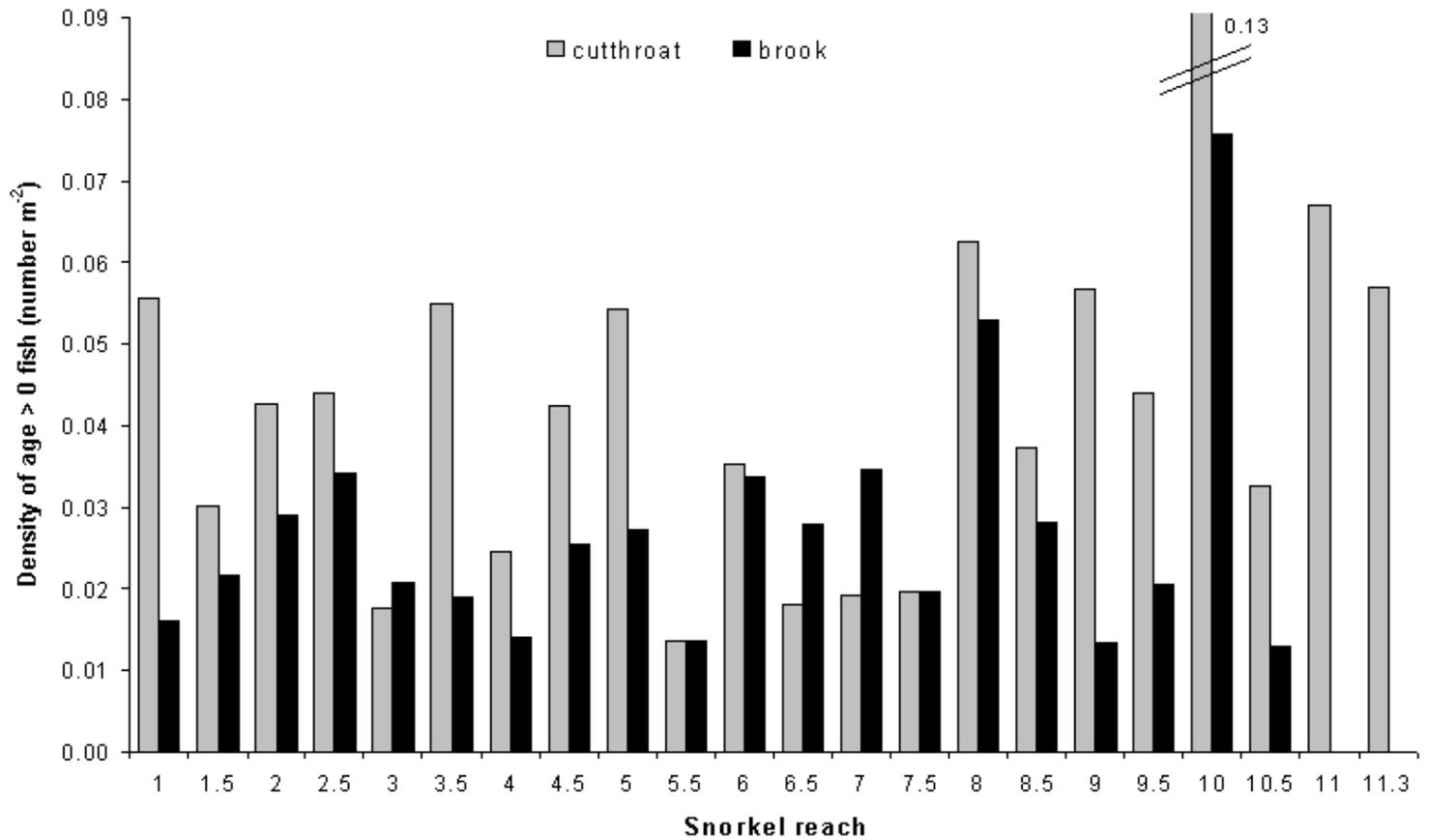


Figure 8. Areal densities (number per [S2] 100 m<sup>2</sup>) of cutthroat trout > 70 mm (estimated age > 0) and age > 0 brook trout in Twelvemile Creek, Montana. Density indices were derived from night snorkel counts conducted in August and September, 1997.

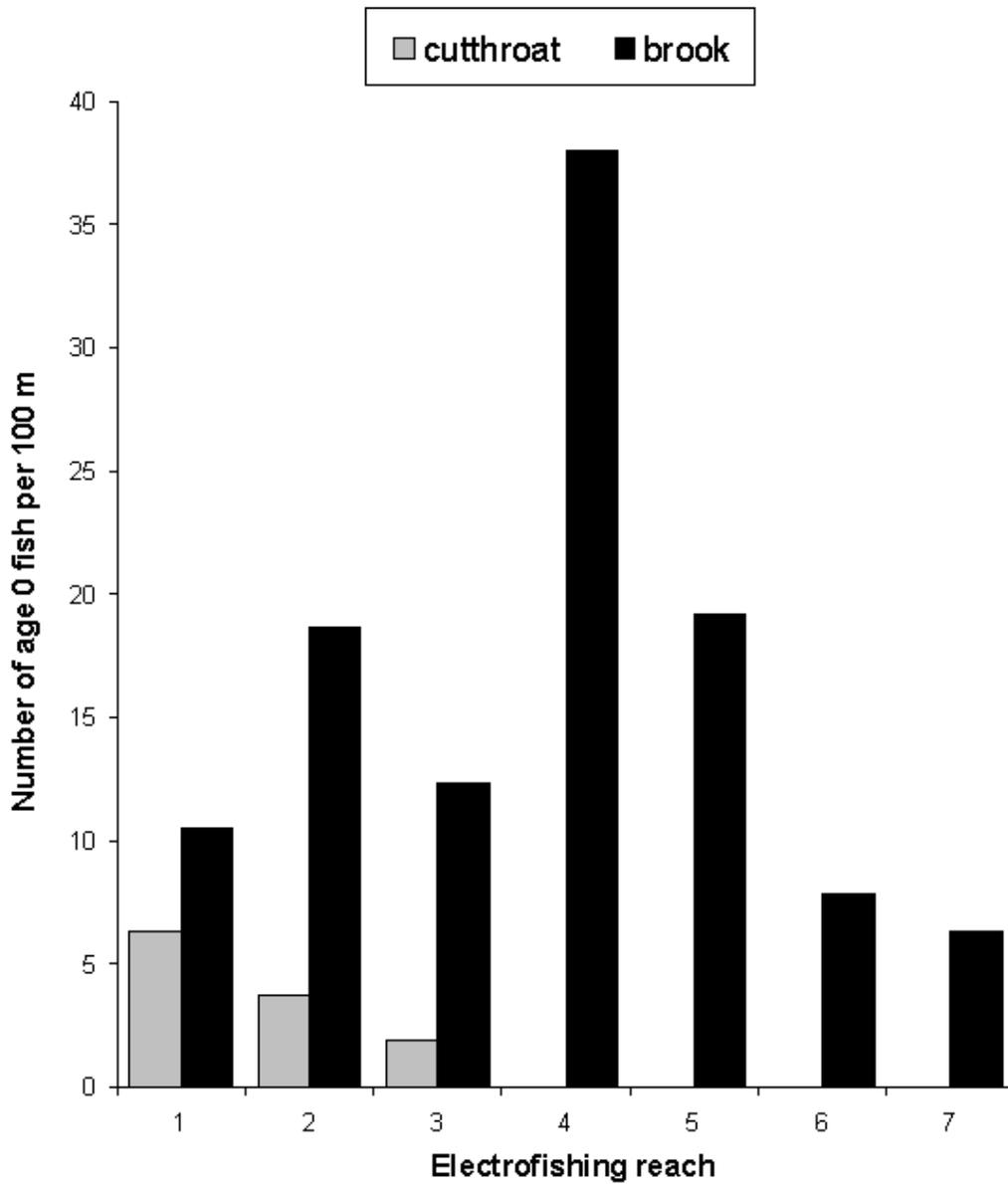


Figure 9. Linear densities (number per 100 m) of cutthroat trout  $\geq$  55 mm (estimated age 0) and age 0 brook trout in Moore Creek, Montana. Density indices are based on 2-pass electrofishing in September and early October, 1997.

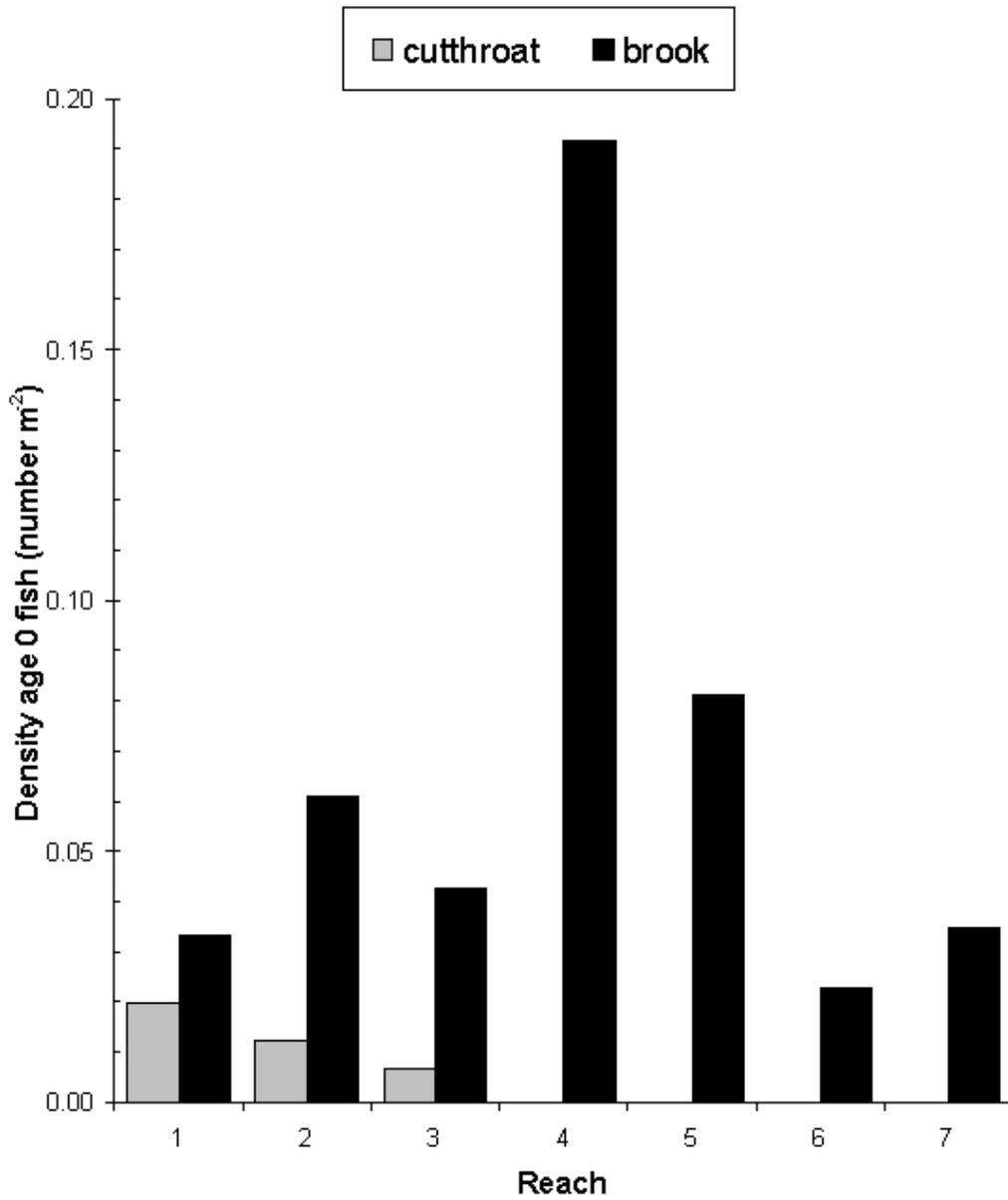


Figure 10. Areal densities (number per [S3](#) 100 m<sup>2</sup>) of cutthroat trout  $\leq$  55 mm (estimated age 0) and age 0 brook trout in Moore Creek, Montana. Density indices are based on the number of fish captured during 2-pass electrofishing in September and early October, 1997.

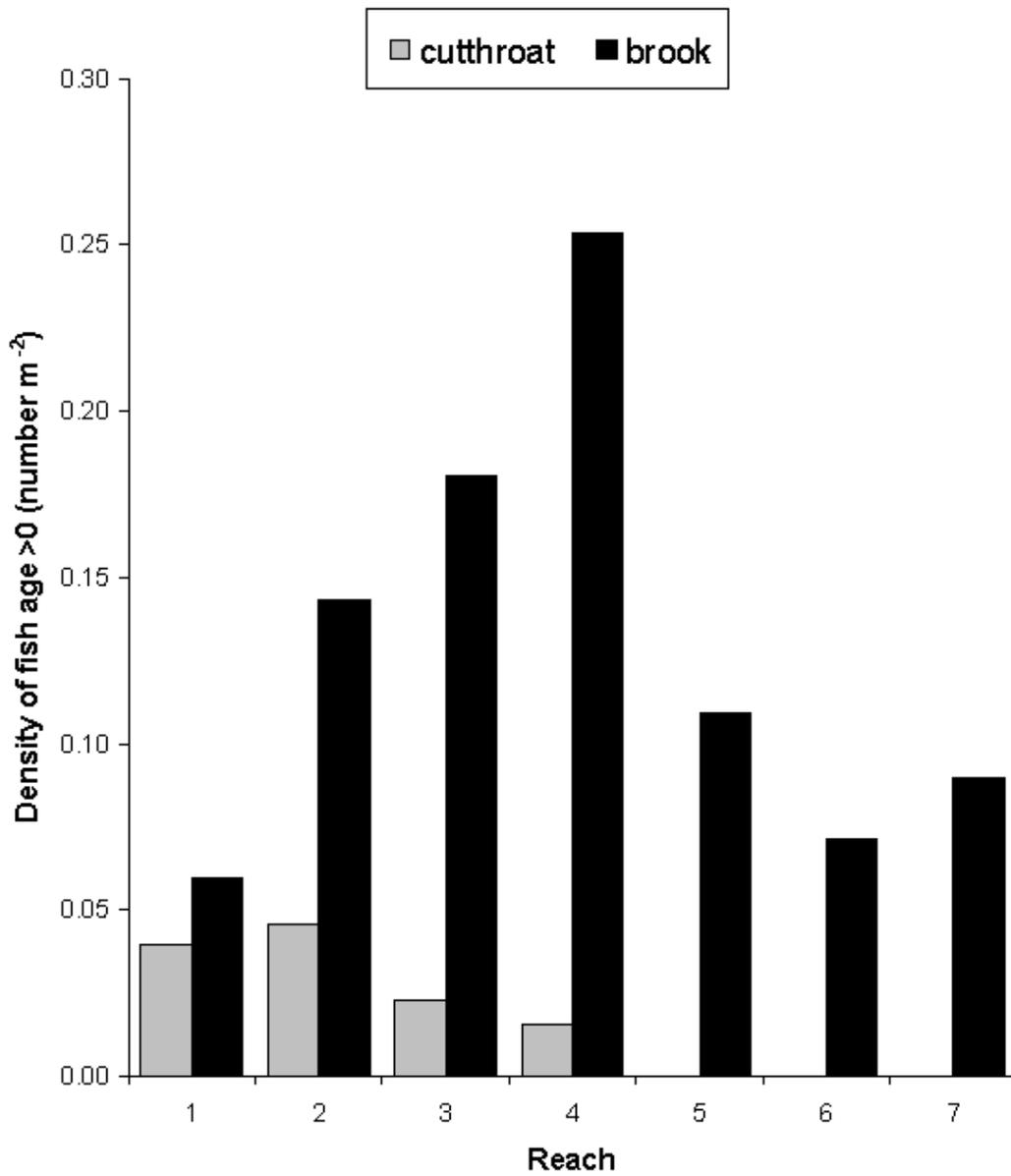


Figure 11. Areal densities (number per [\[S4\]](#) 100 m<sup>2</sup>) of cutthroat trout > 55 mm (estimated age > 0) and age 0 brook trout in Moore Creek, Montana. Density indices are based on the number of fish captured during 2-pass electrofishing in September and early October, 1997.

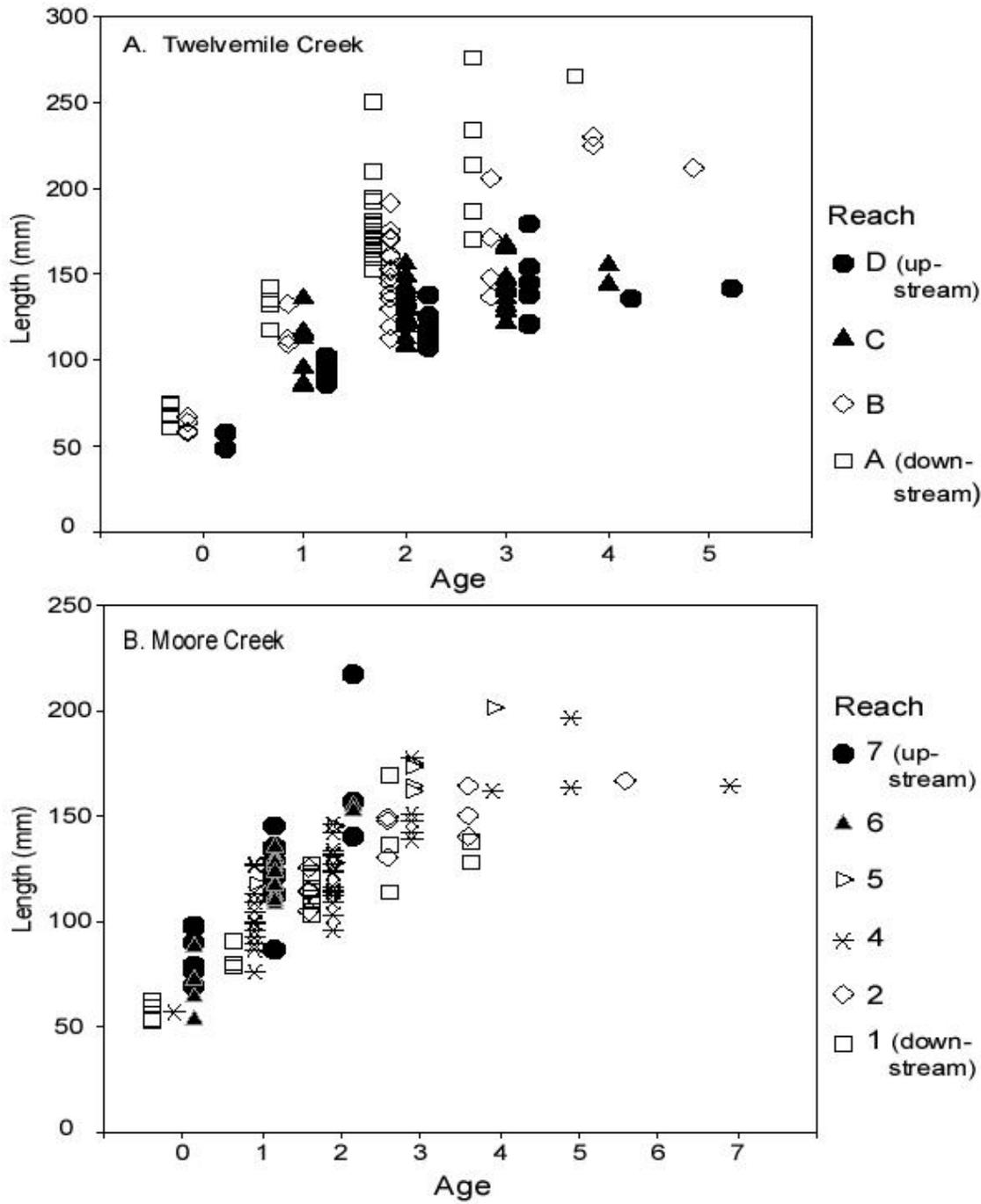


Figure 12. Age and total length of brook trout aged by otoliths. Fish were collected in September and early October, 1997, from Twelvemile (A) and Moore (B) creeks, Montana.

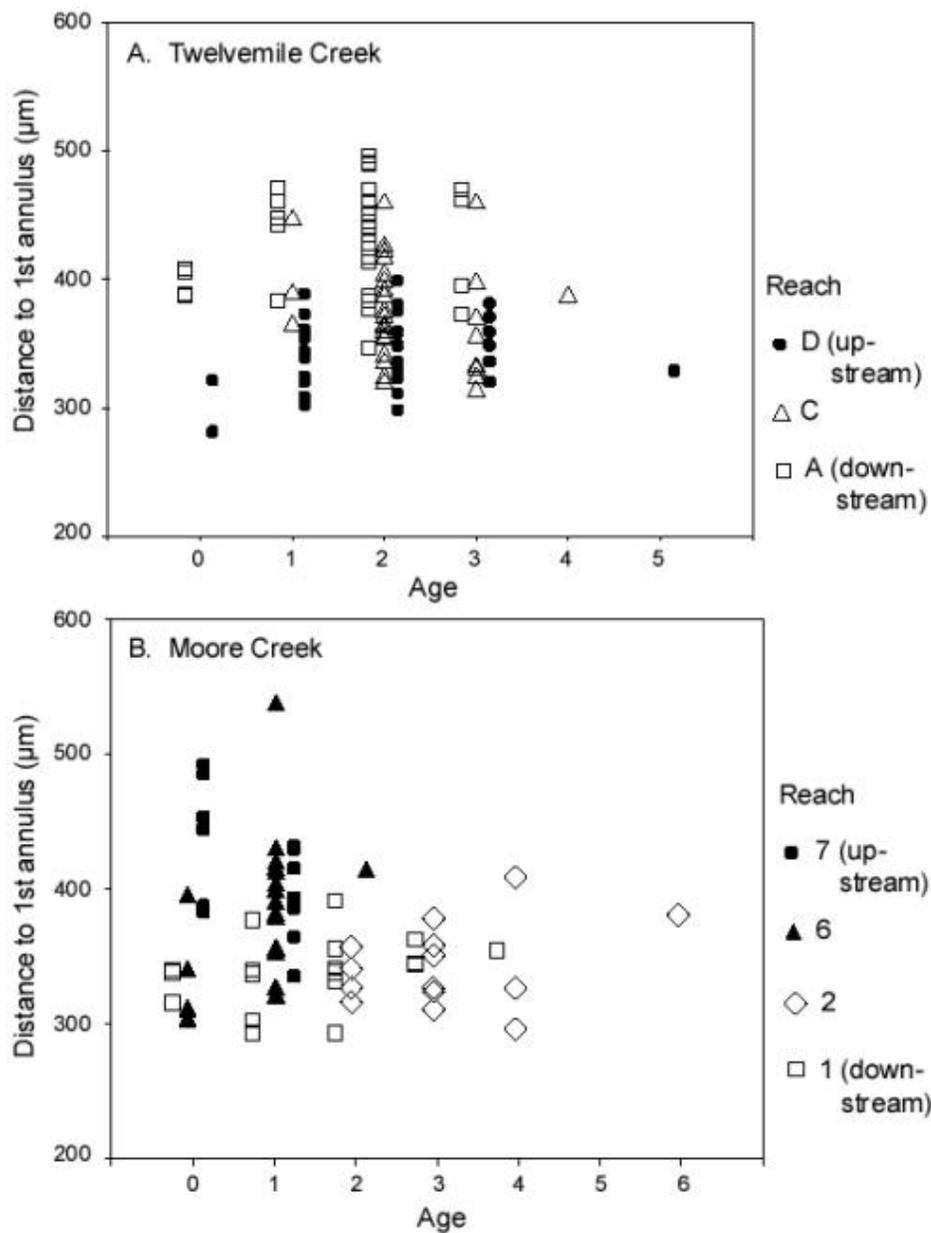


Figure 13. Distance from the core of the sagitta to the first in annulus for brook trout of various ages from Twelvemile (A) and Moore (B) creeks, Montana. Fish were collected in September and October, 1997. For age 0 fish, which had not yet formed annuli, the distance shown is from the core to the edge of the otolith and does not represent complete growth for the first year of life.

Figures on following pages:

Figure 14. Length-frequency histograms of brook trout collected in September 1997 from four reaches of Twelvemile Creek, Montana. All brook trout captured, those aged by otoliths as well as those whose ages were estimated, are included in the histograms.

Figure 15. Length-frequency histograms of brook trout collected in September and early October 1997 from seven, 100-m-long reaches of Moore Creek, Montana. All brook trout captured, those aged by otoliths as well as those whose ages were estimated, are included in the histograms.

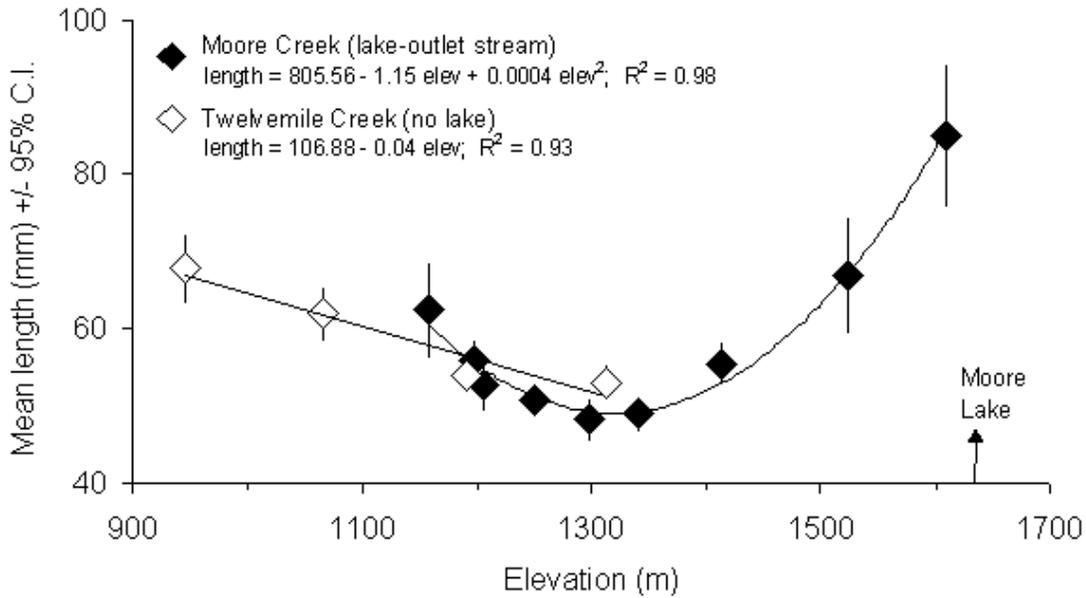


Figure 16. Mean lengths of age 0 brook trout from Twelvemile and Moore/South Fork Little Joe (SFLJ) creeks, Montana, versus elevation of reach where fish were collected. In the Moore Creek/SFLJ system, stream temperatures were highest at the outlet of Moore Lake. With distance downstream, temperatures cooled dramatically and then warmed slightly. In Twelvemile Creek, the warmest temperatures were at the downstream site. Bars represent 95% confidence intervals. Fish were collected between 11 September and 6 October, 1997.

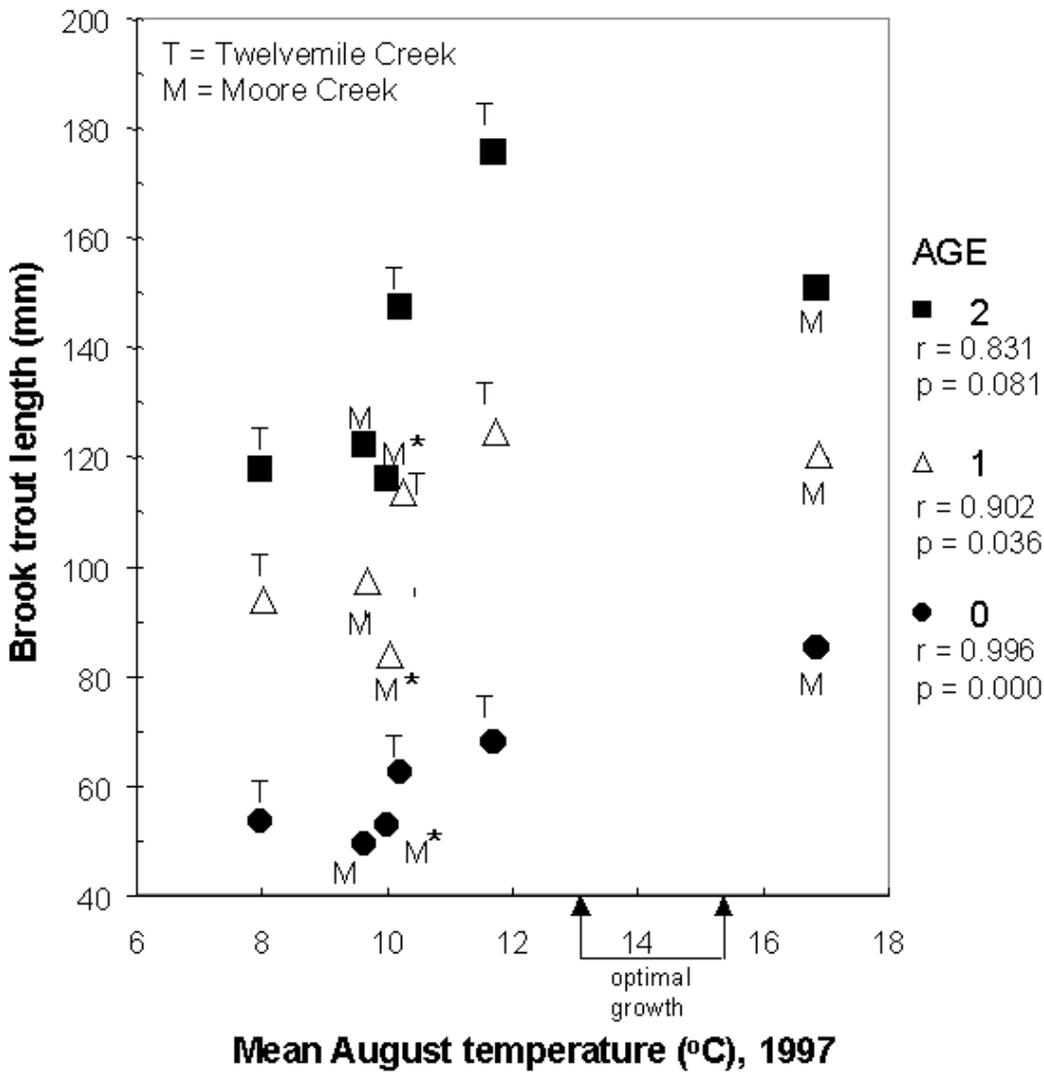


Figure 17. Mean lengths of age 0, 1, and 2 brook trout in September/October 1997 versus mean August stream temperature recorded near or in the reach where the fish were sampled. Beneath each age are the partial correlation coefficients of fish length and stream temperature, controlling for stream. The "M" marked by an asterisk represents Moore Creek reach 1. Optimal growth of brook trout in a laboratory setting occurs at a temperature of about 13 °C (see Discussion). I show data for Moore Creek reaches 1, 4, and 7 and Twelvemile Creek areas A, B, and D.

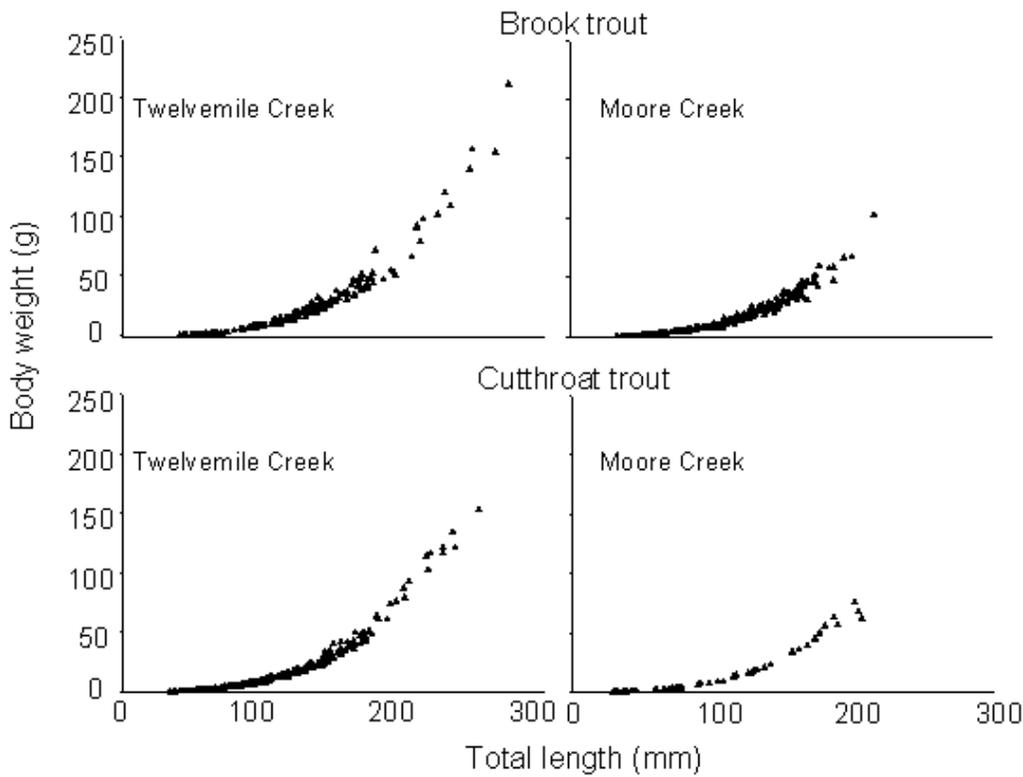


Figure 18. Body weight (excludes gonad weight for mature brook trout) versus total length of brook and cutthroat trout collected in September/October 1997 in the two study streams. Fish from all reaches are included.

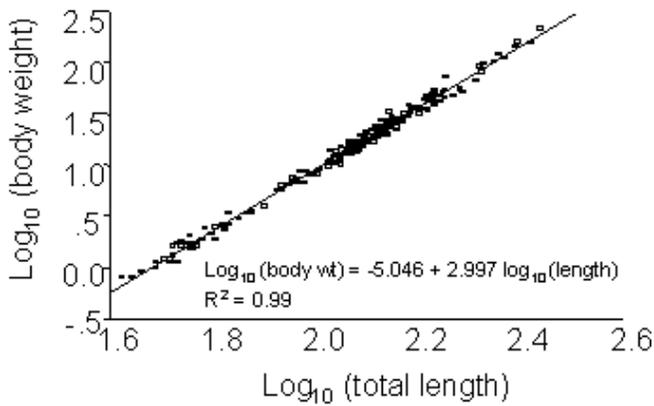


Figure 19.  $\log_{10}$  body weight (excludes gonad weight for mature fish) versus  $\log_{10}$  total length of brook trout collected in September 1997 from Twelvemile Creek, Montana. The linear regression line and equation are shown.

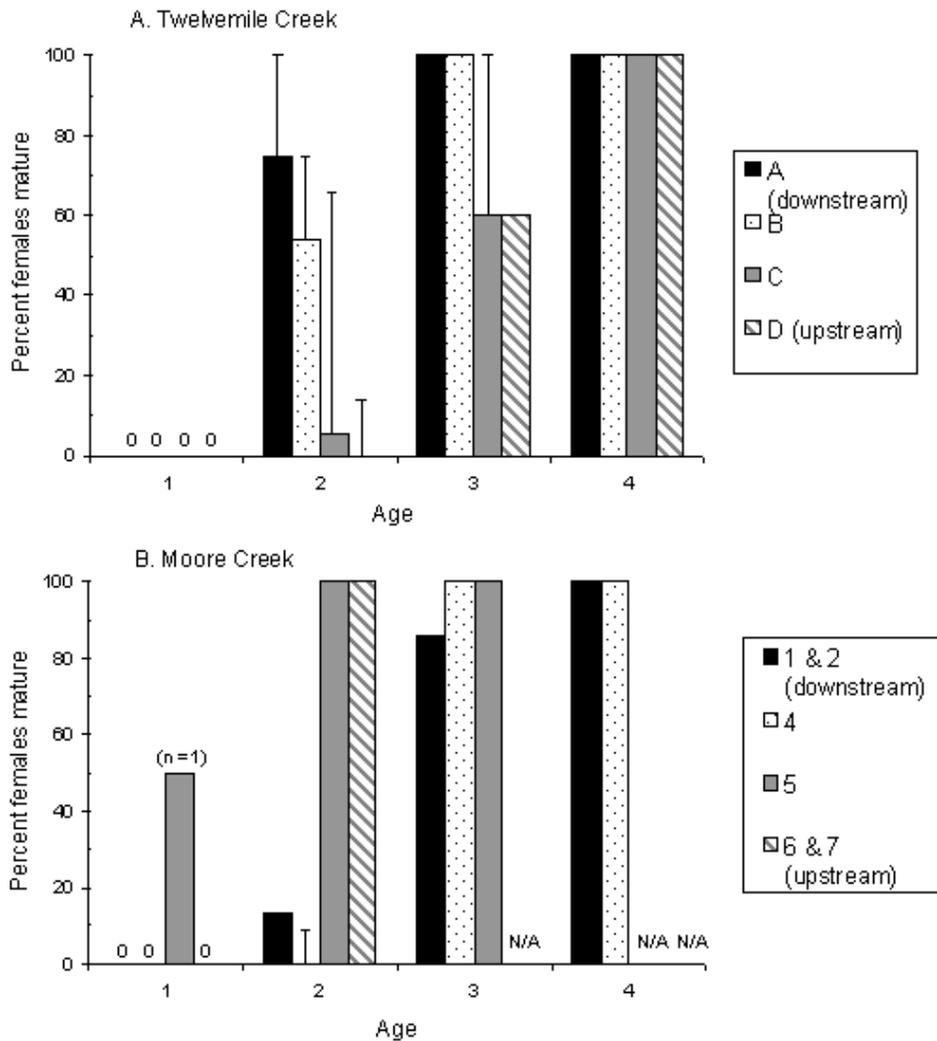


Figure 20. Percent of female brook trout ages 1 through 4 that were mature in each sampling reach of Twelvemile Creek (A) and Moore Creek (B) in September/October 1997. I found one age 1 female that was mature. The error bars represent the potential error in measuring maturity. Sources of error were my inability to sex some immature fish and uncertainty about whether some females were immature or spent. The columns represent my best estimates of the percent of females mature. "N/A" indicates that no females in the age group were collected from the reach.

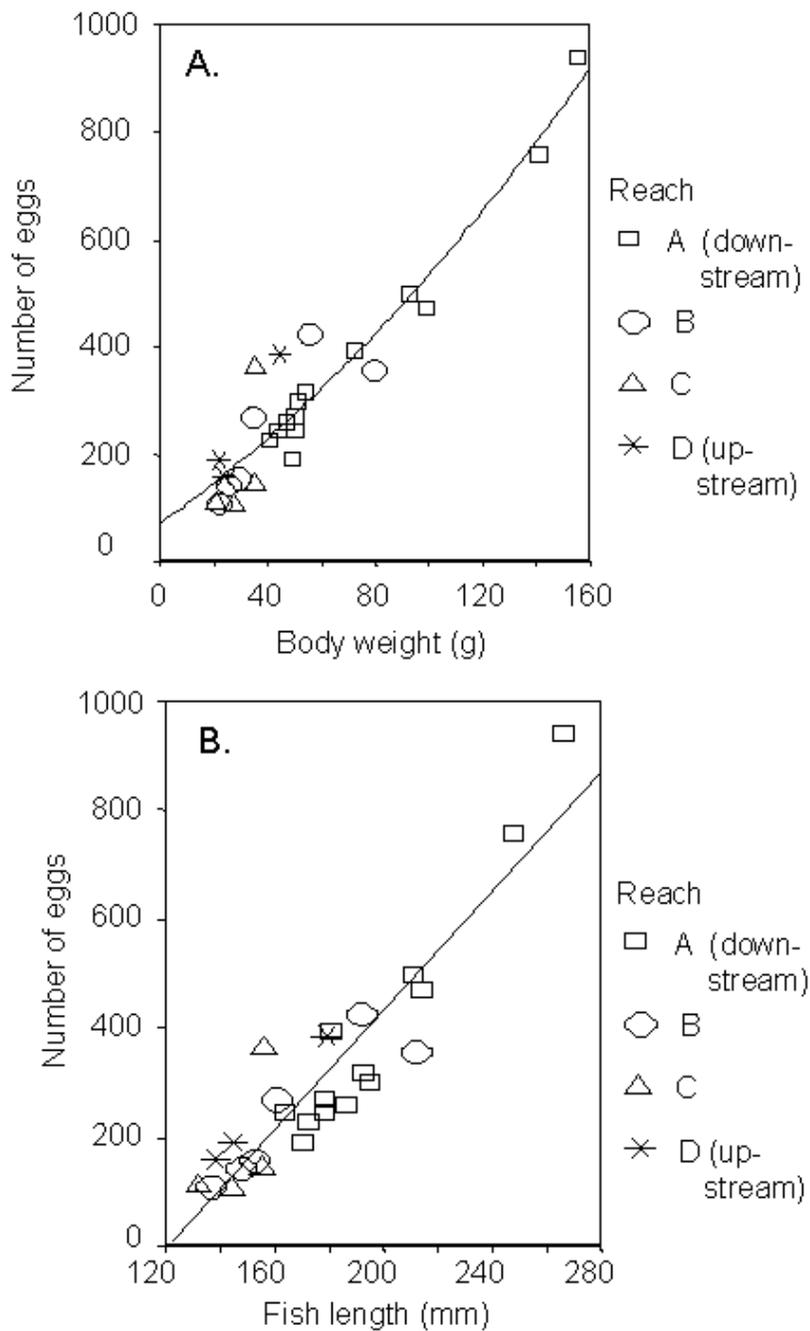


Figure 21. Plots of the number of eggs versus body weight (A) and versus total length (B) for female brook trout collected in September 1997 from Twelvemile Creek, Montana. Body weight excludes gonad weight. Regression equations are given in Table 6. Females that may have started spawning or that had egg counts that were low outliers are excluded.

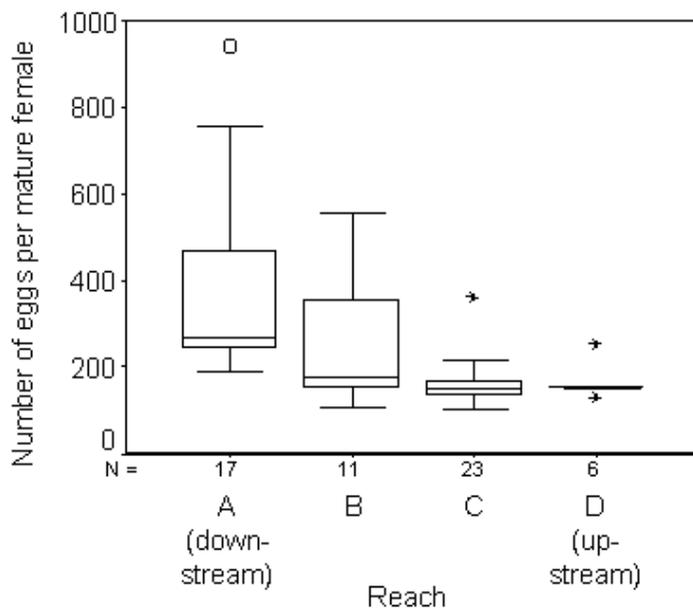


Figure 22. Box plots of the number of eggs per mature female for four reaches of Twelvemile Creek, Montana. Horizontal lines are medians, and boxes enclose the 75<sup>th</sup> and 25<sup>th</sup> percentiles. Outliers further than 1.5 times the box length from the median are indicated by asterisks and circles. Females for which I estimated the number of eggs based on the equation in Table 6 are included. The number of females is indicated.

## Appendix A. Habitat Data

Table A1. Physical characteristics of snorkel reaches in Twelvemile Creek and electrofishing reaches in Moore and South Fork Little Joe (SFLJ) creeks. Measurements were taken during low water in early autumn. Total area includes main channel and side channel areas. Channel slope was measured with a rod and level except were otherwise indicated. Percent pools is the percent of the reach length that was pool habitat. The average of the maximum depths of all pools in each reach is shown (avg. max. pool depth).

Stream	Reach	Elevation (m)	Reach length (m)	Average wetted width (m)	Main channel area (m <sup>2</sup> )	Side Channel area (m <sup>2</sup> )	Total area (m <sup>2</sup> )	Channel slope (%)	Average bankfull width (m)	Percent pools	Avg. max. pool depth (m)
12-mile	1	957	101.1	5.52	558.1	0.0	558.1	2.07	8.46	54	0.69
12-mile	1.5	975	103.9	5.77	599.1	49.1	648.2	2.22	8.23	31	0.66
12-mile	2	985	95.4	6.13	585.1	0.0	585.1	2.49	8.63	44	0.69
12-mile	2.5	1009	94.6	9.60	908.2	76.2	984.4	1.76	11.94	53	0.84
12-mile	3	1024	95.3	6.56	625.2	50.8	675.9	2.21	9.38	27	0.56
12-mile	3.5	1036	101.1	5.75	581.3	223.1	804.4	2.08	8.82	50	0.77
12-mile	4	1045	91.9	6.23	572.8	0.0	572.8	2.30	8.06	15	0.68
12-mile	4.5	1058	105.1	5.60	588.6	12.8	601.4	1.26	9.20	74	0.57
12-mile	5	1079	98.1	5.63	552.1	83.1	635.2	1.68	6.74	49	0.47
12-mile	5.5	1088	95.3	7.68	732.2	10.9	743.1	1.99	10.06	53	0.53
12-mile	6	1100	96.8	6.74	652.4	0.0	652.4	2.44	8.90	56	0.58
12-mile	6.5	1116	98.3	6.20	609.5	26.0	635.5	3.11	8.98	38	0.54
12-mile	7	1143	101.7	5.12	520.3	0.0	520.3	3.52	6.76	30	0.52
12-mile	7.5	1161	91.8	4.98	457.4	0.0	457.4	3.40	6.31	30	0.40
12-mile	8	1192	95.1	5.55	527.8	13.9	541.7	4.00	6.55	62	0.46
12-mile	8.5	1210	98.8	3.25	321.1	0.0	321.1	4.18	4.53	38	0.39
12-mile	9	1253	93.0	3.22	299.1	9.9	309.0	4.13	5.26	50	0.40
12-mile	9.5	1271	96.0	3.55	340.8	28.2	369.0	5.09	5.53	46	0.39
12-mile	10	1314	91.7	2.73	250.6	0.0	250.6	4.43	3.68	22	0.43
12-mile	10.5	1362	109.8	4.20	461.2	9.5	470.6	8.12	4.68	33	0.43
12-mile	11	1420	95.0	3.62	343.5	3.5	347.0	6.26	5.36	35	0.37
12-mile	11.25	1463	96.2	2.55	245.3	0.0	245.3	8.12	3.51	56	0.39
12-mile	11.5	1487	96.3	2.50	240.8	n/a	240.8	7.15	2.98	55	0.40
12-mile	11.75	1500	109.7	1.78	195.6	n/a	195.6	7.82	3.13	28	0.41

MECHANISMS LIMITING A VERTEBRATE INVASION:

SFLJ	1	1158	110.0	8.04	884.4	74.8	959.2	7.34 <sup>a</sup>	14.00	72	0.64
SFLJ	2	1198	107.5	6.06	651.5	35.3	686.8	6.90 <sup>a</sup>	7.90	46	0.66
Moore	1	1207	95.2	3.17	301.5	0.0	301.5	13.28 <sup>a</sup>	4.72	36	0.467
Moore	2	1250	107.1	3.07	328.4	0.0	328.4	15.19 <sup>a</sup>	4.20	52	0.432
Moore	3	1298	105.5	2.88	304.2	0.0	304.2	11.03 <sup>a</sup>	3.78	62	0.435
Moore	4	1341	97.4	1.98	193.2	0.0	193.2	10.69 <sup>a</sup>	2.80	29	0.384
Moore	5	1414	104.4	2.10	219.2	27.6	246.9	11.67	4.36	16	0.367
Moore	6	1524	102.4	2.73	279.9	73.4	353.3	13.29	3.72	12	0.308
Moore	7	1609	94.5	1.77	167.0	4.9	171.8	19.17	3.00	29	0.228

<sup>a</sup>. Slopes were measured with a clinometer, and the channel slope reported is the mean of the slopes measured within the reach weighted by the distance over which each slope was measured.

## Appendix B. Fish Data

Table B1. Numbers and densities of brook and cutthroat (cutt.) trout observed while snorkeling at night in Twelvemile Creek, Montana in August and September 1997. The relatively large number of unidentified (unident.) salmonids in reaches 1 and 5 were due to one inexperienced observer on one night. Based on the sizes of the unidentified fish, I inferred that at least 60 % in reach 1 and 50 % in reach 5 were cutthroat trout. The area measure used to calculate densities of age 0 fish included side channel areas (Table A1). Side channel areas were *not* included in density calculations of older/larger fish.

Reach	Reach length (m)	Number cutt. £70 mm	Number brook age 0	Number unident. salmonids £70 mm	Number cutt. > 70 mm	Number brook > age 0	Number unident. salmonids > 70 mm	Number sculpin	Density cutt. £70 mm (# / m2)	Density brook age 0 (# / m2)	Density unident. salmonids £70 mm (# / m2)	Density cutt. > 70 mm (# / m2)	Density brook > age 0 (# / m2)
1	101.1	14	7	12	31	9	1	9	0.025	0.013	0.022	0.056	0.016
1.5	103.9	13	7	0	18	13	2	4	0.020	0.011	0.000	0.030	0.022
2	95.4	20	2	1	25	17	0	10	0.034	0.003	0.002	0.043	0.029
2.5	94.6	18	38	0	40	31	0	15	0.018	0.039	0.000	0.044	0.034
3	95.3	14	6	0	11	13	0	12	0.021	0.009	0.000	0.018	0.021
3.5	101.1	28	5	2	32	11	0	13	0.035	0.006	0.003	0.055	0.019
4	91.9	12	0	2	14	8	0	6	0.021	0.000	0.003	0.024	0.014
4.5	105.1	21	2	2	25	15	0	16	0.035	0.003	0.003	0.042	0.025
5	98.1	16	20	11	30	15	4	20	0.025	0.031	0.020	0.054	0.027
5.5	95.3	39	7	2	10	10	0	21	0.052	0.009	0.003	0.014	0.014
6	96.8	16	11	0	23	22	0	24	0.025	0.017	0.000	0.035	0.034
6.5	98.3	6	6	0	11	17	0	12	0.009	0.009	0.000	0.018	0.028
7	101.7	9	0	0	10	18	0	7	0.017	0.000	0.000	0.019	0.035
7.5	91.8	2	5	1	9	9	0	11	0.004	0.011	0.002	0.020	0.020
8	95.1	14	2	0	33	28	0	13	0.026	0.004	0.000	0.063	0.053
8.5	98.8	7	5	1	12	9	0	6	0.022	0.016	0.003	0.037	0.028
9	93.0	3	0	0	17	4	1	14	0.010	0.000	0.000	0.057	0.013
9.5	96.0	5	0	0	15	7	1	10	0.014	0.000	0.000	0.044	0.021
10	91.7	13	8	0	33	19	1	1	0.052	0.032	0.000	0.132	0.076
10.5	109.8	1	0	2	15	6	0	0	0.002	0.000	0.004	0.033	0.013
11	95.0	10	0	0	23	0	0	0	0.029	0.000	0.000	0.067	0.000
11.25	96.2	3	0	0	14	0	0	0	0.012	0.000	0.000	0.057	0.000
11.5	96.3	0	0	0	0	0	0	0	0.000	0.000	0.000	0.000	0.000
11.75	109.7	0	0	0	0	0	0	0	0.000	0.000	0.000	0.000	0.000

Table B2. Numbers and densities of brook and cutthroat trout captured during the first two electrofishing passes in Moore Creek, MT, in late September and early October 1997. The area measure used to calculate densities of age 0 fish included side channel areas (Table A1). Side channel areas were *not* included in density calculations of older/larger fish.

MECHANISMS LIMITING A VERTEBRATE INVASION:

Reach	Reach length (m)	Number cutthroat <=55 mm	Number brook age 0	Number cutthroat > 55 mm	Number brook > age 0	Density cutthroat <= 55 mm (# / m2)	Density brook age 0 (# / m2)	Density cutthroat > 55 mm (# / m2)	Density brook >age 0 (# / m2)
1	95.2	6	10	12	18	0.020	0.033	0.040	0.060
2	107.1	4	20	15	47	0.012	0.061	0.046	0.143
3	105.5	2	13	7	55	0.007	0.043	0.023	0.181
4	97.4	0	37	3	49	0.000	0.192	0.016	0.254
5	104.4	0	20	0	24	0.000	0.081	0.000	0.109
6	102.4	0	8	0	20	0.000	0.023	0.000	0.071
7	94.5	0	6	0	15	0.000	0.035	0.000	0.090

Table B3. Means, standard deviations (st. dev.), and ranges of total lengths of brook trout captured by electrofishing from four areas of Twelvemile Creek, Montana, in September 1997. Included are fish aged by their otoliths and fish for which I estimated ages. N = number of fish.

Reach		Age					
		0	1	2	3	4	5
Reach A (down-stream)	Mean	67.7	124.5	175.2	223.6	266	---
	St. dev.	7.818	13.416	13.6	35.22	---	---
	Range	54-80	109-143	153-210	170-276	---	---
	N	12	8	18	8	1	---
Reach B	Mean	61.9	113.6	147	165.5	227.5	212
	St. dev.	5.821	7.844	21.342	30.49	3.536	---
	Range	52-72	107-133	112-192	137-206	225-230	---
	N	10	9	20	4	2	1
Reach C	Mean	54	106.2	130.4	144.4	153	---
	St. dev.	1.414	16.962	10.153	13.381	8.185	---
	Range	53-55	85-136	108-156	122-171	144-160	---
	N	2	9	30	16	3	---
Reach D (up-stream)	Mean	53.1	94.3	117.4	138.3	136	142
	St. dev.	5.275	4.968	7.802	20.548	---	---
	Range	42-60	86-102	107-138	121-179	---	---
	N	18	14	14	8	1	1
<i>All fish</i>	<i>Mean</i>	<i>59.4</i>	<i>107.4</i>	<i>142.05</i>	<i>163</i>	<i>188</i>	<i>177</i>
	<i>St. dev.</i>	<i>8.743</i>	<i>15.587</i>	<i>24.45</i>	<i>40.34</i>	<i>51.202</i>	<i>49.498</i>
	<i>Range</i>	<i>42-80</i>	<i>85-143</i>	<i>107-210</i>	<i>121-276</i>	<i>136-266</i>	<i>142-212</i>
	<i>N</i>	<i>42</i>	<i>40</i>	<i>82</i>	<i>36</i>	<i>7</i>	<i>2</i>

Table B4. Means, standard deviations (st. dev.), and ranges of total lengths of brook trout captured by electrofishing from seven reaches of Moore Creek, Montana, in late September and early October 1997. Included are fish aged by their otoliths and fish for which I estimated ages. N = number of fish.

Reach		Age							
		0	1	2	3	4	5	6	7
Reach 1 (down-stream)	Mean	52.5	84	115.6	136	143.7	188	---	---
	St. dev.	5.84	6.442	8.541	20.286	19.14	---	---	---
	Range	43-63	78-91	103-127	114-169	128-165	---	---	---
	N	13	5	7	5	3	1	---	---
Reach 2	Mean	50.6	87.9	118.2	137.2	152.3	---	168	---
	St. dev.	3.268	6.6	5.21	8.077	12.66	---	1.414	---
	Range	45-59	77-99	105-125	125-152	135-164	---	167-169	---
	N	20	8	13	18	6	---	2	---
Reach 3	Mean	48.2	92.5	118.4	137.9	156	172	---	---

MECHANISMS LIMITING A VERTEBRATE INVASION:

	St. dev.	5.134	13.907	6.768	10.643	5.657	8.246		
	Range	38-60	75-115	105-130	129-160	152-160	165-185		
	N	13	17	23	8	2	5		
Reach 4	Mean	48.9	97.7	121.7	147.5	159.7	179.5	---	164
	St. dev.	7.472	16.101	13.94	13.038	40.42	23.335		---
	Range	34-68	76-127	96-146	136-177	155-162	163-196		---
	N	40	21	19	8	3	2		1
Reach 5	Mean	55.45	105.67	138.625	166.167	201	---	---	---
	St. dev.	6.565	11.59	7.405	10.521	---			
	Range	45-64	95-118	127-146	152-188	---			
	N	20	3	8	12	1			
Reach 6	Mean	67	121.4	156.5	---	---	---	---	---
	St. dev.	11.007	8.157	12.61					
	Range	54-88	108-135	144-174					
	N	8	16	4					
Reach 7 (lake outlet)	Mean	85	120.2	150.5	217	---	---	---	---
	St. dev.	11.781	17.1	7.594	---				
	Range	69-98	87-145	140-157	---				
	N	6	10	4	1				
<i>All fish</i>	<i>Mean</i>	<i>54.2</i>	<i>105.3</i>	<i>127.2</i>	<i>148.7</i>	<i>155.8</i>	<i>175.88</i>	<i>168</i>	<i>164</i>
	<i>St. dev.</i>	<i>11.34</i>	<i>18.78</i>	<i>16.399</i>	<i>19.694</i>	<i>18.6</i>	<i>12.334</i>	<i>1.414</i>	<i>---</i>
	<i>Range</i>	<i>34-98</i>	<i>76-145</i>	<i>96-174</i>	<i>114-217</i>	<i>128-201</i>	<i>163-196</i>	<i>167-169</i>	<i>---</i>
	<i>N</i>	<i>107</i>	<i>63</i>	<i>55</i>	<i>44</i>	<i>13</i>	<i>8</i>	<i>2</i>	<i>1</i>

Table B5. Means, standard errors (S.E.), and ranges of body weights of brook trout captured by electrofishing from four areas of Twelvemile Creek, Montana, in September 1997. Body weight excludes gonad weight for mature fish. Included are fish aged by their otoliths and fish for which I estimated ages. N = number of fish.

		Age						
Site		0	1	2	3	4	5	
Reach A (down- stream)	Mean	2.86	17.38	48.81	113.73	155.30	---	
	S.E.	0.192	2.245	3.293	19.624	---		
	Range	1.7-3.9	11.1-27.8	33.5-91.0	47.5-212.2	---		
	N	12	8	18	8	1		
Reach B	Mean	1.80	12.04	27.21	40.40	111.55	79.40	
	S.E.	0.138	0.957	2.607	10.24	8.95	---	
	Range	1.1-2.4	9.5-18.8	11.3-55.6	21.9-66.0	102.6-120.5	---	
	N	9	9	20	4	2	1	
Reach C	Mean	1.70	11.31	21.37	29.66	33.27	---	
	S.E.	0.1	1.675	0.941	2.575	2.826		
	Range	1.6-1.8	5.7-20.5	13.8-35.7	17.1-52.8	27.7-36.9		
	N	2	9	30	16	3		
Reach D (up- stream)	Mean	1.36	7.60	14.76	23.14	22.80	23.30	
	S.E.	0.084	0.281	0.926	3.789	---	---	
	Range	0.8-1.9	5.6-9.1	10.6-24.9	13.6-45.0	---	---	
	N	18	14	14	8	1	1	
<i>All fish</i>	<i>Mean</i>	<i>1.91</i>	<i>11.39</i>	<i>27.69</i>	<i>48.09</i>	<i>71.57</i>	<i>51.35</i>	
	<i>S.E.</i>	<i>0.123</i>	<i>0.823</i>	<i>1.665</i>	<i>7.471</i>	<i>20.234</i>	<i>28.05</i>	
	<i>Range</i>	<i>0.8-3.9</i>	<i>5.6-27.8</i>	<i>10.6-91.0</i>	<i>13.6-212.2</i>	<i>22.8-155.3</i>	<i>23.3-79.4</i>	
	<i>N</i>	<i>41</i>	<i>40</i>	<i>82</i>	<i>36</i>	<i>7</i>	<i>2</i>	

Table B6. Means, standard errors (S.E.), and ranges of body weights of brook trout captured by electrofishing from seven reaches of Moore Creek, Montana, in late September and early October 1997. Body weight excludes gonad weight for mature fish, except those from reach 3. Included are fish aged by their otoliths and fish for which I estimated ages. N = number of fish.

Reach		Age							
		0	1	2	3	4	5	6	7
Reach 1 (down- stream)	Mean	1.26	4.86	12.76	23.64	24.43	47.20	---	---
	S.E.	0.0988	0.595	1.017	5.886	6.288	---	---	---
	Range	0.8-1.9	3.7-6.5	9.5-17.6	12.3-46.2	15.1-36.4	---	---	---
	N	12	5	7	5	3	1	---	---
Reach 2	Mean	1.04	5.96	13.86	23.56	31.15	---	31.45	---
	S.E.	0.0467	0.515	0.543	0.879	3.917	---	1.55	---
	Range	.7-1.5	3.9-8.2	10.2-16.7	16.0-28.9	21.2-42.2	---	29.9-33.0	---
	N	20	7	13	18	6	---	2	---
Reach 3 <sup>a</sup>	Mean	1.00	7.86	15.90	25.90	36.80	47.40	---	---
	S.E.	0.0892	0.865	0.792	2.041	0.8	3.423	---	---
	Range	.6-1.8	3.7-13.9	10.1-25.9	19.9-36.7	36.0-37.6	36.8-57.6	---	---
	N	13	17	23	8	2	5	---	---
Reach 4	Mean	1.00	8.12	15.56	26.11	29.73	50.60	---	40.60
	S.E.	0.0813	0.87	1.258	2.476	0.328	15.9	---	---
	Range	.2-2.7	3.9-16.9	7.2-25.9	18.4-41.3	29.1-30.2	34.7-66.5	---	---
	N	40	21	19	8	3	2	---	1
Reach 5	Mean	1.44	10.07	21.63	40.47	67.20	---	---	---
	S.E.	0.103	1.889	1.668	2.976	---	---	---	---
	Range	.8-2.2	7.7-13.8	15.1-27.6	27.7-59.5	---	---	---	---
	N	20	3	8	12	1	---	---	---
Reach 6	Mean	2.74	15.69	42.50	---	---	---	---	---
	S.E.	0.614	0.812	4.665	---	---	---	---	---
	Range	1.3-5.9	11.1-21.6	37.2-51.8	---	---	---	---	---
	N	7	16	3	---	---	---	---	---
Reach 7 (lake outlet)	Mean	5.53	15.86	28.65	102.50	---	---	---	---
	S.E.	0.93	1.988	3.074	---	---	---	---	---
	Range	2.7-8.2	5.3-26.8	21.8-36.3	---	---	---	---	---
	N	6	10	4	1	---	---	---	---
<i>All fish</i>	<i>Mean</i>	<i>1.44</i>	<i>10.25</i>	<i>17.48</i>	<i>29.74</i>	<i>32.68</i>	<i>48.20</i>	<i>31.45</i>	<i>40.60</i>
	<i>S.E.</i>	<i>0.116</i>	<i>0.615</i>	<i>0.859</i>	<i>1.985</i>	<i>3.214</i>	<i>3.673</i>	<i>1.55</i>	<i>---</i>
	<i>Range</i>	<i>0.2-8.2</i>	<i>3.7-26.8</i>	<i>7.2-51.8</i>	<i>12.3-102.5</i>	<i>15.1-67.2</i>	<i>34.7-66.5</i>	<i>29.9-33.0</i>	<i>---</i>
	<i>N</i>	<i>118</i>	<i>79</i>	<i>77</i>	<i>52</i>	<i>15</i>	<i>8</i>	<i>2</i>	<i>1</i>

a. Weights included gonad weights for all fish in reach 3.

Table B7. Regression equations of log<sub>10</sub> body weight (g) on log<sub>10</sub> total length (mm) for cutthroat trout captured in late September and early October, 1997. All regressions and parameters are significant at p < 0.000.

Stream	Species	N	Constant	Slope	S.E. of estimate	R <sup>2</sup>
Twelvemile	cutthroat	281	-5.030	2.990	0.053	0.992
Moore	cutthroat	56	-5.043	2.985	0.067	0.994

# Chapter VI. Intrapopulation Variation in Nonnative Brook Trout Growth: demographic modelling of the potential for fish growth rate and source-sink dynamics to determine invasion limits

## Abstract

I used age-structured, time-invariant matrix models to explore whether slower brook trout growth upstream translates into reductions in population growth rate ( $\lambda$ ) sufficient to create the upstream distribution limit in Twelvemile Creek, Montana. I also evaluated the potential effects of several anthropogenic impacts on population growth. I used life-stage simulation analysis to estimate vital rate effects on  $\lambda$ . Assuming that slower brook trout growth is not largely compensated by increased survival, the subtle changes in fish growth rate upstream are sufficient to create an upstream distribution limit. Unless mean survival rates up to age 2 increased by 40 %, the upstream subpopulation should not persist ( $\lambda = 0.73$ ) without immigration from downstream. Simulations in Ramas / stage indicated that in the absence of any fishing, the downstream subpopulation could just provide the number of emigrants per 200 m needed to stabilize the upstream subpopulation. The results are consistent with the hypothesis that source-sink dynamics operate within stream populations of brook trout and may be an important factor in determining distribution limits. Fishing had a substantial influence on  $\lambda$  of the downstream subpopulation and has probably helped to limit the population size in the stream. A hypothetical scenario of stream restoration resulting in faster fish growth downstream led to explosive population growth that could support high rates of emigration and thus facilitate invasion of distant reaches.

The importance of most vital rates varied among matrices. Elasticity values and rankings were not necessarily good indicators of a vital rate's contribution to the variation in  $\lambda$  over the 500 replications of a matrix. Survival from egg to age 0 in the fall always had the greatest influence on  $\lambda$  by all measures. In general, variance in  $\lambda$  was attributable more to juvenile than adult survival rates. When the range of plausible vital rate values for the entire stream were simulated, maternity rates contributed a large part of the variance in  $\lambda$ .

Reach- or habitat-specific estimates of survival and dispersal rates are needed to better determine mechanisms creating upstream distribution limits. Insights into the roles of various factors, including interactions with native fishes, in reducing growth rate upstream may assist in prediction and/or prevention of invasions. Finally, any proposed activities that may result in increased brook trout growth or survival rates should be evaluated for their potential to influence invasion of distant stream reaches.

## Introduction

The location of species and population distribution limits can be determined by multiple factors. One approach to studying processes creating distribution limits has been to examine environmental correlates, such as habitat characteristics or interspecific competition, at various sites encompassing the distribution limits (Hengeveld 1990). Another approach is to make inferences about processes creating limits based on demographic changes in the species from the distribution core to boundaries (Caughley et al. 1988; Hengeveld 1990). However, if source-sink dynamics are important within a population, demographic rates in a source area may contribute substantially to defining the population boundary (Pulliam 1988). Substantial reproduction may occur in a sink habitat, but if reproduction is inadequate to replace individuals lost by death or emigration, the subpopulation in the sink will decline unless supplemented by immigration from a source habitat (Pulliam 1988). In such a case, conditions in both the source and sink areas can influence the location of a distribution limit.

The concept of source-sink dynamics is important to invasion theory. In ongoing invasions, distribution limits are, by definition, expanding and the processes controlling the limits may be changing as well. However, it appears that many invasions progress irregularly, stalling in at least some directions before restarting, sometimes more rapidly than before (Johnson and Carlton 1996; Kot et al. 1996). One possible explanation for such irregular progression may be that a source area supports a population beyond the source boundaries. Eventually another source population forms, allowing the population to expand further (Shigesada et al. 1995). The new source population may result from colonization of new habitat, habitat alteration, release from negative interspecific interactions, local adaptation, or stochastic factors, among other possibilities.

In the context of stream fishes, understanding if and how source-sink dynamics influence population boundaries is important for several reasons. First, recognizing when source-sink dynamics are operating will allow people to better predict, and perhaps more effectively control, invasions. Second, by identifying whether localized source areas sustain a broader population, we can predict how alterations that result in demographic changes in a source area (or potential source area, e.g. a new reservoir) influence demographics in sink areas (e.g. tributary streams to a reservoir, as in Erman 1973; Crisp et al. 1984; and Penczak et al. 1984).

Brook trout populations in streams are excellent candidates for study of source-sink dynamics. Brook trout movements can be extensive, even in steep streams (Chapter II), and in many streams where invasions have stalled, limited dispersal ability is clearly not responsible (Chapter III). Furthermore, brook trout appear to persist in stream reaches where little or no reproduction occurs (Chapters II-IV). Reproduction and population densities are frequently high in meandering channels with gradual channel slopes or in beaver ponds (Thompson and Rahel 1996), while densities, and perhaps reproduction, are often lower in steeper stream reaches (Fausch 1989, but see Chapter II). Brook trout will move long distances and ascend steep streams (Chapter II), implying that downstream areas could supply fish to upstream areas. The fact that brook trout have successfully invaded so much of the West is testimony to their tendency to disperse from source populations and their ability to establish new source populations.

The patterns I observed in fish abundance and demographics are consistent with Schlosser and Angermeier's (1995) concept of a hybrid source-sink metapopulation model (hybrid model, hereafter) applicable to stream fishes and functioning at a within-stream scale. According to the hybrid model, source areas in the stream contribute more demographically than sink areas, subpopulations in the latter being supported by fish originating in the source areas. Within stream areas, patchy population processes operate.

Attention to intrapopulation demographic variation when considering population processes is useful for several reasons. Similar to the approach used by Caughley et al. (1988) to assess species distribution boundaries, examining trends in demographic rates from the core to the edge of a population distribution could help in identifying the factors and processes creating the population distribution limit. Ignoring intrapopulation spatial trends in brook trout demographics may lead to erroneous results in population modelling exercises. Hutchings (1993; 1994) demonstrated life history differences between brook trout populations in neighboring streams and suggested that life histories may be locally adapted at a small scale. I presented data on trends in maturity and fecundity within streams (Chapter V). Population models parameterized with data from one population (in Hutchings' case) or one portion of the population (in my case) and applied to the other may lead to erroneous results, such as grossly over- or underestimating the population growth rate.

At least six papers published since 1995 have described brook trout demographic models with various objectives (Power and Power 1995; Ries and Perry 1995; Marschall and Crowder 1996; Power 1996; Clark and Rose 1997b; Clark and Rose 1997a). While some of the models included individual- or population-level variation in demographic parameters, only one considered spatial ramifications (Ries and Perry 1995), and none included spatial differences in model parameterization. For predictions of population growth or persistence and of distribution expansion, spatial variation in demographics may be critical.

I applied matrix projection models to demographic data on brook trout from Twelvemile Creek, Montana (Chapter V), to explore four general questions:

- 1) Does the trend of slower individual brook trout growth upstream in Twelvemile Creek translate into lower subpopulation growth rates upstream? I expressed differences in fish growth in the models via changes in age at maturity, fecundity, and age at recruitment to the fishery. Survival estimates were taken from the literature. I compared subpopulation growth rates (as measured by the finite rate of increase,  $\lambda$ ) of fish from four reaches distributed along the length of Twelvemile Creek.
- 2) Do the demographic data support the hypothesis that source-sink dynamics help maintain the brook trout distribution in the stream? I used Ramas / stage to model various levels of emigration from the downstream subpopulation and immigration into the upstream subpopulation.
- 3) How are various levels of fishing pressure and increases in fish growth likely to influence invasion in the stream? I modelled four levels of fishing pressure in the upstream and downstream subpopulation. I also modelled an increase in fish growth resulting from a hypothetical stream restoration project in the downstream segment of Twelvemile Creek.
- 4) Which vital rates contribute the most to variations in  $\lambda$ ? I used life-stage simulation analysis (Wisdom et al. Accepted; Mills et al. In press) to analyze the sensitivity and empirical effects of the vital rates on  $\lambda$ .

## Terminology

Where terminology typically used in fisheries versus demography literature are at odds, I have tried to be consistent with the former. Fish are age 0 from the time of emergence from the gravel in the spring until January 1 of the next year. Thus age class 0 is equivalent to stage 1 in the matrix models. Egg to age 0 survival (Segg) refers to the survival rate of eggs just before spawning to age 0 fish the next fall. Thus, the first summer mortality of age 0 fish is included in Segg. Fecundity refers to the total egg complement in a mature fish (Snyder 1983). I refer to female eggs per mature female as "female fecundity", which I estimated as 50 % of fecundity. Maternity ( $M_x$ ) is the number of female eggs per female of age  $x$  and is equivalent to the life table  $m_x$  function (Caswell 1989). The fertility functions ( $F_x$ ) form the first row of a population projection matrix and represent the number of age 0 fish at time  $t+1$  per female of age  $x$  alive at time  $t$ .

## Methods

I used female-based, birth-pulse, prebreeding matrix projection models (Caswell 1989) for all exercises. Demographic data were collected in September and October just prior to (or during, see Chapter V) spawning from four reaches, each at least 300 m long, distributed along about 17 km of the stream (Chapter V, Figure 2, reaches A-D). The fertility functions in the matrices were the product of Segg and  $M_x$ . I assumed no female mortality occurred between the survey and spawning. Initial population estimates were used only in the Ramas / stage model, and modelled population trends were relatively insensitive to the initial age distribution (unpublished results).

## Age versus stage structure

Both age and stage models have been used to model brook trout populations. Marschall and Crowder (1996) used a stage-structured matrix model to explore the effects of anthropogenic impacts on brook trout populations. Power and Power (1995) compared an individual based model to an age-structured matrix model (Ramas Age) for examining the effects of contaminant stressors on population size and structure.

I chose to use an age-structured model because variation in the time required to reach a given stage (e.g. maturity) was one of the main points of interest. Within Twelvemile Creek, I found large differences among reaches in fish length, fecundity, and percent females mature at a given age (Chapter V). Age at maturity varied much more than length at maturity among sites. I did not have survival data, so one exercise of interest was to compare subpopulation growth rates using the same survival rates among subpopulations. To hold annual survival constant among reaches with different annual growth rates required using an age-structured model.

## Density-dependence

Density-dependence functions and the way they are incorporated into a model can have a large effect on the outcome of population viability models (Marschall and Crowder 1996; Mills et al. 1996), so including density-dependence functions based on wild guesses seems inadvisable. Based on extensive research, Elliott (1994) concluded that brown trout experience density-dependent mortality rates in the first two months after emergence. McFadden (1961) reached a similar conclusion for brook trout in Lawrence Creek, Wisconsin. Although this is likely true of stream salmonids in general, presumably the parameters of the density dependence function vary by species, region, stream reach, and year (McFadden 1961; Latta 1965, 1969). Reaches of Lawrence Creek differed significantly in both the number of nine month old fry produced and the relationship between the number of eggs and the fry mortality rate. Brook trout mortality appears to be typically density-independent after the first (McFadden 1961; Hunt 1969b; Power 1980) or second (McFadden et al. 1967) summer of life. Marschall and Crowder (1996) used data from brook and brown trout populations to parameterize a density dependence function for age 0 brook trout in their matrix model, and the function had a strong influence on the modelling results.

I did not include density-dependence in the models for several reasons. First, I had no data for parameterizing a density-dependence function for a nonnative brook trout population in the West. The highest age 0 brook trout densities in Twelvemile Creek were less than half the densities in Lawrence Creek, where McFadden (1961) reported density-dependence. Second, it is unknown how cutthroat trout densities influence density-dependent processes in brook trout. Therefore, I had little basis for extrapolating a density-dependence function from published data. I felt that it was more appropriate to exclude density dependence than to use data from a different region and a different genus to parameterize the function. Third, one of my main objectives was simulating the influence of variations in individual growth and fecundity on subpopulation growth, and neither brook trout growth (Cooper et al. 1962; Hunt 1969a) nor fecundity (McFadden et al. 1967) in streams is known to be density-dependent, except possibly at very high densities.

## Life-stage simulation analysis

Life-stage simulation analysis (LSA) is a probability-based approach to determining the vital rates that have the greatest influence on (Wisdom et al. Accepted; Mills et al. In press). LSA uses the results of a large number of randomly-generated replicates of matrices to evaluate the relationship between vital rates and lambda. In each replicate, values of each vital rate are randomly selected from an empirical or hypothetical probability distribution. Elasticities of vital rates and variance decomposition analysis are then used to analyze the effects of each rate on lambda over the range of values. In variance decomposition analysis, the values of in the replicates are regressed on the values of the vital rates. The resulting coefficient of determination ( $r^2$ ) indicates the variation in population growth rate accounted for by the vital rate. The  $r^2$  is a function of both the elasticity and the range of the vital rate. Thus, a high  $r^2$  can result from a large elasticity (i.e. a strong influence of infinitesimal changes in the vital rate on  $\lambda$ ) and/or from a large range of values for the vital rate. Variance decomposition analysis differs from elasticity analysis in that the former 1) does not assume linear changes in  $\lambda$  with changes in a vital rate, 2) incorporates simultaneous changes in vital rates instead of holding all but one constant, and 3) incorporates the range of plausible variation in a vital rate rather than addressing only infinitesimal changes.

I used Elastic (written by L. S. Mills and D. F. Doak and revised in January 1999 by L. S. Mills for this project), for conducting time-invariant (excludes environmental stochasticity) matrix projections. Model input included maternity rates ( $M_x$ ), survival from egg to age 0 (Segg), and age-specific annual survival ( $S_x$ ). Vital rates entered in the model separately were treated as uncorrelated. I chose to combine female fecundity and percent of females mature into one maternity function because the two rates are positively correlated over the range of individual growth rates that I observed. The program used the stable age distribution (Caswell 1989) for the initial age distribution.

For each modelling run, the model first calculated a mean matrix. The mean matrix was one including either the mean, the most probable (i.e. for percent mature, see Chapter V), or the observed values for a given vital rate for each subpopulation and scenario. The resulting was equivalent to that from the same mean matrix simulated in the program Ramas / stage. The Elastic program then performed 500 replications of the matrix, randomly selecting values for vital rates from the uniform distributions that I defined for each rate. For each replication, the pertinent output included the vital rate values, elasticity values and rankings for each vital rate, and the resulting  $\lambda$  for each replication.

I used spreadsheet (Excel) and statistics (SPSS) programs to further manipulate the output data. For each set of matrix replicates I examined the distribution of  $\lambda$ 's, the rankings and values of elasticities for each vital rate, and the  $r^2$  for each vital rate. I then compared the results among various subpopulations and scenarios.

## Ramas / stage

I used Ramas / stage to evaluate the effect of hypothetical levels of migration on two subpopulations. Although modelling the population as age-structured, I used Ramas / stage because of the flexibility it allowed in defining immigration and emigration. I modelled only the most upstream and downstream subpopulations and used the same mean matrices as used in the LSA analysis. Variation in parameters was described by variances, rather than ranges, but I created levels of variation similar to those used in Elastic (Appendix A, Table A6). I simulated the amount of immigration necessary to sustain the upstream population and the amount of emigration that the downstream population could sustain. I also modelled the increased emigration that could be sustained in the restoration scenario without fishing. I categorized population trends as increasing, stable, or decreasing over 15 years.

## Scenarios

I first modelled a "base" matrix for each of the four reaches. Vital rates in the base matrices were maternity functions estimated from fish captured in the reach and survival rates calculated from McFadden et al. (1967) without fishing mortality.

I simulated three levels of fishing pressure (light, medium and heavy) on the subpopulations in reaches A and D by changing survival values of all age classes in which at least some fish were longer than 150 mm. Although there was no legal size limit on salmonids harvested in the St. Regis River drainage, I assumed that anglers did not harvest fish smaller than 150 mm. Details on the survival rates used and the method of adjusting survival for the proportion of fish > 150 mm in an age class are in Appendix A.

I simulated the potential effects of habitat restoration on the brook trout population dynamics in the most downstream segment of Twelvemile Creek. Downstream of the study area and the confluence with the East Fork Twelvemile Creek (Chapter V, Figure 2), the stream channel was restricted and separated from its floodplain by a road, the stream channel was aggraded, and little overhead or instream cover existed. I assumed that if habitat were restored in the downstream segment so that a meandering, gradually sloping channel with pools and cover complexity existed, brook trout survival rates and densities would be at least as high as those in reach A. Because the stream segment is on private land, fishing mortality would not *necessarily* increase, although it certainly could. I assumed that the water temperature would be higher in the restored segment than at my downstream temperature recording site (in reach A, see Chapter V, Figure 2) and that food for brook trout would be more abundant. Therefore, individual brook trout growth rates should increase. I examined the influence on and on the number of emigrants per 200 m that the subpopulation in the restored segment could potentially support, assuming that fish growth did increase. I simulated "restoration matrices" without fishing and with medium and heavy fishing pressure.

In order to assess the effects of vital rates on over the entire range of plausible values, I included two "combination" matrices in the analysis. Both matrices used the range of survival values from scenarios without fishing to those with medium fishing. The first matrix ("without growth") included the range of maternity values estimated throughout the stream. The second matrix ("with growth") had the same survival and minimum maternity values as the first but had maximum maternity values from the restoration scenario and so included a hypothetical increase in fish growth.

Finally, I constructed a matrix using maternity values from the Hunt Creek, Michigan, brook trout population (McFadden et al. 1967) to ensure that the survival values (for heavy fishing) and ranges that I used adequately predicted the population dynamics of the population from which they were derived. The survival values for stages 4 and 5 were hypothetical because fish in those stages were found in portions of Twelvemile Creek, but few were found in Hunt Creek.

## Demographic parameters

I estimated the percent of females that were mature in each age class and reach (Table A3) and the number of female eggs per mature female from brook trout captured by electrofishing in four stream reaches during September 1997 (Tables A1 and A2). Methods and estimates are detailed in Chapter V and in Appendix A.

Survival values were based on brook trout survival data for 11 years in Hunt Creek, Michigan (McFadden et al. 1967). The survival values given by McFadden et al. (1967) included mortality from heavy fishing. All age 2 fish were vulnerable to fishing, as were many age 1 and some age 0 fish. I estimated survival values without fishing based on the survival values and fishing mortality presented in McFadden et al. (1967)(Appendix A). I estimated minimum and maximum survivals without fishing by applying the width of the 95% confidence interval with fishing to the mean survival without fishing (Table A4).

I modelled subpopulations in reaches A and D with three levels of fishing. Survival values for scenarios with heavy fishing were based on the values in McFadden et al. (1967). I adjusted survival rates with fishing to account for fish in the two reaches becoming vulnerable to fishing at different ages (Appendix A). Minimum and maximum values of survival with fishing were based on survival ranges over 11 years (McFadden et al. 1967)(Appendix A, Table A4). Medium and light fishing were simulated by increasing the survival values from those in McFadden et al. (1967) by 30 and 60 percent, respectively, and again adjusting the values for the proportion of fish vulnerable to harvest.

I modelled an increase in individual growth that could hypothetically result from habitat restoration of lowest segment of Twelvemile Creek, downstream of the confluence with the East Fork Twelvemile Creek (Chapter V, Figure 2). I first calculated the percent change in mean body weight between neighboring study reaches for each age in Twelvemile Creek. I then increased the mean weight at age in reach A by the mean increase between sites. The width of the 95% confidence interval of weight in reach A was applied to the new mean weight to obtain minimum and maximum weights. I estimated fecundities based on weights by applying a quadratic equation fitted to observed data (Chapter V, Table 6). I determined percent of females mature and proportion of fish vulnerable to fishing based on length. Length was estimated from the linear regression equation:

$$\log_{10} \text{ length} = 1.684 + 0.332(\log_{10} \text{ body weight}) \quad R^2 = 0.992, \quad p = 0.000 \quad \text{Equation 1.}$$

I considered 65 to 97 % of the age 1 females and all older females mature. No age 0 and all age 1 fish were vulnerable to harvest by the next fall.

The Ramas/stage model required an estimate of the initial age distribution. I based that on the abundance and size structure of brook trout observed during night snorkeling of 100 m stream reaches (Chapter V). Based on the length at age relationships determined from fish captured by electrofishing, I assigned ages to fish whose lengths were visually estimated during snorkeling. I combined data from two neighboring 100 m reaches to derive an initial age distribution for each reach modelled in Ramas.

## Results

### Finite rates of increase ( )

The 's of the base matrices (no fishing) for the four subpopulations decreased with distance upstream (Table 1, Figure 1). The mean 's of 500 simulations were greater than one in the two downstream reaches (A and B) and less than one in the two upstream reaches (C and D). For the upstream subpopulation (reach D) a 40 % increase in Segg through S3 over those in the base matrix resulted in = 1.005.

Fishing had a much greater effect on in the downstream than the upstream reach (Figure 2). Simulations with heavy fishing compared to those with no fishing resulted in a 31 % decrease in the mean in the downstream reach and an 8 % decrease in the upstream reach. Fishing had little effect on the upstream subpopulations because relatively few fish reached 150 mm and those that did were in older age classes than downstream. In the simulation of light fishing in reach A, of the mean matrix was 0.906 (Table 1).

In the restoration scenario, increased individual growth in the downstream reach dramatically increased population growth rates (Figure 3). When an increase in growth was modelled without fishing, population growth was explosive (mean matrix = 1.62) and the simulations aborted when a combination of very high vital rates was selected. Lambda of the mean matrix with growth and heavy fishing was 1.29, higher than that of the downstream reach with no additional growth and no fishing.

Simulation of the Hunt Creek, Michigan, population indicated that the survival values were appropriately applied. Lambda of the mean matrix was 1.06, which is in accord with the findings of McFadden et al. (1967) that the population was remarkably stable over an 11 year period.

## Elasticities and variance decomposition

Survival values of life stages prior to maturity had the highest elasticity values and the highest elasticity rankings of all vital rates for both the downstream and upstream reaches (Figure 4A,B). Because fish matured later upstream, the elasticity of S3 was higher upstream than downstream.

In the variance decomposition analyses of the base matrices, Segg was by far the most important influence on , followed by S1 and maternity rates of various stages (Figure 4C). Segg explained 74 to 79 % of the variation in in all four subpopulations. The relationship between Segg and was linear (Figure 5). Stage 1 survival was an important contributor to variance in , but maternity rates were more important than survival rates in later stages. In accord with later maturity upstream, M3 was less important upstream than downstream.

Similar to the changes in , the changes in elasticity and variance decomposition values with versus without fishing were greater in the downstream than in the upstream subpopulations (compare Figures 4 and 6). Downstream, Segg, S1, and S2 maintained the first three elasticity rankings with all levels of fishing. However, the elasticity of stage 3 maternity increased relative to that of stage 3 survival with heavier fishing (Figures 4A,B and 6 A,B). The contribution of Segg to the total variance in decreased with fishing. As fishing mortality increased, early stage vital rates contributed more, and later stage rates less, to the variation in (Figure 4C). In contrast, fishing in the upstream reach resulted in no qualitative, and little quantitative, change in elasticity rankings or values. The contribution of Segg to the variation in decreased slightly, compensated primarily by reproductive measures of stages 3 and 4 (Figures 4C and 6C). When heavy fishing mortality was applied to the scenario of increased individual growth in the downstream reach, only Segg, S1, and M2 contributed substantially to the variation in .

Although both elasticity and variance decomposition analyses of base matrices indicated that survival rates had the strongest influence on , changes in reproductive measures were entirely responsible for the large differences in between the downstream and upstream matrices. Combination matrix simulations better indicated each vital rate's importance across the entire range of plausible rates in Twelvemile Creek. The first combination matrix did not include values from the restoration scenarios, whereas the second matrix did. When the range of reproductive values throughout the stream, and the range of survival values representing various amounts of fishing were included in one scenario, the variance decomposition became more equitably distributed among various vital rates (Figure 7C, left). Segg contributed about one third of the variance in , and S2, S3, M3, and M4 contributed most of the remaining variance. In the matrix set incorporating the full range of survival and maternity rates, including the latter from the "growth" scenario, Segg and M2 contributed the bulk of the variation in (Figure 7C, right). Elasticity rankings for the combination matrices reflect the increased importance of reproductive measures. However, S1 survival was ranked as the second or occasionally the first highest elasticity even though it barely contributed to the variance in over the range of possible values.

## Migration

Various combinations of immigrants per stage in the upstream subpopulation resulted in stable or increasing fish numbers over 15 years (Table 2). Stable subpopulation numbers occurred in both the upstream and downstream subpopulations with five immigrants/emigrants, respectively, per year distributed as two stage 1, two stage 2, and one stage 3 fish (the number of migrants was relative to a 200 m reach of stream). More emigration from the downstream subpopulation resulted in a subpopulation decline downstream, particularly when emigrants were in stages 3-5. Under the scenario of increased individual growth and no fishing, the downstream subpopulation could support almost twice as much emigration as could be supported under the "base" scenario (Table 2).

## Discussion

The substantial upstream decline in subpopulation growth rate is consistent with the hypothesis that source-sink dynamics extend brook trout distribution limits beyond where they would occur in the absence of a demographic boost from downstream (Pulliam 1988; Schlosser and Angermeier 1995). The upstream subpopulation growth rate is so low ( $\lambda = 0.73$ ) that without immigration from downstream, brook trout should not persist in at least the upper 25 % of the 1997 distribution in Twelvemile Creek (Chapter V, Figure 2). When modelled without fishing mortality, the two downstream subpopulations were stable or increasing while the two upstream subpopulations were decreasing. In the absence of immigration, Segg through S3 would have to increase 40 % over the values estimated to stabilize the upstream subpopulation (unpublished results). The actual  $\lambda$ 's are not necessarily close approximations of reality since survival estimates were taken from a radically different environment, but it is the relative changes in that are of interest. Probably the most realistic scenarios are of light fishing downstream and no fishing upstream. The mean for the downstream scenario with light fishing was still considerably larger than without fishing upstream, although both were less than 1. Thus, either the light fishing scenario overestimated fishing mortality or survival rates of egg and early age classes were underestimated.

When modelled without fishing mortality, the amount of emigration that could be supported by the downstream subpopulation was about

equal to that necessary to sustain the upstream subpopulation. However, if modelled with fishing mortality or if additional mortality were imposed on migrants, the downstream subpopulation would no longer be capable of sustaining the upstream subpopulation per 200 m of stream. However, I did not calculate relative stream lengths that supported various subpopulation growth rates. Data on reach-specific survival rates are necessary to further explore the actual amount of migration needed to sustain the present distribution of brook trout in the stream. I operated four weirs in the creek throughout the summer and fall of 1997 (Chapter V, Figure 2). Few fish moved from one weir to another and none moved between the most upstream and downstream weirs (unpublished data). In a Colorado stream, brook trout moved most during the spring (Gowan and Fausch 1996b), so I may have missed some longer movements before weirs were installed. Analysis of the distance to the first annulus on otoliths suggested that some fish originating in reach C or D may have moved downstream to reach A, but I observed no evidence of the opposite migration (Chapter V). However, sample sizes were small and the method requires further validation to be reliable. Furthermore, immigration from downstream may support the upstream subpopulation in a leap frog fashion. For example fish from reach A move to reach B while fish from reach B move to reach C, et cetera. In that case, important migrations may not be evident from analysis of otoliths.

The modelling results indicated that individual growth rate, as reflected in age at maturity and fecundity, is very important to population growth rate. Because survival rates and ranges were the same, the differences in for the base matrices of the four subpopulations were due entirely to differences in the maternity functions. Also, the large increase in in the restoration scenario over the base matrix for the downstream reach was due solely to changes in maternity functions resulting from hypothetical increases in individual growth.

LSA analyses of matrices incorporating the full range of  $M_x$  and  $S_x$  values revealed the importance of maternity rates to  $\lambda$ , a result much less evident from traditional elasticity analyses (Wisdom et al. Accepted; Mills et al. In press). Previous modelling efforts have generally identified survival of early age classes, particularly age 1, as the vital rates contributing largely to  $\lambda$  (Marschall and Crowder 1996; Clark and Rose 1997b). Likewise, when I modelled individual subpopulations, early life stage survivals were nearly always the most important in both elasticity and variance decomposition analyses. However, when the vital rates of all of the subpopulations were combined, and especially when the restoration scenario was included, variance decomposition analyses revealed that maternity functions of the early age classes had large effects on  $\lambda$ . For example, in the upstream reach, no stage 2 females were mature so the elasticity and variance contributions of  $M_2$  were zero. However, in the matrix incorporating the range of possible survival values and plausible increases in growth,  $M_2$  explained 26 % of the variance in  $\lambda$ . Thus, over the range of plausible rates in the population, maternity rates in the early age classes have a powerful effect on population growth rate.  $S_{eg}$  and  $S_1$  always had the largest effect on  $\lambda$  when only small changes were considered, as in elasticity analyses. However, because the plausible range of maternity values was so large, maternity functions had a substantial effect on  $\lambda$ .

Egg to age 0 survival contributed the most to the variance in  $\lambda$  in every matrix modelled. Elasticities of  $S_1$  and  $S_{eg}$  were always equal, but the range of  $S_{eg}$  was greater. The range of  $S_{eg}$  represented the maximum and minimum estimates over 11 years in Hunt Creek (McFadden et al. 1967). The range of  $S_1$  was slightly smaller than that observed in Hunt Creek because I removed the effect of fishing from the minimum, but not the maximum, value. However, it is probable that in the absence of fishing the survival range would be even larger. Thus, a conservative assumption would be that the contribution of  $S_1$  to the variance in  $\lambda$  is somewhere between the values indicated in the results for  $S_1$  and  $S_{eg}$ .

Other modelling papers also suggest that brook trout survival rates in the early life stages are more important than in the later life stages. Based on results of an individual-based demographic model, Clark and Rose (1997b) concluded that management strategies aimed at decreasing interspecific competition in the age-0 life stage or circumventing the stage by stocking juveniles were the best options for restoring southern Appalachian brook trout populations. Marschall and Crowder (1996) used a size-classified matrix model of southern Appalachian brook trout and concluded that population growth was most sensitive to survival of large juveniles and small adults. Both models incorporated density dependence of juvenile stages which reduced the importance of egg to age 0 survival.

The extreme spatial variation in densities of age 0 brook trout observed in Twelvemile Creek (Chapter V, Figures 6 and 7) and the importance of early survival rates to population growth rate indicate that patchy demographic processes, in addition to longitudinal trends, are likely very important to population dynamics (Pulliam et al. 1992). Based on the distribution of age 0 brook trout, I expect that they have higher first summer survival in shallow side channel or lateral habitats than in deeper habitats associated with the main channel. Brook trout spawning, and presumably egg to emergence survival, are closely associated with upwelling groundwater in many regions (Benson 1953; Snucins et al. 1992; Curry and Noakes 1995a; Essington et al. 1998). Alluvial stream reaches bounded downstream by constricted channels are likely to contain both side channel or lateral habitats and upwelling groundwater (Stanford and Ward 1993; Baxter 1997) and thus, are predicted to have high egg to age 0 survival. Such reaches may serve as reproductive nodes and provide migrants or dispersers to neighboring or distant stream reaches. As fish growth rate declines upstream, increased survival rates provided by reproductive nodal areas may become increasingly important to subpopulation stability. However, in upstream reaches of mountain streams where slow growth is the norm, the incidence of alluvial reaches often declines. Slow individual growth and low survival in early age classes would reduce subpopulation growth rate, and the lower the subpopulation growth rate, the more immigration is necessary to sustain the subpopulation. Thus, a combination of slow growth and low survival in early age classes likely contributes to limiting upstream brook trout invasion of many mountain streams.

The potential importance of changes in local demographics to locations of distribution limits provides insight into how habitat alteration may facilitate brook trout invasion in some instances. As modelled, habitat changes that result in increased individual growth rates will likely lead to increased population growth rate. The changes need not occur near the distribution limit to cause an expansion of the limit. If source-sink dynamics do, in fact, apply to brook trout in streams, then changes in population growth rate in a "source" area can influence the demographics of peripheral populations (Pulliam 1988; Pulliam et al. 1992), as has been documented upstream of newly created reservoirs (Erman 1973; Crisp et al. 1984; Winston et al. 1991). Examples of anthropogenic alterations that have potential to increase individual brook trout growth include stream warming (within limits) via riparian canopy removal (Chamberlin et al. 1991; Hicks et al. 1991) or global warming (Ries and Perry 1995), or increased nutrient loading resulting from livestock grazing or upslope land disturbances, such as logging and road construction (Hicks et al. 1991).

Any proposed ecosystem alterations that could increase the growth rates of nonnative brook trout should be considered potential triggers for population expansion and further invasion. I modelled the potential demographic effects of a stream channel restoration scenario to highlight two

common oversights. First, the offsite, and particularly upstream, effects of ecosystem alteration are frequently overlooked, particularly when the alteration itself is confined to a discrete area. Second, the potential response of invasive species is often overlooked in restoration planning (Jude and DeBoe 1996). The presence of nonnative species may qualitatively alter the community response to restoration and must be accounted for in restoration planning (Moyle and Yoshiyama 1994; Young 1995b). Restoration projects may inadvertently increase invasion of distant habitats by at least two mechanisms: 1) creation of suitable conditions for the establishment or growth of source populations (Jude and DeBoe 1996), as modelled here, or 2) "improvement" of dispersal corridors.

A more direct impact on brook trout populations results from fishing. The impact of fishing on simulated subpopulations was evident both from the decline in with increased fishing mortality and from the increase in the effect of S2 and S3 on when the full range of plausible survival estimates, rather than just one fishing scenario, was considered (Figure 7C, left). In the population described by McFadden et al. (1967), rapid individual growth resulting in early maturation allowed the population to sustain high fishing mortality. However, the slower growth and later maturity of brook trout in the downstream reach of Twelvemile Creek than in Hunt Creek apparently caused the population to be less robust to fishing. In the upstream end of Twelvemile Creek, fish reached a harvestable size at such a late age, if ever, that fishing mortality had little impact on the population dynamics.

Typically, brook trout population growth is probably less sensitive to fishing than that of cutthroat or bull trout. Brook trout typically mature early (age 1 or 2) and have low adult survival resulting in short life spans (often less than 3 or 4 years)(Power 1980). Although the pattern holds in many systems where fishing pressure is light (e.g. Warner 1970; Flick and Webster 1975; Quinn et al. 1994), unexploited high altitude or northern systems may include longer-lived, later maturing individuals (Flick 1977; Reimers 1979; Power 1980). The early maturing brook trout populations are relatively insensitive to depletion by fishing (Shetter 1969). Some native stream salmonids in the west, such as cutthroat trout and bull trout, tend to mature later and live longer, characteristics that should make them more susceptible to the effects of fishing. For example, westslope cutthroat trout females may begin maturing at age 3, but typically do not spawn until age 4 or later (McIntyre and Rieman 1995; Downs et al. 1997). In addition, westslope cutthroat trout are generally easier to catch than brook trout which should exacerbate the effects of fishing on the population (MacPhee 1966). Several studies have documented increases in population size and mean body size of westslope cutthroat trout after reductions in fishing (reviewed in McIntyre and Rieman 1995). Population-specific demographic rates and the intensity of fishing could be important factors in determining the degree of coexistence of cutthroat and brook trout. Slower growth and later maturity compared to the Hunt Creek, Michigan, population indicate that the Twelvemile Creek brook trout population is more vulnerable to the effects of fishing. Furthermore, because fishing pressure is relatively light in the stream, the effect on cutthroat trout is probably less than in other more heavily fished streams where native cutthroat trout have been replaced by brook trout. In some streams, the combination of rapid brook trout growth and heavy fishing could greatly facilitate replacement of cutthroat trout by brook trout. Similarly, I expect that both brook trout growth and fishing pressure typically decline upstream in the small, headwater stream segments where vestigial cutthroat trout populations often persist.

## Limitations of the models

The primary intent of the models presented here was to explore the influence of subtle demographic changes on distribution limits, not to predict the actual population dynamics in Twelvemile Creek. The most obvious limitation to the latter is the lack of reach-, stream-, or even region-specific survival rates. For lack of more specific data, I applied survival rates uniformly to all subpopulations. However, survival is probably not uniform throughout the population. The lack of density dependence in survival may have had little effect on the results for the upstream reaches, but would probably influence the results for reach A, particularly under the restoration scenario.

Survival from the egg stage to age 0 or 1 may be lower upstream than downstream. Size-dependent winter mortality of age 0 salmonids, including brook trout, is apparently a common, but not universal, phenomenon (Quinn and Peterson 1996), and seems to be exaggerated in harsher conditions. In some environments, smaller fish within an age 0 cohort tend to have higher mortality than larger fish (Smith and Griffith 1994; Meyer and Griffith 1997), possibly due to early winter energy deficits (Cunjak et al. 1987). Thus, because age 0 fish are smaller and winter temperatures are presumably colder and persist longer upstream, survival of age 0 brook trout may be lower in the upstream than downstream reaches of Twelvemile Creek in a typical year. However, Latta (1969) suggested that in systems where groundwater dominates upstream reaches, age 0 brook trout survival may be higher upstream than downstream.

Predicting changes in survival of fish ages 2 and older is more difficult. Several factors should favor increased adult survival upstream. First, angling mortality was low upstream compared to downstream. I observed no fishing activity in the upper one half of the study area. Second, survival appears to increase with a decrease in fish growth rate (Carlander 1969; Reimers 1979). Third, post-reproductive, winter mortality of brook trout can be high for brook trout, particularly for small females (Hutchings 1994). Therefore, fish maturing later in upstream reaches may have higher age-specific overwinter survival rates prior to maturity than those maturing earlier in downstream reaches. However, increased predation by diving/wading predators and emigration of the largest fish from upstream reaches may counteract the other forces (Chapter V).

Although cutthroat trout outnumbered brook trout throughout the stream and may be an important influence on brook trout demographics, they were not included in the modelling primarily because I lacked demographic data for them. Lethal sampling would have been necessary to obtain accurate demographic data, and I felt that such sampling at the scale necessary was inappropriate, given the sensitive status of the species. Furthermore, the influence of cutthroat trout on brook trout demographics is unknown. Cutthroat trout in Twelvemile Creek may reduce brook trout survival and/or growth rates in the early age classes. Age 0 brook trout hatch and emerge before age 0 cutthroat trout, so the former appear to have a length advantage at least through the first year. However, cutthroat trout estimated as age 1 were about the same size or slightly larger than age 0 brook trout in late summer (unpublished data). Thus age 1 cutthroat trout may have negative effects on age 0 brook trout. The largest cutthroat trout were larger than the largest brook trout, so the former may also have had detrimental effects on the latter in the adult stages. Conversely, the effect of cutthroat trout on brook trout may be negligible, with the demographics of the latter limited primarily by other factors discussed above.

In both Elastic and Ramas / stage, vital rates were treated as uncorrelated. Although some correlation of survival or maternity functions among age classes over time seems plausible, I found no correlations among either in the 11 year data set of McFadden et al. (1967). Heavy fishing

pressure may have dampened synchronous correlations in that system. Including correlations should increase the variation in in LSA.

Catastrophic events, such as droughts and floods, are undoubtedly important in structuring brook trout populations (Seegrist and Gard 1972; Erman 1986). Clark and Rose (1997a) modelled brook and rainbow trout populations and concluded that more frequent year class failures could explain the dominance of rainbow over brook trout. While year class failures likely occur in Twelvemile Creek, they would only exacerbate the effects of low individual growth rates on population growth.

## Conclusions

Gradual reductions in individual growth rates with distance upstream are apparently sufficient to limit the distribution of brook trout in Twelvemile Creek. Large (about 40 %) increases over Hunt Creek survival rates would be necessary to achieve positive growth of the upstream subpopulation in Twelvemile Creek. Clearly, reach- or habitat-specific estimates of survival, are needed to better understand the relationship between longitudinal changes in fish growth and changes in subpopulation growth rates within streams. Such survival estimates for early age classes would help to establish whether certain reaches function as reproductive nodes, and if so, the importance of the nodes to invasibility of streams.

The results support the hypotheses that source-sink dynamics can function within brook trout populations and can help define the limits of invasion and distribution. Recognizing the potential significance of source-sink dynamics will help to: 1) improve our ability to understand and predict invasions, and 2) focus attention not only on human influences occurring at the invasion front, but also those in core areas possibly far removed from the distribution limits. Identifying factors that stimulate dispersal will help identify the conditions under which source-sink dynamics operate.

I have demonstrated that longitudinal trends in growth rates of brook trout have important demographic consequences that likely translate into consequences for population dynamics. However, the roles of various factors in creating the growth trends are not entirely clear. Stream temperature is probably an important, but not exclusive, factor. Nutrient loading, sunlight, food availability, habitat, and genetic control are some other possible factors. The importance of competition or other behavioral interactions with other species is a possible factor that has proved elusive to quantify, but is exceedingly relevant to understanding invasion processes.

Table 1. Lambdas of mean matrices for each scenario and reach. "Growth" scenarios are those with individual growth increased beyond that documented in reach 1.

Scenario	Reach			
	A	B	C	D
Base matrix (no fishing)	1.14	0.95	0.75	0.73
Light fishing	0.91	---	---	0.67
Medium fishing	0.85	---	---	0.67
Heavy fishing	0.78	---	---	0.66
Growth without fishing	1.62	---	---	---
Growth with medium fishing	1.36	---	---	---
Growth with heavy fishing	1.29	---	---	---

Table 2. Subpopulation responses to various combinations of emigrants per stage from reach A (downstream) and immigrants per stage to reach D (upstream). The rows in bold show the combination of migrants resulting in stable subpopulations in both reaches A and D. Migrants were added to or subtracted from annual stage tallies in projections of base matrices in Ramas / stage. Initial abundances were based on snorkel estimates for 200 m long stream reaches. For each combination of migrants the program ran 500 simulations over 15 years.

1	Stage				Subpopulation trend
	2	3	4	5	
<i>Reach A, emigrants</i>					
-	4	-	-	-	increasing
-	4	1	-	-	stable
-	1	2	-	-	stable
<b>2</b>	<b>2</b>	<b>1</b>	-	-	<b>stable</b>
2	2	2	-	-	decreasing
-	1	2	1	-	decreasing
<i>Restoration scenario without fishing, emigrants</i>					
-	4	3	2	-	stable
<i>Reach D, immigrants</i>					
-	1	2	1	-	increasing then stable
2	2	2	-	-	increasing then stable
<b>2</b>	<b>2</b>	<b>1</b>	-	-	<b>stable</b>
-	2	2	-	-	negligible decrease
-	4	1	-	-	slight decrease

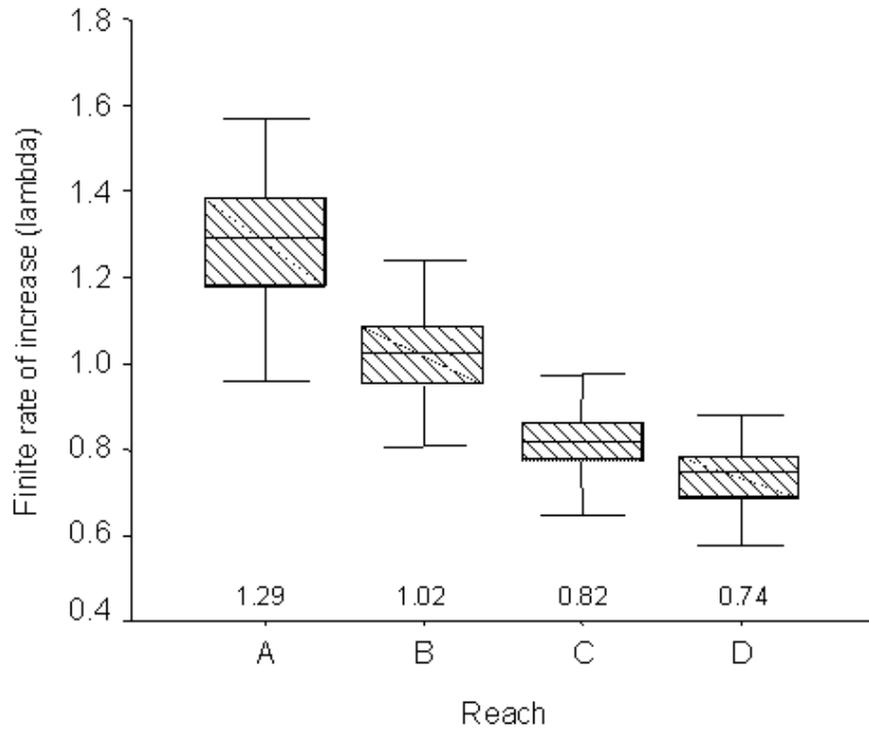


Figure 1. Boxplots of  $\lambda$ 's for 500 simulations of the base matrices of brook trout vital rates for four stream reaches in Twelvemile Creek, Montana. Reach lettering begins with the downstream reach and proceeds upstream. The base matrices included survival estimates from brook trout in Hunt Creek, Michigan calculated without fishing mortality (McFadden et al. 1967). The horizontal line in each box is the median. Boxes enclose the 75th and 25th percentiles. Error bars include the range or 1.5 times the box length from the median, whichever is smaller. The numbers along the horizontal axis are the means of the 500  $\lambda$ 's for each scenario.

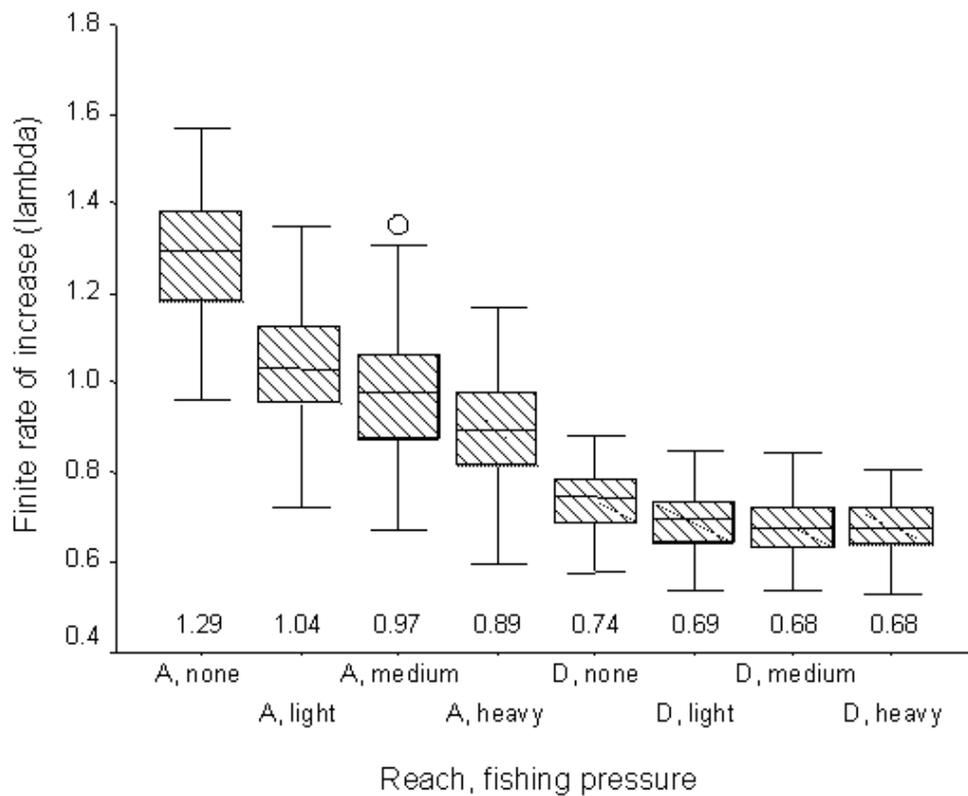


Figure 2. Boxplots of  $\lambda$ 's for 500 simulations of matrices representing four levels of fishing intensity for reaches A and D in Twelvemile Creek, Montana. The matrices with no fishing were the same as those shown in Figure 1. All survival estimates were calculated from data in McFadden et al. (1967). Boxplots are as described for Figure 1. The circle indicates an outlier further than 1.5 times the box length from the median.

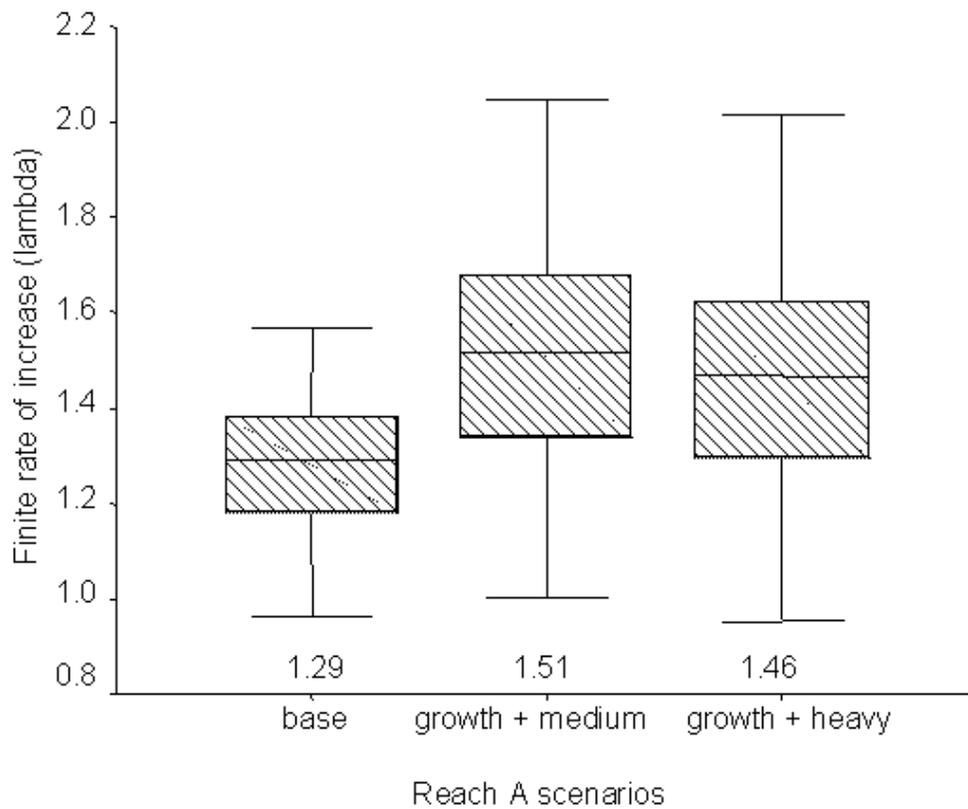


Figure 3. Boxplots of I's for 500 simulations of the base matrix and matrices including increased brook trout growth and two levels of fishing intensity for the downstream reach (A) in Twelvemile Creek, Montana. The base matrix was the same as in Figure 1. All survival estimates were calculated from data in McFadden et al. (1967). Boxplots are as described for Figure 1.

Figure on following page:

Figure 4. Comparisons of elasticity and variance decomposition analyses for base matrices (no fishing mortality) of brook trout in reach A (downstream) and reach D (upstream), Twelvemile Creek, Montana. The bar graphs (A) show the percent of the 500 simulations for which the elasticity of each vital rate ranked one through five. In ties between the elasticities of  $S_{egg}$  and  $S_1$ ,  $S_{egg}$  was ranked higher. Boxplots (B) display the distribution of elasticity values over 500 simulations for each vital rate with an elasticity greater than zero. Boxplots are as explained in Figure 2. The pie charts (C) show variance decomposition values greater than 0.04 and associated vital rates. The contribution of vital rates to the variation in  $\lambda$  for the 500 simulations are indicated by the  $r^2$  values for regressions of  $\lambda$  on each vital rate. Note that  $\lambda$  was sensitive to changes in  $S_2$  and  $S_3$ , but because they had relatively low variance, they had little influence on  $\lambda$  in the simulations.

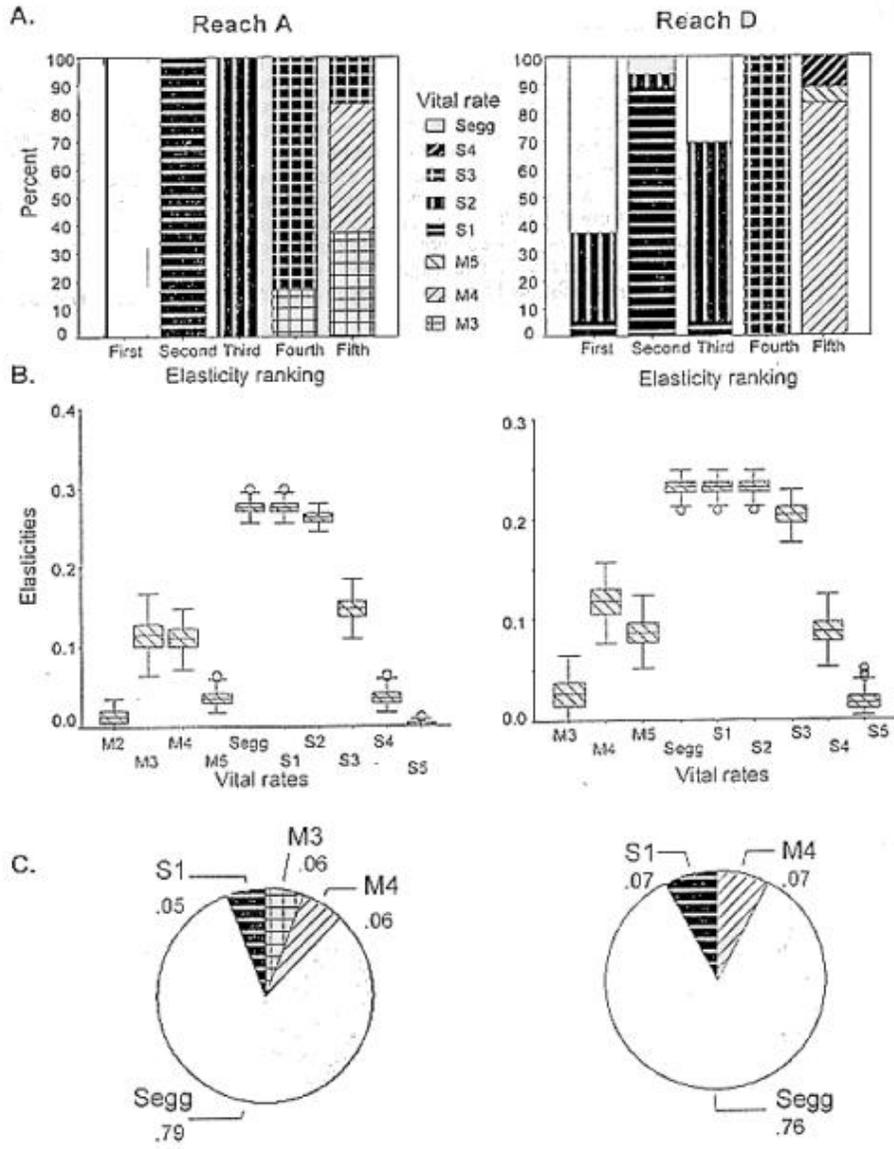


Figure 4.

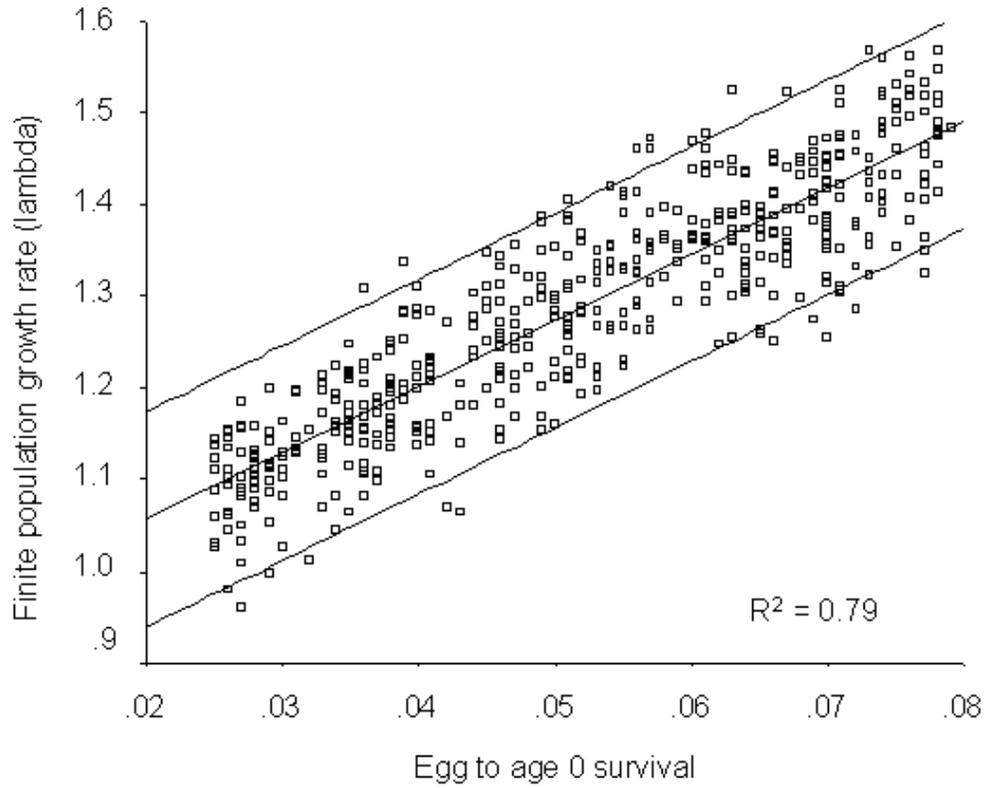


Figure 5. Plot of  $\lambda$  on the values of  $Segg$  used in 500 simulations of the base matrix of brook trout demographics without fishing in reach A, Twelvemile Creek. Lines are the linear regression line and the 95 % confidence intervals of point estimates.

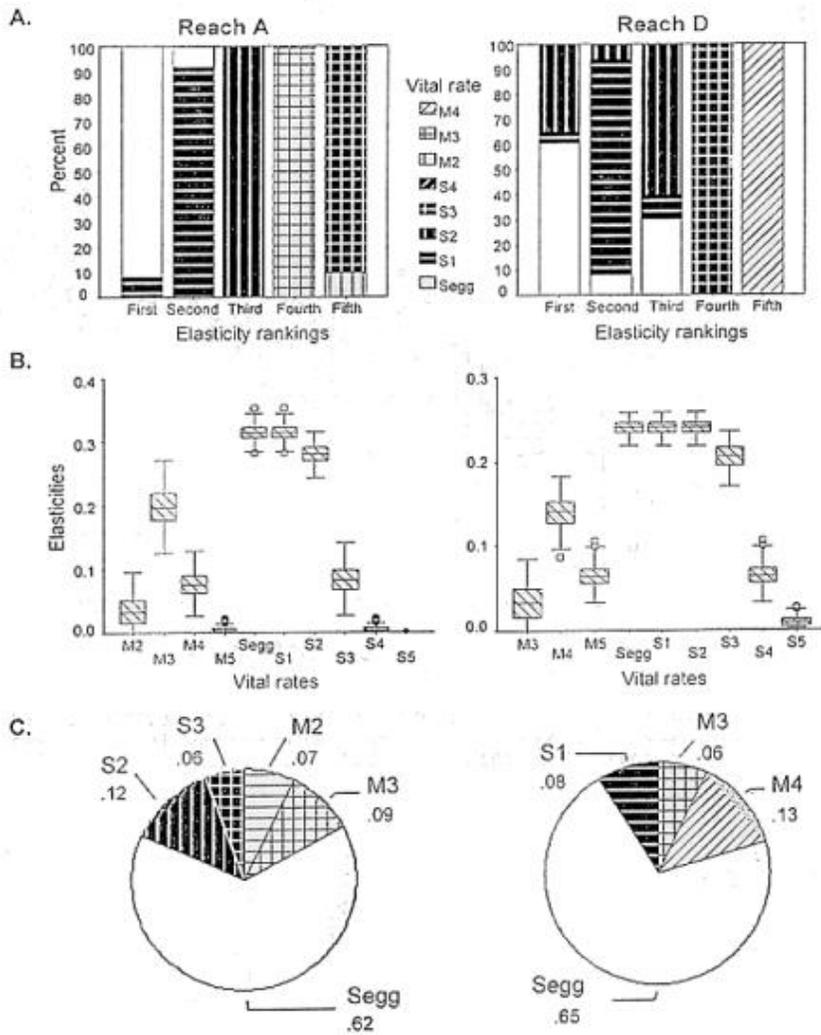


Figure 6. Elasticity rankings (A) and values (B) and variance decomposition values (C) for brook trout subpopulations subjected to heavy fishing in reaches A and D of Twelvemile Creek, Montana.

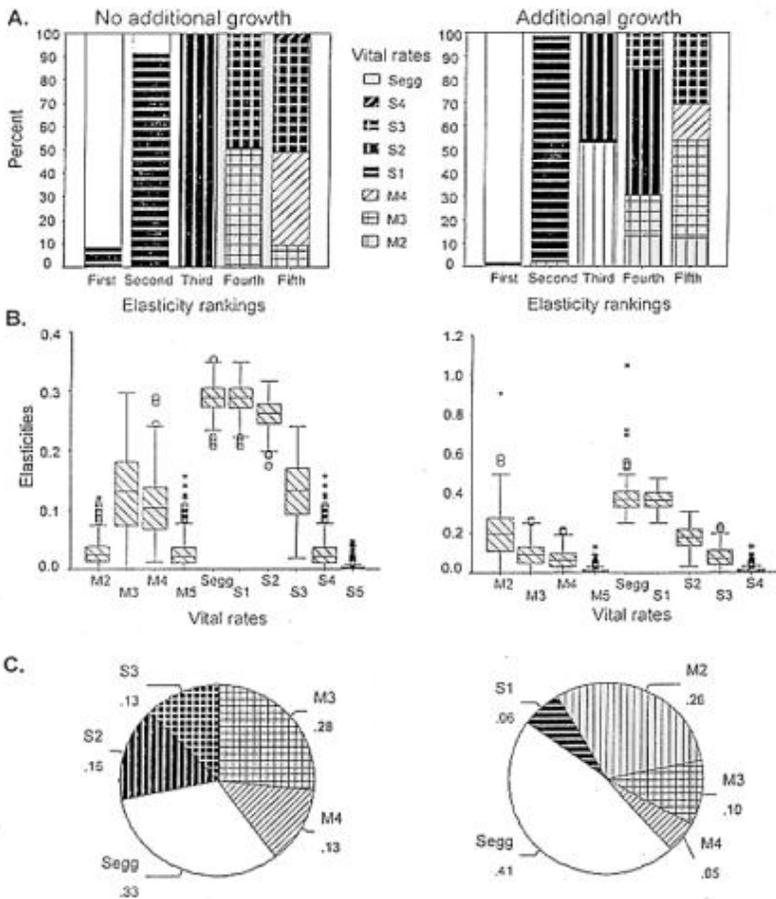


Figure 7. Elasticity rankings (A) and values (B) and variance decomposition values (C) for brook trout "combination matrices" (see text) from Twelvemile Creek, Montana. The left column shows results of 500 simulations in which the minimum survival rates were those from reach A with heavy fishing, and the maximums were those without fishing. The maternity values ranged from the minimum from reach D to the maximum from reach A. The right column shows results from a matrix with the same survival and minimum maternity values but with maximum maternity values from the scenario of increased growth of fish from reach A. Charts are as explained in Figure 4.

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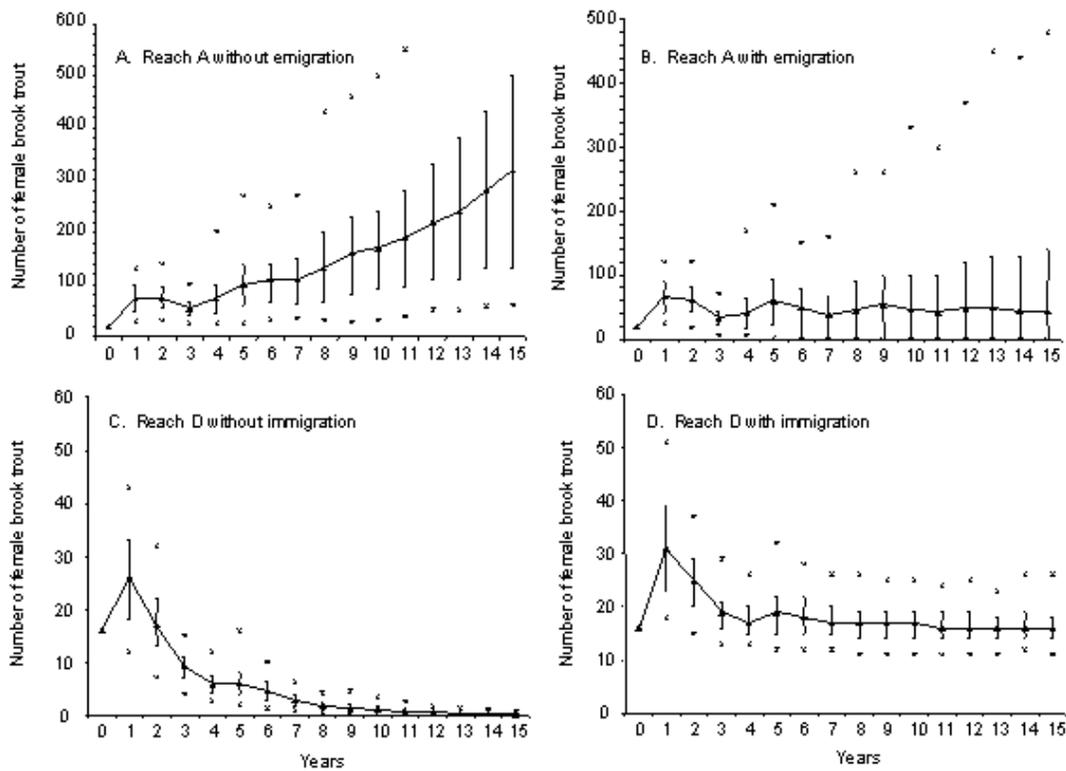


Figure 8. Ramas / stage projections of subpopulation sizes over 15 years for: (A) reach A without migration, (B) reach A with emigration, (C) reach D without migration, and (D) reach D with immigration. The projections in (B) and (D) included five emigrants or immigrants, respectively, per year distributed as two each from stages 1 and 2 and one from stage 3. The solid lines and error bars indicate the mean  $\pm$  one standard deviation for 500 simulations. Asterisks indicate the minimum and maximum values. Abundances include female brook trout of all stages.

### Appendix A. Estimation of demographic parameters.

## Reproduction

I calculated female fecundity values (number of female eggs per mature female) by a different approach for mean, than for maximum and minimum matrices. The values in the mean matrices are averages for the females captured during electrofishing. Some females had begun spawning before capture, so I estimated the number of eggs using the quadratic regression equation on weight (Chapter V, Table 6). I then averaged the estimated and counted eggs and divided by two to obtain an estimate of female fecundity (Table A1). For minimum and maximum values, I used the quadratic regression equation on weight to estimate the number of eggs for fish at the lower and upper 95 % confidence limits of weight for each age and reach, and divided by two (Table A2). In several cases (e.g. all ages in reach C) the "observed" fecundity was smaller than the estimated minimum. In such cases, the "observed" value was used for the minimum.

Chapter V details how values for the percent females mature were obtained. For the mean matrices, I used what I judged to be the best estimate of the percent mature (Table A3). In minimum and maximum matrices I used the minimum and maximum ranges of possible values for the fish collected.

I multiplied the percent mature by the female fecundity to obtain maternity rates. In reach D, only the largest age 3 fish were mature, so the minimum and maximum estimates were biased low. Therefore, I added 5 to both the minimum and maximum values. The ranges of the maternity values are probably conservative because they do not incorporate the expected annual variation in fish growth, rather they are based solely on variation within the 1997 samples.

## Survival

All survival estimates were based on values in McFadden et al. (1967)(Table A4). I estimated survival values without fishing based on survival and harvest data (McFadden et al. 1967). I first calculated mean annual survivals (S) of age groups 0 to 2 from the mean lx for 11 years (Table XIII in McFadden et al. 1967) as:

$$S = l_x(t+1) / l_x(t),$$

where t is time in years. I calculated annual mortality (A) by:

$$A = 1 - S.$$

The average percentage of the annual total loss in each age group (0 to 2) that was attributable to fishing (% loss to fishing) was reported (page 1455 in McFadden et al. 1967). I calculated natural mortality (D) by:

$$D = (1 - \% \text{ loss to fishing})(A) .$$

Then,

$$\text{survival without fishing} = 1 - D.$$

The following table shows the value for each parameter from Hunt Creek.

Ages	S	A	% loss to fishing	D	Survival without fishing
0 - 1	.3996	.6003	.017	.5901	.4099
1 - 2	.1776	.8224	.236	.6283	.3717
2 - 3	.0927	.9073	.351	.5888	.4112

For scenarios with fishing, I adjusted the survival values to account for varying ages of entry into the fishery among reaches. Although no minimum size limit for harvesting trout existed in Twelvemile Creek, I assumed that few fish smaller than 150 mm were harvested. I first estimated the percent of fish of each age that would be over 150 mm by the next fall, based on length-frequency distributions of fish observed and caught. I then added 10 % to each estimate (not to exceed 100 %) in reaches A and B and 5 % to each estimate in reaches C and D to account for the faster-growing fish that were harvested before I sampled (Table A5). The upper site has a lower correction factor because it has been subjected to less fishing. Then I applied survival rates with fishing according to the following equation:

$$S_{x\text{combined}} = (V)(S_{x\text{with fishing}}) + (1-V)(S_{x\text{without fishing}}) \quad \text{Equation A1.}$$

Where  $S_{x\text{combined}}$  is the overall survival rate for age class x in a reach, and V is the proportion of fish in age class x that will be vulnerable to fishing by the next fall. Minimum and maximum values of survival with fishing were calculated by the same method using survival ranges over 11 years (McFadden et al. 1967).

Table A1. Female fecundity values (number of female eggs per mature female) used to calculate  $M_x$  for mean base matrices. Values are means of the observed or predicted number of eggs in mature females captured by electrofishing divided by two. Numbers in parentheses are the sample sizes. More details on determining fecundity are presented in Chapter V. The value for reach C, age 2, excludes one fish that had a large number of immature eggs.

Age	Stage	Reach			
		A	B	C	D
2	3	136.79 (10)	111.35 (6)	68.50 (9)	64.83 (9)
3	4	230.93 (6)	101.05 (3)	79.46 (10)	93.52 (3)
4+	5	469.50 (1)	227.72 (2)	77.37 (3)	77.14 (2)

Table A2. Minimum and maximum female fecundity values used to calculate the minimum and maximum  $M_x$  values for base matrices. In most cases, I calculated the values by using the quadratic equation in Chapter V, Table 6 to estimate fecundity for the upper and lower 95 % confidence

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limits of the weights of fish for each age and reach. The observed values (Table A1) for reach C fish were smaller than the predicted minimum, so I used the former for minimum values.

Stage	Reach			
	A	B	C	D
2	56.16 - 74.44	---	---	---
3	120.12 - 150.87	75.12 - 97.33	68.50 - 77.50	56.09 - 63.54
4	201.71 - 433.40	71.38 - 163.73	79.46 - 102.66	61.76 - 93.45
5	319.78 - 582.50	207.66 - 342.29	77.37 - 111.95	61.58 - 93.25

Table A3. Percent of females that were mature in each stage and reach. The minimum and maximum values are shown in parentheses. Minimum and maximum values represent the possible range of error in my estimates. Values used in the mean matrix represent my best estimate.

Stage	Reach			
	A	B	C	D
1	0	0	0	0
2	0 (0 - 10)	0	0	0
3	75 (60 - 90)	54.55 (44 - 65)	5.56 (4 - 7)	14.29 (0 - 17)
4	100	100 (80 - 100)	100 (80 - 100)	60 (38 - 60)
5	100	100	100	100 (90 - 100)

Table A4. Mean, minimum, and maximum survival values for each age under various degrees of fishing based on McFadden et al. (1967). I used the values shown to calculate "adjusted survival values" that accounted for the proportion of fish vulnerable to fishing in each age class. Survival values for egg to age 0 and for age 0 to 1 fish were unchanged in the various fishing scenarios.

Age	Mean	Minimum	Maximum
egg	0.0424	0.02515	0.07905
0	0.4099	0.3758	0.5388
<i>No fishing</i>			
1	0.3717	0.3490	0.3944
2	0.4112	0.3896	0.4328
3	0.2596	0.2420	0.2772
4	0.1000	0.0500	0.2000
<i>Light fishing</i>			
1	0.2862	0.1687	0.3585
2	0.1517	0.0835	0.2819
3	0.0213	0.0160	0.1333
4	0.0213	0.0160	0.1333
<i>Medium fishing</i>			
1	0.2326	0.1371	0.2913
2	0.1232	0.0678	0.2290
3	0.0173	0.0130	0.1083
4	0.0173	0.0130	0.1083
<i>Heavy fishing</i>			
1	0.1789	0.1054	0.2240
2	0.0948	0.0522	0.1762
3	0.0133	0.0100	0.0833
4	0.0133	0.0100	0.0833

Table A5. Proportions of fish in each age group and reach that are expected to be vulnerable to fishing (> 150 mm TL) by the next fall. Proportions are adjusted to account for fishing mortality that has already occurred.

Reach	Age				
	0	1	2	3	4

MECHANISMS LIMITING A VERTEBRATE INVASION:

A	0	0.85	1	1	1
D	0	0	0.30	0.45	0.55

Table A6. Means, variances, and distributions of vital rates used in Ramas / stage modelling of migration in subpopulations in reaches A and D.

Rate	Reach A			Reach D		
	Mean	Variance	Probability distribution	Mean	Variance	Probability distribution
Segg	0.0424	2.23 x 10-4	uniform	0.0424	2.23 x 10-4	uniform
S1	0.4099	3.32 x 10-3	uniform	0.4099	3.32 x 10-3	uniform
S2	0.3717	1.47 x 10-3	uniform	0.3717	1.47 x 10-3	uniform
S3	0.4112	1.33 x 10-3	uniform	0.4112	1.33 x 10-3	uniform
S4	0.2596	8.92 x 10-4	uniform	0.2596	8.92 x 10-4	uniform
S5+	0.1000	8.92 x 10-4	uniform	0.1000	8.92 x 10-4	uniform
F1	0.000	-	invariant	0.000	-	invariant
F2	0.100	3.42	lognormal	0.000	-	invariant
F3	102.579	256	uniform	9.274	7.41	uniform
F4	230.927	3364	uniform	56.115	56.65	uniform
F5	469.500	4356	uniform	77.141	89.44	uniform

## Appendix B. Vital rates for each matrix

Table B1. Form of matrices used in LSA. Egg to age 0 survival (Segg) was entered independently of maternity values (Mx) so that the values of both rates could be randomly selected. Age at maturity and female fecundity were entered as one maternity value because I assumed that the two values were correlated. Conditions leading to faster fish growth, probably led to both earlier age at maturity and higher fecundity at age. Other survival values are indicated by Sx.

(Segg)(M1)	(Segg)(M2)	(Segg)(M3)	(Segg)(M4)	(Segg)(M5)
S1	0	0	0	0
0	S2	0	0	0
0	0	S3	0	0
0	0	0	S4	S5+

Table B2. Mean, minimum and maximum vital rates used in base matrices for Twelvemile Creek reaches A through D. The base matrices include no fishing mortality. Values in the first row are egg to age 0 survival rates (Segg) on the left and maternity rates (Mx, eggs per female of age x) on the right. Values in the second row are survival (Sx) rates.

	Stages				
	1	2	3	4	5
Reach A, mean base rates	0	0	(0.0424)(102.6)	(0.0424)(230.9)	(0.0424)(469.5)
	0.4099	0.3717	0.4112	0.2596	0.1000
Reach A, minimum base rates	0	0	(0.0252)(72.1)	(0.0252)(201.7)	(0.0252)(319.8)
	0.3758	0.3490	0.3896	0.2420	0.0500

Reach A, maximum base rates

MECHANISMS LIMITING A VERTEBRATE INVASION:

0	(0.0791)(7.4)	(0.0791)(135.8)	(0.0791)(433.4)	(0.0791)(582.5)
0.5388	0.3944	0.4328	.2772	0.2000

Reach B, mean base rates

0	0	(0.0424)(60.7)	(0.0424)(101.0)	(0.0424)(227.7)
0.4099	0.3717	0.4112	0.2596	0.1000

Reach B, minimum base rates

0	0	(0.0252)(32.8)	(0.0252)(57.1)	(0.0252)(207.7)
0.3758	0.3490	0.3896	0.2420	0.0500

Reach B, maximum base rates

0	0	(0.0791)(63.7)	(0.0791)(163.7)	(0.0791)(342.3)
0.5388	0.3944	0.4328	.2772	0.2000

Reach C, mean base rates

0	0	(0.0424)(3.8)	(0.0424)(79.5)	(0.0424)(77.4)
0.4099	0.3717	0.4112	0.2596	0.1000

Reach C, minimum base rates

0	0	(0.0252)(3.0)	(0.0252)(63.6)	(0.0252)(77.4)
0.3758	0.3490	0.3896	0.2420	0.0500

Reach C, maximum base rates

0	0	(0.0791)(5.2)	(0.0791)(102.7)	(0.0791)(112.0)
0.5388	0.3944	0.4328	0.2772	0.2000

Reach D, mean base rates

0	0	(0.0424)(9.3)	(0.0424)(56.1)	(0.0424)(77.1)
0.4099	0.3717	0.4112	0.2596	0.1000

Reach D, minimum base rates

0	0	0	(0.0252)(28.7)	(0.0252)(55.4)
0.3758	0.3490	0.3896	0.2420	0.0500

Reach D, maximum base rates

0	0	(0.0791)(10.9)	(0.0791)(58.8)	(0.0791)(93.2)
0.5388	0.3944	0.4328	.2772	0.2000

Table B3. Mean, minimum and maximum vital rates used in matrices for Twelvemile Creek reaches A and D with three levels of fishing mortality. Formatted as described in Table B2.

	1	2	Stages 3	4	5
Reach A, mean rates with light fishing	0	0	(0.0424)(102.6)	(0.0424)(230.9)	(0.0424)(469.5)
	0.4099	0.2991	0.1517	0.0213	0.0213
Reach A, minimum rates with light fishing	0	0	(0.0252)(72.1)	(0.0252)(201.7)	(0.0252)(319.8)
	0.3758	0.1957	0.0835	0.0160	0.0160

MECHANISMS LIMITING A VERTEBRATE INVASION:

Reach A, maximum rates with light fishing

0	(0.0791)(7.4)	(0.0791)(135.8)	(0.0791)(433.4)	(0.0791)(582.5)
0.5388	0.3639	0.2819	.1333	0.1333

Reach A, mean rates with medium fishing

0	0	(0.0424)(102.6)	(0.0424)(230.9)	(0.0424)(469.5)
0.4099	0.2534	0.1232	0.0173	0.0173

Reach A, minimum rates with medium fishing

0	0	(0.0252)(72.1)	(0.0252)(201.7)	(0.0252)(319.8)
0.3758	0.1689	0.0678	0.0130	0.0130

Reach A, maximum rates with medium fishing

0	(0.0791)(7.4)	(0.0791)(135.8)	(0.0791)(433.4)	(0.0791)(582.5)
0.5388	0.3067	0.2290	.1083	0.1083

Reach A, mean rates with heavy fishing

0	0	(0.0424)(102.6)	(0.0424)(230.9)	(0.0424)(469.5)
0.4099	0.2078	0.0948	0.0133	0.0133

Reach A, minimum rates with heavy fishing

0	0	(0.0252)(72.1)	(0.0252)(201.7)	(0.0252)(319.8)
0.3758	0.1420	0.0522	0.0100	0.0100

Reach A, maximum rates with heavy fishing

0	(0.0791)(7.4)	(0.0791)(135.8)	(0.0791)(433.4)	(0.0791)(582.5)
0.5388	0.2496	0.1762	.0833	0.0833

Table B3. continued.

	1	2	Stages 3	4	5
Reach D, mean rates with light fishing	0	0	(0.0424)(9.3)	(0.0424)(56.1)	(0.0424)(77.1)
	0.4099	0.3717	0.3333	0.1524	0.0567
Reach D, minimum rates with light fishing	0	0	0	(0.0252)(28.7)	(0.0252)(55.4)
	0.3758	0.3490	0.2978	0.1403	0.0313
Reach D, maximum rates with light fishing	0	0	(0.0791)(10.9)	(0.0791)(58.8)	(0.0791)(93.2)
	0.5388	0.3944	0.3875	.2125	0.1633
Reach D, mean rates with medium fishing	0	0	(0.0424)(9.3)	(0.0424)(56.1)	(0.0424)(77.1)
	0.4099	0.3717	0.3248	0.1506	0.0545
Reach D, minimum rates with medium fishing					

MECHANISMS LIMITING A VERTEBRATE INVASION:

0	0	0	(0.0252)(28.7)	(0.0252)(55.4)
0.3758	0.3490	0.2931	0.1390	0.0297

Reach D, maximum rates with medium fishing

0	0	(0.0791)(10.9)	(0.0791)(58.8)	(0.0791)(93.2)
0.5388	0.3944	0.3717	.2012	0.1496

Reach D, mean rates with heavy fishing

0	0	(0.0424)(9.3)	(0.0424)(56.1)	(0.0424)(77.1)
0.4099	0.3717	0.3163	0.1488	0.0523

Reach D, minimum rates with heavy fishing

0	0	0	(0.0252)(28.7)	(0.0252)(55.4)
0.3758	0.3490	0.2884	0.1376	0.0280

Reach D, maximum rates with heavy fishing

0	0	(0.0791)(10.9)	(0.0791)(58.8)	(0.0791)(93.2)
0.5388	0.3944	0.3558	.1900	0.1358

Table B4. Mean, minimum and maximum vital rates used in matrices for Twelvemile Creek reach A under the restoration scenarios with increased fish growth and three levels of fishing mortality. Formatted as described in Table B2.

	Stages				
	1	2	3	4	5
Restoration scenario, mean rates without fishing	0	(0.0424)(62.6)	(0.0424)(196.3)	(0.0424)(633.5)	(0.0424)(738.4)
	0.4099	0.3717	0.4112	0.2596	0.1000
Restoration scenario, minimum rates without fishing	0	(0.0252)(44.1)	(0.0252)(179.6)	(0.0252)(490.0)	(0.0252)(585.2)
	0.3758	0.3490	0.3896	0.2420	0.0500
Restoration scenario, maximum rates without fishing	0	(0.0791)(84.3)	(0.0791)(213.4)	(0.0791)(791.6)	(0.0791)(905.9)
	0.5388	0.3944	0.4328	.2772	0.2000
Restoration scenario, mean rates with medium fishing	0	(0.0424)(62.6)	(0.0424)(196.3)	(0.0424)(633.5)	(0.0424)(738.4)
	0.4099	0.2326	0.1232	0.0173	0.0173
Restoration scenario, minimum rates with medium fishing	0	(0.0252)(44.1)	(0.0252)(179.6)	(0.0252)(490.0)	(0.0252)(585.2)
	0.3758	0.1371	0.0678	0.0130	0.0130
Restoration scenario, maximum rates with medium fishing	0	(0.0791)(84.3)	(0.0791)(213.4)	(0.0791)(791.6)	(0.0791)(905.9)
	0.5388	0.2913	0.2290	.1083	0.1083
Restoration scenario, mean rates with heavy fishing	0	(0.0424)(62.6)	(0.0424)(196.3)	(0.0424)(633.5)	(0.0424)(738.4)
	0.4099	0.1789	0.0948	0.0133	0.0133

MECHANISMS LIMITING A VERTEBRATE INVASION:

Restoration scenario, minimum rates with heavy fishing

0	(0.0252)(44.1)	(0.0252)(179.6)	(0.0252)(490.0)	(0.0252)(585.2)
0.3758	0.1054	0.0522	0.0100	0.0100

Restoration scenario, maximum rates with heavy fishing

0	(0.0791)(84.3)	(0.0791)(213.4)	(0.0791)(791.6)	(0.0791)(905.9)
0.5388	0.2240	0.1762	.0833	0.0833

Table B5. Minimum and maximum vital rates used in combination matrices for Twelvemile Creek as a single population. Mean matrices were not evaluated. Formatted as described in Table B2.

	Stages				
	1	2	3	4	5
Combination matrix without additional fish growth from restoration scenario, minimum values					
0	0	0	0	(0.0252)(28.7)	(0.0252)(55.4)
0.3758	0.1689	0.0678	0.0130	0.0130	0.0000
Combination matrix without additional fish growth from restoration scenario, maximum values					
0	(0.0791)(7.4)	(0.0791)(135.8)	(0.0791)(433.4)	(0.0791)(582.5)	
0.5388	0.3944	0.4328	.2772	0.2000	
Combination matrix with additional fish growth from restoration scenario, minimum values					
0	0	0	(0.0252)(28.7)	(0.0252)(55.4)	
0.3758	0.1689	0.0678	0.0130	0.0000	
Combination matrix with additional fish growth from restoration scenario, maximum values					
0	(0.0791)(84.3)	(0.0791)(213.4)	(0.0791)(791.6)	(0.0791)(905.9)	
0.5388	0.3944	0.4328	.2772	0.2000	

Table B6. Mean, minimum and maximum vital rates used in matrices for the Hunt Creek, Michigan brook trout population as presented in McFadden et al. (1967). Survival rates for stages 4 and 5 are hypothetical. Formatted as described in Table B2.

	Stages				
	1	2	3	4	5
Hunt Creek, mean rates					
0	(0.0424)(38.0)	(0.0424)(129.9)	(0.0424)(308.5)	(0.0424)(508.0)	
0.4099	0.1789	0.0948	0.0133	0.0133	
Hunt Creek, minimum rates					
0	(0.0252)(35.8)	(0.0252)(122.6)	(0.0252)(286.6)	(0.0252)(490.4)	
0.3758	0.1054	0.0522	0.0100	0.0100	
Hunt Creek, maximum rates					
0	(0.0791)(41.0)	(0.0791)(136.5)	(0.0791)(319.7)	(0.0791)(525.6)	
0.5388	0.2240	0.1762	.0833	0.0833	

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