DISSERTATION

POPULATION ECOLOGY OF AN INVASION: DEMOGRAPHY, DISPERSAL, AND EFFECTS OF NONNATIVE BROOK TROUT ON NATIVE CUTTHROAT TROUT

Submitted by
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In partial fulfillment of the requirements
For the Degree of Doctor of Philosophy
Colorado State University
Fort Collins, Colorado
Fall 2002

UMI Number: 3075375

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7 October 2002

WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY DOUGLAS PAUL PETERSON ENTITLED POPULATION ECOLOGY OF AN INVASION: DEMOGRAPHY, DISPERSAL, AND EFFECTS OF NONNATIVE BROOK TROUT ON NATIVE CUTTHROAT TROUT BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY

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ABSTRACT OF DISSERTATION

POPULATION ECOLOGY OF AN INVASION: DEMOGRAPHY, DISPERSAL, AND EFFECTS OF NONNATIVE BROOK TROUT ON NATIVE CUTTHROAT TROUT

Invasions are population-level phenomena, but are seldom studied as such. To test for population-level mechanisms by which nonnative brook trout (*Salvelinus fontinalis*) replace native Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*), I conducted a four-year removal experiment and mark-recapture study in long segments of four Rocky Mountain headwater streams with sympatric trout populations. Two streams were at moderate (2500 – 2700 m) and two were at high (> 3150 m) elevation, and brook trout were removed annually from two streams (treatments), but not the other two (controls). At moderate elevation, age-0 and -1 cutthroat trout survived at rates 2 – 13 times higher on average where brook trout were removed, but age-0 cutthroat trout survived at rates nearly 10 times lower than age-0 brook trout where they were not removed. At high elevation, cutthroat trout recruitment failed despite brook trout removals apparently because of cold water temperatures, but adult cutthroat trout at all elevations survived at similar rates whether brook trout were removed or not (mean survival 44 – 47%). Brook trout reduced survival of juvenile cutthroat trout through biotic interactions, leading to population declines. Weirs operated in three streams indicated that cutthroat trout tended to emigrate downstream during summer, but removing brook trout did not change this behavior. In comparison, brook trout, primarily mature adults, immigrated upstream at high rates and could rapidly recolonize reaches where their populations had been removed. Immigration may help sustain invasions in harsh habitats where environmental conditions limit recruitment. Brook trout immigrated from a range of distances. Although 46 – 89% of brook trout recaptured in three streams moved < 50 m, 6 – 36% moved > 250 m, and some individuals moved up to 2 km within a season. Brook trout invasions appear to be driven by two simultaneous processes: a wave of local movement that exerts biotic pressure on the downstream limit of the cutthroat trout population, and jump dispersers moving upstream past the invasion front facilitating rapid population spread. Prevention or complete eradication are the best management options, but two within-year brook trout removals repeated in consecutive years may forestall extirpation of invaded cutthroat trout populations.

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INTRODUCTION

Native cutthroat trout in the western USA have been in decline since the mid 19th century, and currently occupy less than 5% of their historic ranges (Benhke 1992). Habitat modification and negative interactions with nonnative salmonid species are the two major factors responsible for the decline and continued imperilment of these fishes (Young 1995; Harig et al. 2000; Harig and Fausch 2002). Brook trout have been widely introduced into western streams, and generally extirpate cutthroat trout where the two come into contact (Behnke 1992). Despite this well-known pattern of replacement, the mechanisms causing it have been difficult to isolate (Griffith 1988; Fausch 1988, 1989). Habitat relationships have been measured in the field (Griffith 1972; Schroeter 1998; Dunham et al. 1999), and individual-level competition (Griffith 1972; Cummings 1987; DeStaso and Rahel 1994; Wang and White 1994; Thomas 1996; Hilderbrand 1998; Schroeter 1998; Novinger 2000) or predation (Novinger 2000) have been observed or tested in laboratory tanks, small enclosures, or short stream reaches. However, results tended to depend on scale and the size or age classes tested, and replicated manipulations at appropriate spatial and temporal scales are lacking, making generalization and management recommendations difficult. Thus, I argue that initial efforts to understand invasions of this type should: 1) focus on the population biology of the invading and affected species, 2) include appropriately scaled experiments that measure changes in reproduction, survival, and movement, and 3) detect how these mechanisms vary by age class. Results based on this demographic approach will be relevant to scales at which managers make decisions, and motivate smaller-scale experiments to test proximate individual-level mechanisms (i.e., competition, predation) among the appropriate ages or sizes of brook trout and cutthroat trout. This dissertation is composed of three sections, which describe: 1) a conceptual framework for testing mechanisms of stream fish invasions, 2) the results of a four-year removal experiment based on this framework to test the effects of brook trout on demography of cutthroat trout, and 3) empirical data on movement of brook trout that drives their invasion.

Chapter 1 presents a conceptual framework for testing population-level mechanisms of invasion by nonnative stream salmonids and their effects on native salmonids. This chapter is based on the principle that invasions are population-level processes (Parker 2000), so the demographic processes of births, deaths, immigration, and emigration are the appropriate response variables for mechanistic studies. This chapter also promotes the idea that targeted, taxon-specific invasion studies are necessary to provide the empirical basis for prediction (Lodge 1993). Using the example of stream salmonid invasions, a widely introduced group of mobile vertebrates, I review the existing literature, provide a simple framework to study the population biology of these invasions, and offer specific suggestions to improve the design of such studies. I conclude by demonstrating how the framework can be applied to design a study to measure population-level mechanisms by which brook trout replace native cutthroat trout in small streams.

Chapter 2 presents results from a four-year, large-scale field removal experiment designed using the framework in Chapter 1. The experiment measured the demography

of brook trout invasions and tested mechanisms by which they replace Colorado River cutthroat trout in small, headwater streams at two different elevations. Mark-recapture techniques were used to estimate reproduction, survival by age class, and movement of trout in segments of four streams, and results for cutthroat trout were contrasted between streams where brook trout were annually removed or not. Results are used to propose a mechanism by which brook trout cause cutthroat trout population decline, to provide suggestions for more detailed individual-level experiments with the appropriate age classes of trout, and to offer practical suggestions to managers dealing with invasion by nonnative brook trout.

Chapter 3 reports on the movement of brook trout and cutthroat trout in three of the four streams, and its implications for understanding mechanisms of brook trout invasions. Data from trout captured and recaptured during electrofishing, during sampling downstream of the primary study areas, and at two-way fish weirs were used to test hypotheses about the timing, direction, rate, distance, and demographic composition of moving trout, primarily brook trout. Results were used to discuss how these characteristics of moving brook trout and their movement patterns contribute to making them potent invaders of cutthroat trout habitat.

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ACKNOWLEDGMENTS

This dissertation was dramatically improved by input from my advisory committee: Kurt Fausch (advisor), Gary White, Kevin Bestgen, and LeRoy Poff. Colden Baxter, Mark Coleman, Amy Harig, Ed Weber, and Mike Young provided valuable comments on various chapters of this dissertation. Financial support was provided by the Colorado Division of Wildlife (CDOW), U.S. Department of Interior Central Utah Project Completion Act (CUPCA), U.S.D.A. Forest Service Fish Habitat Relationships Program (FHR), and Trout Unlimited (TU). I thank Tom Nesler (CDOW), Dave Langlois (CDOW), Ralph Swanson (CUPCA), Nick Schmal (FHR), Dave Winters (FHR), Mike Young (FHR), and Whit Fosburgh (TU) for administering these funds. I was also supported by scholarships from the West Denver Chapter of Trout Unlimited, Cook Memorial Scholarship fund, Peters Scholarship fund, and the Western Division of the American Fisheries Society. Logistic assistance and access to information about field sites was provided by Bruce Rosenlund (US Fish and Wildlife Service), Jake Bennett (CDOW), Dan Brausch (CDOW), Sherman Hebein (CDOW), Greg Horstman, Mike Wunder (Colorado Natural Heritage Program), Amy Harig (Colorado State University), Marsha Raus (USFS), Aaron Boswarth (USFS), Mike Young (USFS-FHR), Mike Kinzer (Bureau of Land Management), and Jay Thompson (BLM). Field assistance was provided by (in alphabetical order): Matt Andre, Holly Antall, Matt Bates, Aaron

Boswarth, Jay Breidert, Warren Colyer, Harry Crockett, Mark Day, Tom Deem, Matt Entz, Kurt Fausch, Ashley Ficke, Mark Fiorini, Tom Fresques, Zephra Gordanier, Wade Johnson, John Hickey, Christine Hirsch, Brandon Hoffner, Ben Kennedy, Chris Kennedy, Jeffrey Kennedy, Matt Kondratieff, Ben Kraft, Jesse Laframboise, Anita Lahey, Tim Lynch, Peter Martin, Seth Martin, Mark Minner, Jeremy Monroe, Eric Odell, Sara Peterson, Dana Pittman, Kim Potter, Andrew Ramey, Robin Revelle, Laurel Saito, Rachel Saylor, Scott Schneider, Julie Scheurer, Zach Shattuck, Cory Sipher, Brett Smithers, Todd Stevenson, Sean Tackley, Chris Vogel, Ed Weber, James Wick, and Joe Zendt. Matt Entz, Brandon Hoffner, Ben Kennedy, Seth Martin, Andrew Ramey, and James Wick helped with laboratory analyses. Gary White, Paul Lucaks, Aaron Ellingson, and Ken Burnham provided assistance with statistical analysis and program MARK.

DEDICATION

To my wife, Sara, whose unconditional support sustained me through my long and arduous graduate education. To my parents, Joan and Paul Peterson, for their lifelong encouragement and guidance. To my grandfather, Knut Lunnum, who fostered a respect for nature. To my daughter, Gabriella Loan, who reminded me what really matters in life.

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CHAPTER ONE: TESTING POPULATION-LEVEL MECHANISMS OF INVASION BY A MOBILE VERTEBRATE: A SIMPLE CONCEPTUAL FRAMEWORK FOR SALMONIDS IN STREAMS

Abstract

Invasion ecology suffers from a lack of the ability to predict the outcome of particular invasions because of reliance on verbal models and lack of rigorous experimentation. More progress is likely to be made by considering invasions as population-level phenomena and initially focusing on specific taxa or particular categories of invasions. To this end, I propose a simple conceptual framework to motivate studies of invasion by salmonids (salmon, trout, grayling, and whitefish) in streams that emphasizes population-level mechanisms affecting native species and promoting spread by the invader. Specifically, the only direct mechanisms by which the abundance of the native species can decline are through decreased reproductive rates or survival at specific life stages, net emigration, debilitating or fatal diseases introduced by the invader, or a combination of these factors. Conversely, abundance of the invader must increase by local reproduction, high survival, net immigration, or a combination of these factors. Review of existing salmonid invasion papers suggests that future studies could be improved by using manipulative field experiments at a spatial and temporal scale appropriate to address population-level processes, characterizing how movement affects the establishment and spread of an invader, and including abiotic context in experimental design. Using the example of brook trout (*Salvelinus fontinalis*) invasion into streams containing native Colorado River cutthroat trout (*Oncorhynchus clarki pleuriticus*) in the central Rocky Mountains (US), I demonstrate how the framework can be used to design a manipulative field experiment to test for population-level mechanisms causing ecological effects and promoting invasion success. Experiments of this type will give invasion ecologists a useful example of how a taxon-specific invasion framework can improve the ability to predict ecological effects, and provide fishery biologists with the quantitative foundation necessary to better manage stream salmonid invasions.

Introduction

Introduced fishes that become invasive are one of the primary causes of endangerment and extinction of native fishes (Williams et al. 1989; Allan and Flecker 1993), yet factors causing these invasions and their resulting effects are rarely understood. Salmonids (salmon, trout, grayling, and whitefish) are among the most widely introduced fishes worldwide (Welcomme 1992), often become invasive, and have effects that include local extinction of native fauna (Townsend 1996). However, in few cases are the mechanisms understood well enough to predict the course of the invasion or its effects, or propose effective control measures, the primary goals of invasion biology (Parker et al. 1999; Sakai et al. 2001).

Invasion biology has traditionally relied on anecdotal or verbal models that describe attributes of invasive species or invasible communities (Lodge 1993a, b; Moyle and Light 1996a; Schrader-Freschette 2001). These models often lack a clear theoretical framework (Townsend 1991, 1996; Kareiva 1996), and have rarely been tested with empirical data (Parker 2000). Furthermore, the predictive power of these models is often low because they are not based on experiments. One recommendation for producing reliable predictions is to develop specific, mechanistic models for invasions by particular taxa (Lodge 1993b) that can be tested with experimental data collected at the appropriate level of biological organization.

Invasions by vertebrates like fishes have most often been studied at the individual level of biological organization, by measuring interactions for a particular age group (typically adults) to determine proximate mechanisms for effects of the invader on the native invaded species. However, invasions succeed or fail at the population level (Parker 2000). Demographic rates (births, immigration, deaths, and emigration) of the invader are the ultimate mechanisms that determine whether an invading species establishes a reproducing population. Likewise, changes in the vital rates of the native species resulting from interactions with the invader determine whether the native species maintains a viable population. Unless biotic interactions at a particular life stage change demographic rates, measuring these interactions may be inconsequential. Thus, population-level research that identifies the life stages at which critical interactions occur is needed to direct individual-level studies. Like the mechanisms of invasions, the impacts of invaders on native species are of most interest at the population level, because conservation biologists place emphasis on the viability of species' populations. Moreover, impacts are most commonly reported for populations rather than on genetics, individuals, communities, or ecosystems (Parker et al. 1999). Thus, the population level is likely to be the nexus at which useful mechanistic models can be developed for specific taxa or guilds, and for which hypotheses can be tested by experiments at realistic scales of space and time.

Ideally, all aspects of an invasion should be studied so that mechanisms affecting the outcome are not overlooked. However, relatively few studies have followed a particular invasion from beginning to end (Parker 2000; Kolar and Lodge 2001). To motivate more systematic studies, invasions have been variously organized into sequential steps. For example, Vermeij (1996) classified invasions into three stages: 1) arrival – caused by natural or human-assisted dispersal of individuals to the recipient location, 2) establishment – persistence of the invader resulting from local reproduction and recruitment potentially augmented by continued immigration, and 3) integration – due to ecological links that develop between invader and invaded species. Similarly, Kolar and Lodge (2001) discuss four transitions (transportation, release, establishment, and spread) that nonnative species must overcome in order to successfully invade. In practice, however, usually only specific stages or transitions are emphasized. For example, early stages of invasion such as dispersal or transport are generally understudied compared with later stages after ecological impacts are already evident, even though the early stages may be most important for resource managers trying to prevent invasions (Kolar and Lodge 2001). Drawing on examples from fishes introduced via ballast water from ships, Wonham et al. (2000) argued that variability in survival among invasion stages implies that all stages must be sampled. For mobile and long-lived vertebrates like fishes, a meaningful predictive framework for invasions must consider the potentially large spatial and temporal scales of investigation necessary to understand mechanisms that promote or limit invasions, and to determine how invaded populations respond.

In this paper, I propose a simple conceptual framework to motivate and guide studies of invasions by salmonids in streams. This approach emphasizes changes in demographic processes of the invading and native species, and integrates recent understanding about mobile stream salmonid populations (Gowan and Fausch 1996b; Kocik and Ferreri 1998; Rieman and Dunham 2000). I discuss the scales at which answers and experiments are needed, stages of invasions that need to be understood, and ecological contexts that obscure general conclusions and thus limit prediction. Documented stream salmonid invasions are used to develop guidelines for improving the design of future studies. The proposed framework is subsequently applied to a specific salmonid invasion in streams of the Rocky Mountains in western North America. I conclude by briefly relating how results may apply to fishery management and how this framework strengthens the theoretical underpinnings for studying stream fish invasions.

Stream salmonids as a model system

Stream salmonids are an ideal group for developing a habitat- and taxon-specific model of invasion by a mobile vertebrate for five general reasons. First, stream salmonid introductions are globally widespread (Fausch 1988), providing a wealth of examples across geographic regions and ecological contexts. Intercontinental transfer of salmonids has been common, and introduction and naturalization of nonindigenous salmonids has occurred on all continents except Antarctica (Krueger and May 1991). North American rainbow trout (*Oncorhynchus mykiss*) have been particularly successful, with populations introduced in >80 countries throughout South America, Europe, Africa, Asia, and Australasia (Welcomme 1988; Fausch et al. 2001). Eurasian brown trout (*Salmo trutta*) have also been introduced into >30 countries in North America, South America, Africa, and Australasia (Townsend 1996). In North America, these salmonids are two of the top five invasive fish species as judged by number of nonnative occurrences (Gido and Brown 1999; Rahel 2000). Most North American species of Pacific salmon (*Oncorhynchus*) and charr (*Salvelinus*) have also been transferred outside their native range within the continent and abroad (Krueger and May 1991). For example, brook trout (*Salvelinus fontinalis*) from eastern North America have been naturalized into western waters, and rainbow trout from Pacific coast drainages have been successfully transferred to eastern North America, which has contributed to the homogenization of fish faunas (Rahel 2000).

A second reason that stream salmonids are a suitable taxon for developing an invasion framework is that their basic biology and ecology is well understood. Salmonids have been well studied compared with other groups of stream fishes because of their cultural, economic, and recreational importance, so their behavior, physiology, life histories, and ecological roles are relatively well known (e.g., Groot and Margolis 1991; Stolz and Schnell 1991). This robust foundation permits prediction of how specific processes or interactions may influence invasions and what effects can be expected on native salmonids.

Third, salmonids in streams live in bounded linear habitats, facilitating study of distribution and movement of invading taxa. Small streams can be conceptualized as one-dimensional habitats arranged in a hierarchical network (Adams et al. 2001), permitting relatively simple mathematical and statistical analysis of movement patterns (Skalski and Gilliam 2000; Rodríguez 2002). There is a rich body of literature describing movements by stream salmonids (reviewed by Gowan et al. 1994), and recent focus on the role of movement in salmonid invasions in streams (Adams et al. 2000).

Fourth, salmonid invasions are likely to be detected more quickly compared with invasions by more cryptic taxa. Anglers and fishery biologists are keenly interested in the distribution and abundance of stream salmonids, making it probable that many invasions are discovered at early stages (Fausch et al. 2001). In contrast, incipient invasions by smaller or more nondescript organisms may be detected much later, leading to confusion over invasion dynamics. For example, Carey (1996) concluded that outbreaks of Mediterranean fruit fly (*Ceratitis capitata*) in southern California (USA) resulted from 'early stage subdetectability' of an invasion with a long lag phase rather than from multiple reintroductions as was previously assumed. Invading salmonids are more easily identified as introduced because their historical ranges are well known (e.g., Behnke 1992). Many invertebrate and some fish taxa are more cryptogenic and cannot be definitively categorized as native or introduced, obscuring conclusions about invasion routes, community invasibility, and invasion success rates (Carlton 1996).

Fifth, salmonids often invade ecologically simple systems and have the potential to produce large ecological effects. Ecological theory suggests that systems with few taxa are often affected by strongly interacting species (Paine 1980; Power et al. 1996), and stream salmonids are known to display strong interference competition in interspecific dominance hierarchies (Kalleberg 1958; Jenkins 1969) and strong piscivory (Strange et al. 1992; McIntosh 2000). Accordingly, aquatic ecologists have argued that waters suitable for salmonids are often more vulnerable to invasion than other aquatic systems because of low fish species diversity, low primary production, or habitat degradation (Moyle 1986; Krueger and May 1991). For example, Moyle and Light (1996a, b) observed that piscivorous fishes are more likely to successfully invade and alter fish assemblages than omnivores or detritivores. Thus, the piscivorous nature of brown trout may, in part, explain its relative success as an invader and its potential to harm native fish faunas (e.g., Moyle and Vondracek 1985; Townsend 1996). Nonindigenous stream salmonids often replace native salmonid species (Moyle 1986; Gresswell 1988; Behnke 1992) and influence community structure and function (Moyle et al. 1986; Flecker and Townsend 1994), so consequences of salmonid invasions are well established even if the mechanisms causing them are not well understood (Krueger and May 1991).

A conceptual framework for studying salmonid invasions in streams

To promote a more thorough understanding of the mechanisms underpinning salmonid invasions, I present a simple conceptual framework based on first principles of population biology which emphasizes measuring changes in demographic rates of native and invading salmonid populations (Table 1.1). Here I define 'native' as the salmonid whose habitat is being invaded, even though that species may itself be naturalized. The 'invader' is a nonnative species that is attempting to establish a naturalized population.

I illustrate the framework with a field removal experiment using a two-species system with one invading nonnative and one native salmonid (Table 1.1). In a natural setting, a common outcome for this invasion is for the invading salmonid to replace the native salmonid. This pattern leads to two hypotheses: 1) the invader must cause the native species to decline by reducing its reproduction, reducing survival at some age class, causing emigration, or transferring disease, and 2) the invader must increase by increased local reproduction, high survival through some or all age classes, or immigration. Predictions from these hypotheses can be tested where the invader and native species occur in sympatry using a removal experiment. For example, the first prediction is that the native salmonid will increase in treatment streams where the invader is removed, compared to control streams, by one or more of six possible mechanisms: increased birth rate, increased survival (at young-of-the-year, juvenile, or adult life stages), decreased emigration, or decreased incidence of disease (see Table 1.1.A). The second prediction is that the invading salmonid will increase in control streams by one or more of five possible mechanisms: increased birth rate, increased survival (at young-of-the-year, juvenile, or adult life stages), or increased immigration (see Table 1.1.B). The data needed to test these mechanisms logically follow from the predictions. For example, to determine if survival by native young-of-the-year (YOY) fish is affected by nonnative invasion, the appropriate data to collect are abundance estimates of YOY (e.g., by electrofishing, seining, or visual estimation techniques), and interannual survival estimates for YOY (e.g., using capture-recapture techniques) which could then be compared between experimental groups. An increase in survival rates for the native YOY fish in the treatment streams, compared to controls, implies that treatment fish have been released from biotic interaction with the nonnative; thus I infer that presence of the nonnative salmonid reduces native salmonid YOY survival rates. Next, I highlight the need for this framework by reviewing published reports of stream salmonid invasions and offer five proposals to improve the design of field studies given current knowledge of salmonid population dynamics.

Focus on population-level processes

Field studies of stream salmonid invasions have usually revealed clear patterns at the population and community level, such as reduced abundance or replacement of native species (Table 1.2), but the mechanisms behind these patterns are not well understood (Fausch 1988). For example, introduced brown trout replaced brook trout in a stream in the upper Mississippi River basin (US) over 15 yr (Waters 1983), but based on the data collected, it was not possible to identify how demographic rates of brook trout changed because of the invasion. Establishing which population-level mechanisms are important and on which life stage they act remains a gap in our understanding of salmonid invasions, and often prevents managers from developing control measures that reduce effects of invading salmonids.

In contrast to larger-scale observational studies, smaller-scale experimental studies have often focused on individual-level biotic interactions at a single age class or life stage (Table 1.2). A survey of the stream salmonid invasion literature suggests that investigators have made an inductive leap from observing that a native population is declining to conducting individual-level tests of competition or predation. However, without knowing at which life stage the invader reduces survival of the native species, studies of individual-level interactions may focus on the wrong stage and never reveal mechanisms that can explain population-level patterns. This is important for salmonids, because juveniles and adults can have different ecological requirements (Baltz and Moyle

1993; Elliot 1994), and thus different survival and movement rates. For example, introduced rainbow trout commonly replace native brook trout in eastern North American streams from the southern Appalachian Mountains north through Newfoundland (Larson and Moore 1985; Fausch 1988; Krueger and May 1991). However, individual-level studies of competition (typically measuring behavior and growth) between these two species have been unable to establish a probable mechanism causing such replacement (Cunjak and Green 1983, 1984, 1986; Magoulick and Wilzbach 1998a, b). Perhaps these studies were not designed to consider the potential role of emigration or immigration, suffered enclosure effects, or missed important biotic interactions because they did not consider all life stages. Interestingly, models that included all life-stages did suggest a population-level mechanism whereby rainbow trout can replace brook trout. Changes in egg or juvenile survival of brook trout had a larger effect on brook trout population dynamics than changes in survival of adult fish using age-structured (Marschall and Crowder 1996) or individual-based models (Clark and Rose 1997b; Clark et al. 2001). In warmer habitats, higher fecundity may favor rainbow trout and lead to replacement of brook trout (Clark and Rose 1997b). Ultimately, appropriate field data on vital rates of these populations must be collected to validate simulations and to suggest empirical studies of important proximate individual-level mechanisms (e.g., competition or predation) at the proper life stage.

Select appropriate scales for study

The spatial and temporal extent for studies of stream salmonid invasions will also need to be expanded if we hope to address the population-level processes outlined in the framework. Most stream salmonid invasion studies were at spatial scales inadequate to detect the importance of movement, and temporal scales too short to measure changes in survival (Table 1.2). Future studies should explicitly consider the space required by native and invading species to complete their life histories, the potential for immigration to catalyze invasions or emigration to produce effects, and the time required to detect changes in abundance or survival (Connell and Sousa 1983). Stream fishes often require several distinct habitats through ontogeny that are dispersed in space and time to provide favorable growing conditions, refugia during periods of environmental stress, and spawning and incubation sites (Schlosser 1995; Schlosser and Angermeier 1995). Ranging movements to find these suitable habitats (Dingle 1996), and movement among habitat patches, are critical population-level processes for mobile vertebrates including salmonids (Fausch and Young 1995; Rieman and Dunham 2000). Although habitat requirements for salmonids are relatively well understood, the spatial juxtaposition of these habitats and the movement required to link them have seldom been thoroughly considered in previous salmonid invasion studies reporting population-level effects (Fausch et al. 2002). To understand invasion dynamics and effects, it will be necessary to identify places on the landscape that may be sources (Pulliam 1988) or nodes of production (Adams 1999) versus sinks or areas lacking reproduction for invading and native populations. Moreover, natural spatial variability in density of stream salmonids (Hankin and Reeves 1988) and the potential for interspecific biotic interactions to occur only at certain places on the landscape (Fausch et al. 2002) may lead to inaccurate conclusions when the scales of these processes are not considered in design and sampling.

Landscape ecologists refer to grain (the smallest unit measured) and extent (overall area encompassed) when describing the lower and upper boundaries of the scale of investigation (Wiens 1989). Sampling grain typically corresponds to the observation unit, or the scale at which replication and thus the strongest inferences are made, so it is a useful metric to compare the spatial scale of different studies. The spatial sampling grain of many salmonid invasion studies reporting population-level effects typically ranged from tens to hundreds of meters (5 of 8 studies reviewed; Table 1.2), whereas only two studies encompassed more than one kilometer (spatial scale of the remaining study was not reported). The spatial scale of these studies may have been appropriate for the particular questions asked, but if the goal is to quantify demographic rates that are influenced by mechanisms operating over thousands of meters of aquatic habitat, then the scale will need to be expanded to the landscape level.

Stream salmonids also have age-structured populations, so repeated annual sampling is needed to detect changes in demographic rates. Many stream-resident salmonids begin reproducing in their second or third year of life (McFadden 1961; Behnke 1992), so measuring rates over more than one generation requires monitoring populations a minimum of three or four years. Connell and Sousa (1983) suggested that community persistence studies should account for at least one complete turnover of the assemblage, or in practical terms, at least two generations for a consistently reproducing species (e.g., Moyle and Vondracek 1985). Stream fishes like salmonids are easily marked or tagged (Skalski and Gilliam 2000), permitting researchers to follow the fate of individuals. Using capture-recapture techniques and assuming constant capture probabilities, a single estimate of interannual survival requires two primary sampling periods ~1 yr apart (White and Burnham 1999). Three such survival estimates, the minimum number to detect a trend, would thus require monitoring the population over 4 yr. For example, Gowan and Fausch (1996a) reported on an 8-yr study to determine effects of habitat manipulation on abundance and survival of brook trout, which encompassed four generations. Such long-term data are critical to assess the relative importance of movement (emigration and immigration) versus survival, and changes in juvenile versus adult demography (Riley and Fausch 1995; Gowan and Fausch 1996a, b).

Long-term data are also required to detect effects of biotic interactions under fluctuating environmental conditions. For example, effects of competition and predation influenced by the timing of floods over a 10-yr period produced a pattern of fluctuating coexistence among three species of introduced salmonids in a Sierra Nevada (US) stream (Seegrist and Gard 1972; Moyle and Vondracek 1985; Strange et al. 1992). A shorter, snapshot study might have incorrectly attributed changes in abundance to either biotic or environmental effects, and missed the interaction between these factors. Effects of species manipulations often require substantial time to become evident in natural systems (Power et al. 1996), so careful consideration must be given to the pre- and post-manipulation data required to make robust conclusions about factors influencing population-level processes. If salmonid populations have inherently variable interannual abundance, the power to detect demographic trends within a few years may be low (Ham and Pearsons 2000). Small runoff-driven streams have higher environmental stochasticity than large rivers or lakes (Matthews 1998), and regional differences in hydrology may prevent accurately predicting invasion dynamics and species coexistence across broad geographic areas (Moyle and Light 1996a). Thus, researchers should consider the natural variability of the system they plan to study which may limit the ability to detect a clear trend.

Adopt an experimental approach

Experiments conducted at the population level are needed to establish cause-and-effect relationships and define mechanisms responsible for success and impacts of stream salmonid invasions. Kareiva (1996) proposed that invasion ecology has lagged far behind other fields in ecology in using manipulative field experiments, and this is also true of stream salmonid invasion studies (Table 1.2). Most experiments have been done in the laboratory using artificial channels or in small field enclosures (ca. 0.5-10 m^2), and have emphasized individual-level mechanisms. Most studies reported that invaders harmed native salmonids via competition measured by niche shifts or behavioral dominance (e.g., DeWald and Wilzbach 1992; McIntosh et al. 1992; Wang and White 1992), whereas fewer measured changes in attributes that more directly affect fitness, such as growth (Fausch and White 1986), survival (McIntcsh 2000) or incidence of fatal disease (DeWald and Wilzbach 1992). In contrast, most population- and community-level studies were observational. Moore et al. (1983, 1986) conducted the only known long-term, replicated population-level manipulation of an invading salmonid. They reduced the abundance of rainbow trout over 4-6 yr in six Appalachian Mountain streams and observed an increase in the abundance of native brook trout. Despite the clear population-level response of brook trout in treatments, more detailed research would have been required to make stronger inferences concerning the causal mechanisms (Fausch 1988).

The lack of experimental manipulations of invading salmonids and measurement of ultimate population-level mechanisms (Table 1.1) makes it difficult to isolate factors contributing to success of invaders and their effects on native species, and therefore to advise managers on mitigation and restoration efforts. Without rigorous experimental studies, fishery biologists responsible for restoring invaded populations of native salmonids may be unable to select among alternative explanations for the decline of native stocks. For example, the replacement of brook trout by brown trout observed by Waters (1983), could have also been affected by concurrent land use changes and unusual environmental conditions. Moreover, managers will not know what actions may improve success of native populations if mechanisms responsible for declines are not identified. Observational studies are needed first to document ecological patterns, but large-scale manipulative experiments on populations will be required to develop a robust mechanistic understanding and improve the ability to predict the outcome of stream salmonid invasions.

Focus on movement by the invader

Increased emphasis should be placed on measuring and interpreting movement by invaders because this is the least-understood element of stream salmonid invasions. Studies measuring ecological effects other than movement are over represented in the literature, and there were virtually no data reported showing how dispersal of the invading species contributed to the success or effects of these invasions (Table 1.2). Two specific components of movement warrant attention. First, the rate and timing of immigration by invaders should be measured at the invasion front to assess the potential for rapid population expansion. Individuals at the advancing edge of the invasion may be far-ranging elements of the population that promote rapid spread. Long distance movement by stream fishes is apparently common (Gowan et al. 1994; Young 1994, 1996), and may be a general property of invasive organisms across many taxa (Suarez et al. 2001). Skalski and Gilliam (2000) developed a two-compartment theoretical model, with slow- and fast-moving population segments, based on movement measured in an assemblage of non-salmonid stream fishes. Rodríguez (2002) proposed a similar model for sedentary and mobile stream salmonids based on data from the literature. Skalski and Gilliam (2000) suggested that the fast-moving individuals that compose the long tails of the leptokurtic movement distribution might explain how 'jump dispersal' facilitates high rates of population spread (Kot et al. 1996; Lewis 1997). In jump dispersal, some propagules establish ahead of the main population front and subsequently produce more propagules for further colonization, leading to explosive population spread (Turchin 1998). Recent evidence suggests that stream salmonid populations include individuals that move many different distances, with the most mobile individuals moving many kilometers within a season (Riley et al. 1992; Gowan et al. 1994; Gowan and Fausch 1996b; Young 1996; Northcote 1997; Hilderbrand and Kershner 2000). If leptokurtic movement distributions are common for stream fishes like salmonids, then long-distance movements must be considered to develop a comprehensive and predictive framework at the population level. In addition, examination of movement should also consider the primary direction of invasion and the potential for non-lethal dispersal of younger fishes during high flow events. Many stream salmonid invasions are upstream directed (Fausch 1989), but downstream invasions are also possible, particularly where headwater lakes provide a source population of invaders. For example, downstream-directed invasions may proceed more rapidly than those directed upstream because dispersal barriers are easier to overcome (Adams et al. 2001). High flow can disperse young fishes downstream (reviewed by Gowan et al. 1994), distributing propagules for further invasion if individuals survive (K. Bestgen, Larval Fish Laboratory, Colorado State University, Fort Collins, CO, USA, personal communication).

The role of immigration in increasing local abundance of the invader or sustaining an invasion in a sink habitat (Vermeij 1996) is a second component that must be documented to establish the relative importance of movement versus survival and reproduction in facilitating the invasion. Overall, the arrival stage of salmonid invasions may be difficult to study because it can happen rapidly. The capability for invading salmonids to spread rapidly via jump dispersal means that some invasions are not detected until after native species have been harmed (Behnke 1992). Nonetheless, stream salmonids are still a suitable model for studying arrival, because their invasions are often detected at an earlier stage than other invasive taxa (Fausch et al. 2001). Releasing an invasive salmonid into a natural system to measure invasion rates (or effects) is unethical (McIntosh 2000). However, one alternative afforded by the framework is to remove established invaders from a stream reach, then measure recolonization as a surrogate for the arrival stage of the invasion.

Incorporate context into design

Invasion success or effects may be greater under certain abiotic conditions than others (Dunson and Travis 1991), so experimental designs that account for these factors hold promise to improve predictive power. The role of these covariates may also change with scale, from environmental factors that influence physiology and behavior at the local scale (Taniguchi and Nakano 2000), to abiotic filters that limit invaders at the landscape scale (Poff 1997). Important abiotic factors shown to alter invasion or biotic interactions among stream salmonids include: flow regime (Seegrist and Gard 1972; Moyle and Light 1996a, b; Fausch et al. 2001), temperature (Reeves et al. 1987; Taniguchi and Nakano 2000), disturbed habitats (Moyle and Light 1996a, b) and gradient (Fausch 1989). Two examples show the importance of such context (sensu Power et al. 1996) to biotic interactions and invasion dynamics of salmonids. First, Strange et al. (1992; Strange and Foin 1999) reported that hydrologic conditions controlled the recruitment of spring- versus fall-spawning salmonid and other fishes in a Sierra Nevada stream (USA). Thus an abiotic factor set the context within which competition and predation by introduced brown trout altered the native fish community. Second, Taniguchi and Nakano (2000) demonstrated in laboratory streams that temperature affected the outcome of competition between two native charr species (*Salvelinus leucomaenis* and *S. malma*) which come in contact in mountain streams of northern Japan. One species reduced survival of the other by behavioral dominance at warm temperatures, whereas the second species survived longer than the first at cold temperatures because of higher physiological tolerance. This second study also showed how changes in behavior can be linked to changes in demographic parameters which can ultimately explain the population-level patterns observed in the field. Abiotic context must be explicitly included in the design of salmonid invasion studies in natural streams if investigators hope to isolate the underlying mechanisms and their effects.

Application to brook trout invasion of cutthroat trout streams

Here I apply this framework and the concepts emphasized above to test population-level mechanisms of the widespread invasion by brook trout into streams inhabited by cutthroat trout (*Oncorhynchus clarki*). The 12 extant subspecies of cutthroat trout in the interior of the western USA now each occupy less than 5% of their historic range (Gresswell 1988; Behnke 1992), and are the focus of large-scale recovery efforts (USFWS 1998; CRCT Task Force 2001). Habitat loss, overfishing, hybridization with nonindigenious rainbow trout and cutthroat trout, and competitive replacement by nonindigenous salmonids are the main factors thought to have caused this decline (Allendorf and Leary 1988; Young 1995). Encroachment by introduced trout, particularly brook trout, is thought to be the greatest current threat to remaining populations (Young 1995; Young et al. 1996; Harig et al. 2000).

Brook trout replace most subspecies of interior cutthroat trout, but there is little direct evidence for ultimate population-level mechanisms. Brook trout typically extirpate cutthroat trout from downstream reaches of streams, although zones of sympatry of variable length or allopatric cutthroat trout may exist upstream (Griffith 1988; Fausch 1989). When brook trout were present, stream-dwelling Lahontan cutthroat trout (*O. c. henshawi*) were restricted to higher elevations (Dunham et al. 1999) and had lower biomass (Schroeter 1998). Competition is purportedly the mechanism causing this replacement (Griffith 1988), and several studies have reported that brook trout behaviorally dominate and reduce growth of cutthroat trout, responses to individual-level mechanisms that may ultimately cause declines at the population level (Table 1.3).

However, results often depended on study setting, design, or sizes or age classes of individuals on which interactions were measured. For example, in two studies there was weak evidence, or no evidence, for a niche shift by adult cutthroat trout when brook trout were removed in a field experiment (Cummings 1987) or added to an artificial stream channel (Griffith 1972). Griffith (1972) reported that adult cutthroat trout even supplanted adult brook trout that were given the advantage of prior residence. Schroeter (1998) also found that adult Lahontan cutthroat trout were equal competitors with brook trout in an artificial channel when brook trout did not hold a numerical advantage. However, when the density of brook trout was increased, the same cutthroat trout failed to hold profitable positions (sensu Fausch 1984) resulting in a lower feeding rate. In contrast to adults, juvenile cutthroat trout demonstrated niche shifts to less favorable positions (Cummings 1987) or reduced growth and lipid accumulation (Thomas 1996) when they interacted with brook trout.

Interactions may also depend on temperature and size differences. Brook trout dominated equal-sized cutthroat trout (age-1 or -2) at 20°C, but not at 10°C (Griffith 1972; DeStaso and Rahel 1994). In contrast, fry of fall-spawning brook trout emerge earlier than those of spring-spawning cutthroat trout, so age-0 brook trout have a ~20 mm size advantage over age-0 cutthroat trout during their first summer (Griffith 1972; Novinger 2000). In competitive trials with age-0 brook trout, the smaller age-0 cutthroat trout were behaviorally subordinate (Griffith 1972; Novinger 2000), grew less, and survived at a lower rate than when alone, in some cases because of predation by age-0 brook trout (Novinger 2000). Larger size usually confers a competitive advantage among interacting stream salmonids (Nakano 1995; Gowan and Fausch 2002).

Studies of brook trout-cutthroat trout interactions, like those of other stream salmonid invasions, have focused on individual-level responses and lack appropriately scaled experiments to measure population-level mechanisms (Table 1.3). Experiments testing effects of competition have been conducted in lab aquaria (Novinger 2000), artificial stream channels (Griffith 1972; DeStaso and Rahel 1994; Thomas 1996; Schroeter 1998), field enclosures (Thomas 1996; Hilderbrand 1998), and unenclosed stream reaches (Cummings 1987). Replicated experiments were conducted at the scale of tens of m or m^2, and never lasted more than one season (e.g., maximum=60 d, Thomas 1996). All population-level studies were observational, demonstrating pattern but not process (e.g., Fausch 1989; Schroeter 1998; Dunham et al. 1999). In addition, the importance of movement in invasions by brook trout has been overlooked until recently (Adams 1999; Adams et al. 2000). To increase our understanding of brook trout invasion and effects on native cutthroat trout, we need to expand the spatial and temporal scale of experiments, and test population-level mechanisms affecting both species.

Study design

To show the utility of the proposed framework, I use it to design an experiment to test mechanisms and effects of brook trout invasion into streams containing Colorado River cutthroat trout (*O. c. pleuriticus*). Colorado River cutthroat trout (CRCT) were historically present in streams and rivers of the upper Colorado River basin draining portions of the central and southern Rocky Mountains and Great Basin in five states (Behnke 1992). Population declines and extirpations in many streams have been attributed to negative interactions with brook trout introduced starting in the late 1800s

(Wiltzius 1985). I propose a population-level manipulative field experiment in replicate small (first- or second-order) headwater streams containing CRCT where invasion by brook trout is ongoing. Of 318 recognized CRCT populations, nearly 40% are invaded by brook trout (Young et al. 1996), providing a sufficient pool from which to draw a sample of streams (Figure 1.1). Low water temperature is thought to reduce recruitment of cutthroat trout in high-elevation streams (Harig and Fausch 2002), and cold temperatures may similarly affect brook trout (Novinger 2000). Thus temperature likely influences invasion resistance by cutthroat trout and ability of brook trout to establish populations and spread. Because elevation and temperature are generally inversely related in the Rocky Mountains (e.g., Hauer et al. 1997), assigning treatments within blocks by elevation may help account for the influence of temperature on these species' population dynamics.

To carry out the experiment, brook trout abundance will be reduced in half the streams (i.e., treatments), randomly selected from within each elevation block, to test the hypotheses that: 1) brook trout cause CRCT populations to decline, and 2) brook trout abundance will increase in control streams. The predictions which follow from these hypotheses are: 1) the abundance of CRCT will increase in treatment streams because of release from biotic interactions with brook trout (mechanisms: increased birth rate, increased survival, or decreased emigration of CRCT) compared to control streams where abundance of brook trout is not manipulated, and 2) abundance of brook trout will increase in control streams as the invasion progresses (mechanisms: increased birth rate, increased survival, or immigration; see Table 1.1). Standard electrofishing removal techniques (Riley and Fausch 1995; Gowan and Fausch 1996a) can be used to estimate abundance (program MARK; White and Burnham 1999), and capture-recapture of trout given individual marks or age-specific batch marks can be used to estimate interannual survival by age class for both the native and invading trout (program MARK). Electrofishing capture probabilities are generally high in small streams where brook trout and cutthroat trout co-occur, so the treatment effect (i.e., removal of nonnative brook trout) will be large. For example, Gowan and Fausch (1996a) electrofished similar streams and captured a median of > 90% of the estimated juvenile and adult trout population. Two-way weirs (Gowan and Fausch 1996b) can be used to estimate immigration into and emigration from study areas. Invaders may introduce diseases into native populations, so brook trout can be tested for presence of diseases such as whirling disease or bacterial kidney disease that can be severely debilitating or fatal to native trout (Nickum 1999).

The study reaches must be long enough to include habitat types critical to the life cycle of these species and have large enough populations to measure changes in demographic rates. In effect, the sampling grain should be extended to the segment scale (10^3 m or greater - Frissell et al. 1986; Fausch et al. 2002), and the temporal extent should ideally account for at least two generations of each species. Toward that end, the study area in each stream should consist of an ~1 km segment where brook trout and CRCT are sympatric. This stream length reflects a trade off between logistic constraints (i.e., the maximum effort that can be allocated to measure trout abundance and remove the invader) and realism (i.e., the minimum amount of habitat required by these fishes to complete their life histories). Even resident salmonids are likely to range farther than 1 km within or between years (Young 1994, 1996; Gowan and Fausch 1996b; Hilderbrand

and Kershner 2000), but encompassing all such movement is logistically prohibitive. To verify the assumption that sufficient habitat exists to meet the history requirements for salmonids, at a minimum the study reach should be selected to include all life stages of the native species.

The life histories of brook trout and cutthroat trout will dictate the temporal extent of the study if changes in population-level parameters are being measured. Fall-spawning brook trout in headwater Rocky Mountain streams begin reproducing in their second or third year of life (Adams 1999; Kennedy et al. *in press*) and spring-spawning CRCT in their third or fourth year (Downs et al. 1997), so a 4-yr study would include one or two generations of each. Another important consideration is deciding when to begin the treatment. This decision reflects a trade off between obtaining pre-treatment estimates of annual variation in survival and movement, versus sufficient post-treatment data to detect a treatment effect for a long-lived species with multiple age-classes. Assuming a 4-yr study, brook trout manipulation should begin the first year to maximize the ability to estimate a response in CRCT populations in treatment versus control streams. A single interannual survival estimate requires a minimum of two years of data so it may be prohibitive to measure pre-treatment survival, but pre-treatment abundance can be estimated at the same time brook trout are removed the first year.

Under this design, the clearest inferences are for those mechanisms by which CRCT are affected by invasion, which are tested by contrasting demographic parameters in treatment versus control streams (Table 1.1.A). Mechanisms promoting successful invasion by brook trout can be tested by comparing the relative importance of immigration, reproduction, and survival by age class in control streams, and by comparing demographic parameters for brook trout to cutthroat trout. However, movement by brook trout is subject to slightly different interpretation in control versus treatment streams. For example, arrival has already occurred in control streams, so net movement of brook trout into the study segment suggests either that the invasion is at an early stage or that immigration is sustaining the invading population in a sink habitat. In contrast, in treatment streams such immigration can be characterized as closer to pure arrival because removing brook trout has created a new invasion front. Brook trout tend to move upstream in Rocky Mountain streams during summer, and some individuals move long distances (Gowan and Fausch 1996b; Adams et al. 2000), so such ranging behavior may be an important factor promoting invasion via jump dispersal. Characterizing this invasion front will be an important initial step toward understanding a little-known aspect of brook trout-cutthroat trout invasion dynamics.

Application to native cutthroat trout management

When population-level mechanisms of brook trout invasion and effects on CRCT are established, they can be used to make recommendations for cutthroat trout conservation. For example, if data indicate that the vital bottleneck for CRCT populations invaded by brook trout is survival during their first year of life, managers could schedule brook trout eradication to reduce the potential for competition when young cutthroat trout are most vulnerable (see Clark and Rose 1997a for another example), or consider habitat modifications to favor young cutthroat trout. A more complete understanding of how populations of these two species interact may allow managers to prioritize restoration efforts for cutthroat trout or control brook trout populations by predicting: a) the rate or trajectory of the invasion, or b) environmental conditions that favor coexistence. Finally, where rigorous population-level data are collected, metrics like the rate of population change (i.e., lambda), which integrates contributions of survival, reproduction, immigration, and emigration, can be used to explore effects of invasion and evaluate potential management actions. Lambda can be indirectly estimated using projection matrices if survival and reproductive rate estimates are available (Caswell 2001), or estimated directly using capture-recapture data (Nichols and Hines 2002), and then used to examine how demographic contributions by specific age-classes changes abundance of the native and invading species.

Improving the theory of stream salmonid invasions

My goals in presenting this framework are to outline a comprehensive study approach for widespread, and often deleterious, invasions by nonnative salmonids in streams, and to demonstrate one method for developing taxon-specific models capable of predicting invasions. Predicting and preventing further invasions should be a primary focus, but the already widespread introduction of nonnative salmonids and continuing impacts on native aquatic fauna requires research biologists and managers to understand mechanisms causing these results. To halt the decline of native salmonid species facing invasion, biologists must collect better data on patterns of invasion and use these to design field experiments capable of determining mechanisms causing invasions and their ecological effects. Ultimately, fishery biologists manage invasions at the landscape scale with the goal of conserving native populations; so to provide sound advice researchers must first understand the ultimate mechanisms causing these population-level interactions. Establishing the population-level mechanisms, and determining at which age class they are most important, will improve the focus of smaller-scale tests of competition or predation and strengthen the causal relationships between these individual-level interactions and population-level mechanisms and responses.

In applying this framework to stream salmonid invasions, I hope to have demonstrated how "practical and precise knowledge of particular taxa" (Schrader-Freschette 2001) and communities (Lodge 1993b) can improve the predictive power of invasion biology by forging a quantitative link between population dynamics and invasion theory (Parker 2000). Despite the conceptual simplicity of the framework, it should help to guide research objectives and recommend appropriate experiments to test underlying mechanisms of invasion (Moller 1996). The successful application of similar population-level frameworks to other invasive taxa may lead to more general theories or empirical rules. Accumulating such rigorous experimental data will be difficult (Simberloff and Van Holle 1999), but necessary if we hope to predict future invasions, the outcome of ongoing invasions, and help biologists manage the ecological and economic consequences.

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Table 1.1. A proposed framework for testing population-level mechanisms of a salmonid invasion in streams using a field removal experiment. The observed pattern is that the invader replaces the native species, leading to the hypotheses: 1) the invader must cause the native species to decline by reducing its reproduction, reducing survival at some age class or classes, causing emigration, or transferring disease, and 2) the invader must increase by increased local reproduction, high survival through some or all age classes, or immigration. Predictions from these hypotheses that can be tested by removal experiment are: 1) The native salmonid will increase in treatment streams where the invader is removed, compared to control streams, by one or more of six possible mechanisms (see part A below), and 2) the invading salmonid will increase in control streams by one or more of five possible mechanisms (see part B below). The predicted mechanisms causing these changes, and the data needed to test them are also presented. Differences among streams in temperature, flow regime, habitat quality, and other abiotic covariates are assumed to be accounted for by the experimental design.

Predictions and predicted mechanisms	Data needed to test mechanisms
A. Abundance of the native salmonid will increase in treatment streams relative to control streams by: [a]	
1. Increased birth rate	Age at maturity, fecundity, spawning behavior, abundance of the young-of-the-year (YOY)[b] cohort
2. Increased YOY survival[c]	YOY survival, abundance of juveniles[d]
3. Increased juvenile survival	Juvenile survival, abundance of adults[e]
4. Increased adult survival	Survival and abundance of adults
5. Low or no net emigration [f]	Net movement across study area boundaries
6. Low incidence of disease [g]	Incidence of debilitating or fatal diseases (e.g., whirling disease, bacterial kidney disease)

Table 1.1. Concluded.

B. Abundance of the invading salmonid will increase in controls streams by:

1. High birth rate	Age at maturity, fecundity, abundance of YOY
2. High YOY survival	YOY survival, abundance of juveniles
3. High juvenile survival	Juvenile survival, abundance of adults
4. High adult survival	Survival and abundance of adults
5. High net immigration	Net movement across study area boundaries

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[a] The converse are the predicted mechanisms by which the native salmonid decreases in control streams relative to the treatments: 1) decreased birth rate, 2) decreased YOY survival, 3) decreased juvenile survival, 4) decreased adult survival, 5) net movement (emigration) from study area, and 6) increased incidence of fatal diseases.

[b] Young-of-the-year (YOY) are age-0 fish in the first year of life.

[c] Interannual survival estimates are from age-0 to age-1, or age-1 to age-2, etc.

[d] Juveniles are age-1 fish in the second year of life.

[e] Adults are age-2 and older fish in the third year of life and older, and are usually sexually mature.

[f] There is no immigration into many populations of native salmonids confined to headwaters because downstream source populations are frequently absent.

[g] Invaders may bring new diseases into native populations in control streams.

Table 1.2. Representative studies of salmonid invasions in streams where investigators sought observational or experimental evidence of effects on native fish species. Methods are abbreviated as observational (Obs), lab experiment (LE), field enclosure experiment (FEE), field removal experiment (FRE), or modeling (Mod). Levels of biological organization are abbreviated as individual (Ind), population (Pop), community (Com), or ecosystem (Eco).

				Scale				
Invading species[a]	Invaded species[b]	Location	Methods	Spatial grain[c]	Temporal duration (d)	Biological[d]	Evidence for main interaction[e]	Reference
Atlantic salmon	Steelhead	British Columbia (Canada)	LE	$0.525\ m^2$	10	Ind	Behavior (=), growth (=)	Volpe et al. (2001)
Brook	Bull, cutthroat	Rocky Mts. (US)	FRE	$102\text{-}163\ m^2$	15	Ind	Behavior (-) for bull, cutthroat not tested	Nakano et al. (1998)
Brown	Brook	Appalachian Mts. (US)	LE	$10.3\ m^2$	12-28	Ind	Behavior (-), growth (-), survival (-)[f]	DeWald and Wilzbach (1992)
Brown	Brook	Great Lakes (US)	FRE	1800 m	34	Ind	Behavior (-)	Fausch and White (1981)
Brown	Brook	upper Mississippi basin (US)	Obs	400 m	~5475	Pop	Replacement (-)[g]	Waters (1983)
Brown	Cutthroat	Rocky Mts.	LE	$2.7\ m^2$	2-5	Ind	Behavior (-)	Wang and White (1992)

Table 1.2. Continued.

Brown	*Galaxias* species	New Zealand	Obs	–[h]	–	Pop	Replacement (-)	Townsend and Crowl (1991)
Brown	*Galaxias* species	New Zealand	FEE Obs	0.8 m^2 15-40 m	2-6 –	Ind Pop	FEE: behavior (-) Obs: density (-)	McIntosh et al. (1992)
Brown	*Galaxias* species	New Zealand	FEE	1.9 m^2	10-11	Com, Eco	Trophic cascade (-), indirect effects (-)	Flecker and Townsend (1994)
Brown	Non-salmonids	Poland	Obs	100-500 m	~9855	Pop, Com	Abundance (-)[g], distribution (-)[g]	Penczak (1999)
Brown	Rainbow, catostomids, cyprinids	Sierra Nevada Mts. (US)	Obs Mod	1000-2700 m –	~1825 –	Com	Obs and Mod: abiotic factors > biotic interactions for community structure	Baltz and Moyle (1993)
Brown, rainbow	Cyprinids, catostomids	Sierra Nevada Mts.	Obs Mod	30-40 m –	~3650 –	Pop, Com	Obs: abiotic factors mediate biotic interactions, predation (-)[i]; Mod: replacement (-)	Strange et al. (1992); Strange and Foin (1999)
Brown, rainbow	*Galaxias* species	New Zealand	FEE[j] Obs	0.823 m^2 20-35 m	2 –	Ind Pop	FEE: predation (-) by brown; Obs: replacement (-)	McIntosh (2000)
Coho	Brook, brown	Great Lakes	LE	1.09 m^2	18.5-20.5	Ind	Behavior (-), growth (-)	Fausch and White (1986)

Table 1.2. Continued.

Rainbow	Brook	Appalachian Mts.	FRE	100-1260 m	1460-2190	Pop	Density (-)[k]	Moore et al. (1983); Moore et al. (1986)
Rainbow	Brook	Appalachian Mts.	Obs	1230-1500 m	~395	Pop	Production (-), growth (-)	Whitworth and Strange (1983)
Rainbow	Brook	Appalachian Mts.	LE FEE Obs	1 m^2 0.75 m^2 20-50 m	≥20 14 90	Ind	LE: behavior (=), growth (=); FEE: growth (=); Obs: growth (=)	Magoulick and Wilzbach (1998a,b)
Rainbow	Brook	Appalachian Mts.	FRE	600 m	~60	Ind	Behavior (-)	Lohr and West (1992)
Rainbow	Brook	Great Lakes	Obs	500 m	120	Ind	Growth (-)	Rose (1986)
Rainbow	Brook	Newfoundland (Canada)	Obs LE FEE	364-573 m^2 1.08 m^2 1.28-1.6 m^2	~300 ~45-95 3-16	Ind	Obs: Behavior (=); LE: Behavior (=); FEE: Behavior (=), growth (=)	Cunjak and Green (1983, 1984, 1986)

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[a] Non-indigenous species abbreviations and scientific names are: Atlantic salmon *Salmo salar*, Brook = brook charr *Salvelinus fontinalis*, Brown = brown trout *Salmo trutta*, Rainbow = rainbow trout *Oncorhynchus mykiss*, and Coho = coho salmon *O. kisutch*.

[b] Native or naturalized fish species abbreviations and scientific names are: Steelhead (anadromous rainbow trout) *O. mykiss*, Bull = bull charr *S. confluentus*, and Cutthroat = cutthroat trout *O. clarki*.

[c] Enclosed areas (m^2) are reported for laboratory or field experiments and survey lengths (m) for observational studies, with some exceptions. Values are listed on the same line as their corresponding method. Grain was selected as the spatial metric because it usually represented the experimental or primary sampling unit.

Table 1.2. Concluded.

[d] Level of biological organization at which effects were detected

[e] Evidence for effect on invaded (native or naturalized) species resulting from biological interactions with nonnative salmonid invader where: (-) indicates a negative outcome on the invaded species and (=) indicates no evidence for an effect on the invaded species. Results are organized by study method where applicable.

[f] Some brook trout died of fungal infection when sympatric with brown trout.

[g] Results were potentially confounded with changes in abiotic conditions.

[h] Dash indicates that data were not reported or not relevant.

[i] Authors presented indirect evidence that predation and competition influenced invaded fish populations, but droughts and floods mediated these biotic interactions.

[j] Experiment was conducted in plastic tanks adjacent to a natural stream.

[k] Negative effect was inferred from an increase in standing crop of brook trout in streams where rainbow trout were removed.

Table 1.3. Representative studies of brook trout and cutthroat trout interactions where investigators sought empirical evidence of effects on native cutthroat trout subspecies. Abbreviations and column headings are as in Table 1.2.

			Scale				
Cutthroat subspecies[a]	Location (US)	Methods	Spatial grain	Temporal duration (d)	Biological	Evidence for main interaction[b]	Reference
Bonneville	Idaho, Utah	Obs FEE	–[c] 12-30 m	– ~2-7	Ind	Obs: behavior (=) from diet analysis; FEE: behavior (-), weak evidence for niche shift	Hilderbrand (1998)
Colorado R.	Colorado	Obs	34-247 m	–	Pop	Replacement (-): brook exclude cutthroat from low-gradient reaches	Fausch (1989)
Colorado R.	Wyoming	LE	1.08 m^2	5	Ind	Behavior: (-) at 20°C, (=) at 10°C; Physiology: brook have greater upper thermal limit	DeStaso and Rahel (1994)
Colorado R.	Wyoming, Utah	LE FEE	1.98 m^2 23.7-37.3 m^2	3 60	Ind	LE: behavior (-), decreased feeding efficiency; FEE: weight (-), lipid content (-), diet preference (=)	Thomas (1996)
Colorado R.	Wyoming	LE LE LE FEE	3.3-420 L[d] 0.29 m^2 1.2 m^2 0.75 m^2	14-73[e] 6-10 3 21-28	Ind	Growth (-), behavior (-), survival (-), predation (-), physiology (-): brook have advantage at upper thermal limit	Novinger (2000)

Table 1.3. Continued.

Greenback	Colorado	FRE	168-519 m	97[f]	Ind	Behavior: > 150 mm length (=), < 150 mm (-) by niche shift	Cummings (1987)
Lahontan	Nevada, California	Obs	25 m	–	Pop	Obs: replacement (-), negative correlation in biomass; FEE: behavior (-) by habitat use and feeding	Schroeter (1998)
		FEE	1.12 m^2	19	Ind		
Lahontan	Oregon, Nevada	Obs	>300 m	–	Pop	Replacement (-): downstream limits of cutthroat higher where brook present	Dunham et al. (1999)
Lahontan	Nevada	Obs	2000 m	2	Ind	Behavior (=): prey selection similar, no predation on cutthroat	Dunham et al. (2000)
Westslope	Idaho	Obs	100 m	–	Ind	Obs: behavior (-) for YOY;	Griffith (1972, 1974)
		Obs	1000 m	–		Obs: diet (-) for age-1 and older [g];	
		LE	7.2-11.8 m^2	3-21		LE: behavior (=) for equal-size competitor, behavior (-) when brook had size advantage	

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[a] Scientific names for cutthroat subspecies are: Bonneville *Oncorhynchus clarki utah*, Colorado River *O. c. pleuriticus*, greenback *O. c. stomias*, Lahontan *O. c. henshawi*, and westslope *O. c. lewisi*

[b] Evidence for effect on cutthroat trout resulting from biological interactions with brook trout where: (-) indicates a negative outcome for the invaded species and (=) indicates no evidence for an effect on the invaded species. Results are organized by study method where applicable.

[c] Dash indicates that data were not reported or not relevant.

Table 1.3. Concluded.

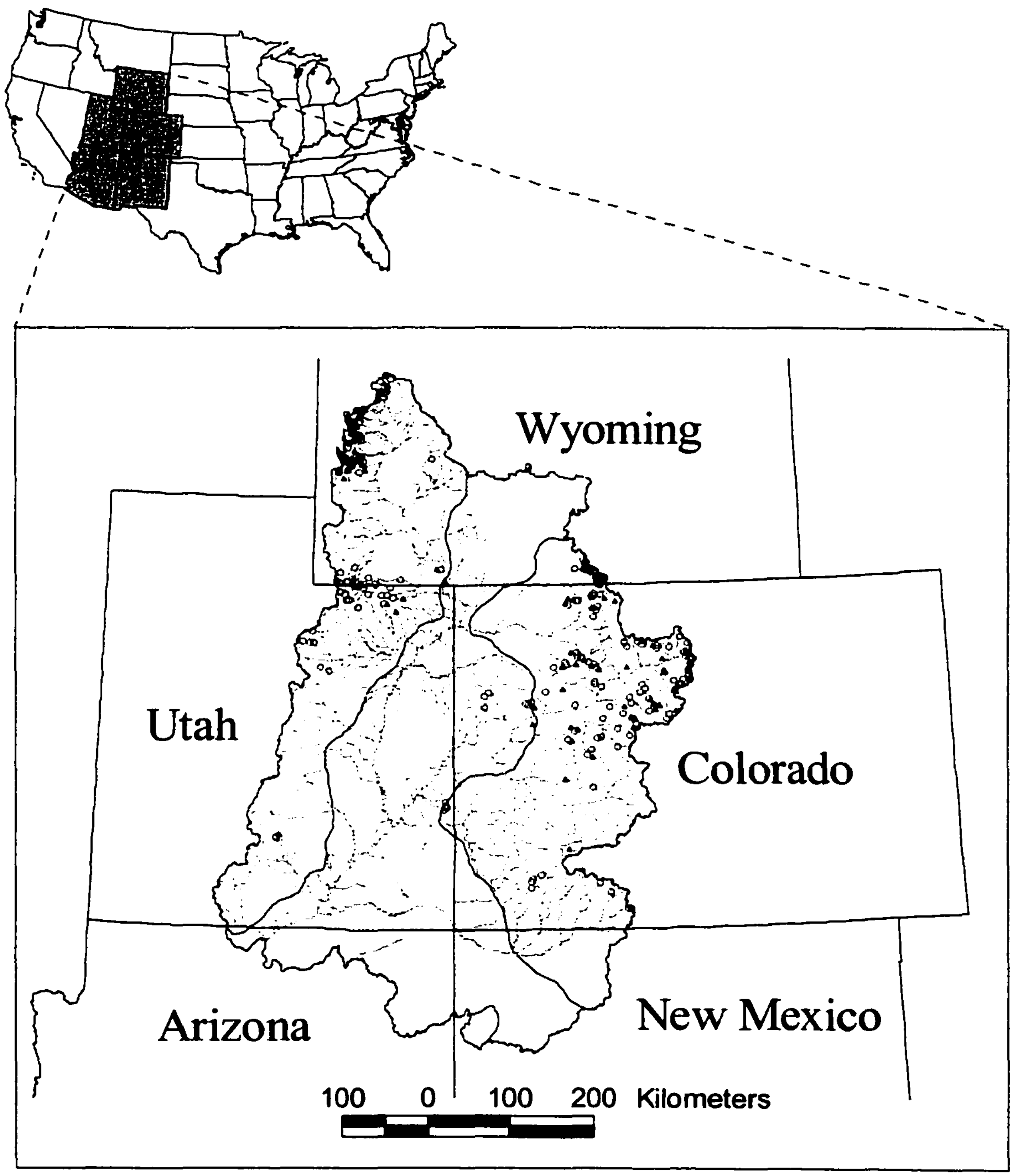
[d] Laboratory physiology experiments conducted in a combination of flumes (100 L), tanks (420 L), respirometers (3.3 L), and aquaria (17.5 L). Behavioral experiments were conducted in various lab (0.29 and 1.2 m^2) and field (0.75 m^2) enclosures.

[e] Duration of short-term physiological performance trials (e.g., sustained and sprint swimming) were not reported here.

[f] Trout were observed in sympatry beginning 19 June, then observations in allopatric treatment versus sympatric control sections were made between 28 August and 23 September (or for ~ 27 d) following brook trout removal, so total study duration was 97 d.

[g] Field observations indicated: a) young-of-the-year (YOY) brook and cutthroat trout segregated by depth, but older fish overlapped in their microhabitat use; b) YOY cutthroat trout selected similar food items in sympatry and allopatry, but older cutthroat showed greater diet selectivity in sympatry presumably because of negative biotic interaction with brook trout

Figure 1.1. Upper Colorado River basin (outline) with historical range of Colorado River cutthroat trout (unshaded area within outline) showing 291 stream populations of CRCT existing without invading brook trout (open circles) or in sympatry with brook trout (closed triangles). Other nonnative salmonids may be present at these sites, and a few of the cutthroat trout populations have been naturalized outside their presumed historical range. Data are from Young et al. (1996) and Biodiversity Associates Inc., Laramie, WY. The Colorado River flows generally from northeast to southwest.


Wyoming
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CHAPTER TWO: POPULATION ECOLOGY OF AN INVASION: EFFECTS OF BROOK TROUT ON NATIVE CUTTHROAT TROUT

Abstract

Invasion by nonnative brook trout (*Salvelinus fontinalis*) usually results in replacement of cutthroat trout (*Oncorhynchus clarki*) in the inland western US, but the underlying mechanisms are unknown. I conducted a four-year removal experiment to test for population-level mechanisms (i.e., changes in recruitment, survival, emigration, and immigration) promoting invasion success of brook trout and causing decline of native Colorado River cutthroat trout (*O. c. pleuriticus*). I chose 700 – 1200-m segments of four small mountain streams with sympatric trout populations, two each at moderate elevation (2500 – 2700 m) and high elevation (3150 – 3250 m), and annually removed brook trout from two streams (treatments), but not the other two (controls). At moderate elevation, age-0 and age-1 cutthroat trout survived at 12 times and 2 times higher rates, respectively, where brook trout were removed. At high elevation sites, recruitment of cutthroat trout failed despite brook trout removals apparently because of cold water temperatures. In contrast, age-2+ cutthroat trout survived at similar rates whether brook trout were removed or not, and regardless of elevation. Cutthroat trout tended to emigrate during summer, whether or not brook trout were removed. In comparison, brook trout immigrated at high rates, rapidly recolonizing depleted segments. Brook

trout reduced survival of juvenile cutthroat through biotic interactions, which led to population declines. In contrast, brook trout survived at the same or higher rates than same-aged cutthroat trout, and immigration may have sustained invasion where harsh environmental conditions limit recruitment. In my study streams, complete eradication of brook trout from watersheds is necessary to eliminate the threat to native cutthroat trout, but twice-yearly removal of 90% of the brook trout population for at least two consecutive years repeated at three-year intervals is one option that may permit cutthroat trout populations to temporarily coexist with brook trout.

Introduction

Invasions by nonnative organisms can harm ecosystems at many ecological levels (Parker et al. 1999), and are regarded as one of the most significant global challenges facing resource managers (Vitousek et al. 1996; Byers et al. 2002). Aquatic species such as Eurasian water milfoil (*Myriophyllum spicatum*), Nile perch (*Lates nilotica*), sea lamprey (*Petromyzon marinus*), and zebra mussel (*Dreissena polymorpha*) have become poster species for invasions, causing major economic and social impacts (Moyle 1986; Smith and Barco 1990; Mills et al. 1994; Pitcher and Hart 1995). Invasions by these high-profile species and others have resulted in the decline and imperilment of native aquatic species (Williams et al. 1989; Allan and Flecker 1993), and a general homogenization of freshwater faunas (Rahel 2000; Marchetti et al. 2001).

Invasions are fundamentally population-level phenomena (Parker 2000), but they are seldom studied as such. Success of an invasion is defined in terms of establishment and growth of a population (Vermeij 1996), which is clearly a function of the ultimate population-level mechanisms of births and immigration (inputs, B and I), and deaths and emigration (outputs, D and E; Gotelli 2001). Accordingly, declines in native species can be described in similar terms (Chapter 1). Identifying the population-level mechanisms of invasion is difficult (Holway 1999; Kiesecker et al. 2001), particularly where populations are age or stage structured (e.g., Kiesecker and Blaustein 1998; Neubert and Caswell 2000). Moreover, asymmetry in interspecific competitive interactions is common for size-structured animal populations like fishes (Persson and Greenberg 1990), and can produce large effects on population and community dynamics (Persson 1988; Persson et al. 1999).

A comprehensive understanding of the population-level mechanisms underpinning invasion success and effects is necessary to design control, mitigation, and recovery plans (Parker et al. 1999; Sakai et al. 2001; Byers et al. 2002). However, comprehensive studies on the population biology of invasions are rare, and experimental evidence has only recently begun to accumulate despite its relevance to understanding invasion dynamics (Kareiva 1996). Population-level approaches have been applied to the study of plant invasions (Dayton and Primack 1999; Downey and Smith 2000; Foster 2000; Parker 2000) and some simple organisms (e.g., protozoans and rotifers – Miller et al. 2002). In contrast, most research of effects of invasive species has been done at the individual level, including studies on insects (Hollway 1999; Juliano 1998), gastropods (Byers and Goldwasser 2001), crustaceans (Hill and Lodge 1999), amphibians (Kupferberg 1997; Kiesecker and Blaustein 1998; Kiesecker et al. 2001) and reptiles (Petren and Case 1996). Results are then scaled up to explain population-level declines in native species. Gabor and Hellgren (2000) provided a unique example of a population-level observational study of invasion by a mobile vertebrate. They compared the demography of collared peccary (*Tayassa tajuca*) in allopatry versus sympatry with the nonnative feral pig (*Sus scrofa*), although they did not detect differences in demographic rates between invaded and uninvaded peccary populations. Thus, to date there is little understanding of the mechanisms that explain invasion by any mobile vertebrate.

Salmonid fishes (trout, salmon, charr, and whitefish) are a widely introduced group of mobile vertebrates (Welcomme 1992; Fuller et al. 1999) known to produce negative effects on native aquatic fauna (Krueger and May 1991). For example, introductions and invasions by nonnative salmonids have been implicated in the decline of native cutthroat trout (*Oncorhynchus clarki*) in the inland western US (Gresswell 1988; Behnke 1992). Cutthroat trout are subject to genetic introgression with rainbow trout (*O. mykiss*; Allendorf and Leary 1988) and other cutthroat trout subspecies, predation by lake trout (*Salvelinus namaycush*; Ruzycki et al. *in press*), and competition with brook trout (*Salvelinus fontinalis*; Novinger 2000) and brown trout (*Salmo trutta*; Wang and White 1992). All subspecies of inland cutthroat trout are considered sensitive, threatened, or endangered (Young and Harig 2001), making their recovery a biological and legal imperative.

Brook trout replace inland cutthroat trout in many streams where they come into contact (Fausch 1989; Behnke 1992), and brook trout invasions are viewed as a major impediment to cutthroat trout persistence (Young 1995; Harig et al. 2000). Despite this consistent pattern of replacement, two problems hamper management. First, the underlying population-level mechanisms that promote invasion by brook trout and harm cutthroat trout are not known. Second, stream salmonids have age- and size-structured populations (Elliott 1994), but the life stages at which these population-level mechanisms operate during the invasion are not known. Competition and predation are individual-level (proximate) mechanisms advanced to explain why brook trout replace cutthroat trout populations (Griffith 1970; Novinger 2000). These factors have been tested in small-scale laboratory or field-enclosure experiments but results differ depending on the ages or sizes of individuals tested (Chapter 1). However, mechanisms driving stream salmonid populations are believed to operate at large spatial and long temporal scales (Gowan and Fausch 1996a, 1996b; Rieman and Dunham 2000; Fausch et al. 2002), so individual-level studies at small scales may not scale-up to explain population patterns (Peckarsky et al. 1997), and may focus on life stages other than those at which effects occur. Moreover, fishery biologists, who focus on the status of populations as their benchmark of success, are uncertain how to apply information at the individual level to management. Thus, I argue that documenting the existence and outcome of biotic interactions, measured at the population level as changes in demographic rates for each life stage, should precede more detailed tests of proximate-level mechanisms.

My goal in this study was to measure the demography of a salmonid invasion at an appropriate scale using a field removal experiment on sympatric populations of nonnative brook trout and native Colorado River cutthroat trout (*O. c. pleuriticus*). To my knowledge, this is the first population-level field experiment of an invasion by a mobile vertebrate. I identified factors promoting invasion success by brook trout and causing declines in invaded cutthroat trout populations by estimating the population parameters (B, I, D, and E) of recruitment, survival by age class, and movement during a four-year study. Survival and abundance of cutthroat trout of various age classes were compared: a) between streams where sympatric brook trout were removed (treatments) or not (controls) to determine at which life stage effects of brook trout invasion are most pronounced, and b) to those of brook trout to identify reasons for invader success. Movement of both species was measured to determine the relative contributions of emigration and immigration to local abundance and invasion dynamics. Integrating these results, I present a conceptual model for the progress of a brook trout invasion in cutthroat trout streams at different elevations, and discuss why population-level experiments are important to reveal underlying mechanisms of invasion by an age- or size-structured population.

Methods

Study sites

I selected four streams in northern Colorado containing sympatric populations of nonnative brook trout and native Colorado River cutthroat trout for study (Figure 2.1). The study streams were selected from 12 streams surveyed during 1998 based on historical fish distribution data from natural resource agencies (e.g., CRCT Task Force 1998), and were representative of cutthroat trout streams in the central Rocky Mountains where populations were isolated in headwater reaches by nonnative salmonids, downstream barriers, or both. Selection criteria included streams having a simple fish assemblage of brook trout and cutthroat trout throughout a long zone of sympatry (>1 km) and without physical barriers to movement, sufficient abundance of genetically pure cutthroat trout for mark-recapture analysis, and a remote location with low levels of angling. Brook trout had invaded all streams, and Indiana Creek was the only location where they had not invaded all available headwater habitats.

Study segments in each stream were at 2500 – 3250 m elevation, and ranged from 700 to 1200 m long (Table 2.1). Streams were first- or second-order, averaged 1.6 – 3.2 m wide, had less than 0.05 $m^3 \cdot s^{-1}$ baseflow, had average gradients of 2.3 – 4.7 %, and gravel and cobble substrate. Streams flowed through basins with mixed stands of lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), and aspen (*Populus tremuloides)*. Habitat alternated between higher-gradient forested reaches and lower-gradient meadow reaches where willow (*Salix* sp.) was the dominant riparian vegetation. Beaver (*Castor canadensis*) inhabited all streams except Willow Creek.

Study design and predictions

Streams were divided into mid-elevation (2500 – 2700 m) and high-elevation (3150 - 3250 m) blocks on the a priori assumption that higher sites would be colder, which might affect the demographic rates influencing the invasion. Streams were randomly assigned to treatment (TRT) or control groups (CTL) within each elevation block, and brook trout populations were removed annually from treatment streams. This removal experiment employs an additive design appropriate for studies of nonnative species invasions (Fausch 1998), where the goal is to demonstrate the existence and measure the strength of interspecific biotic interactions.

I used current knowledge about brook trout invasions to develop specific predictions to test using a removal experiment (Chapter 1). Based on the pattern of replacement of cutthroat trout by brook trout, I hypothesized that brook trout cause cutthroat trout populations to decline by depressing recruitment, reducing survival of one or more age classes, forcing emigration, or introducing diseases and parasites. Given this, I predicted that removing brook trout from treatment streams would increase cutthroat trout recruitment, increase survival of one or more age classes, reduce emigration rates, or eliminate a vector for parasites and diseases brought by brook trout (e.g., whirling disease), when compared to control streams where brook trout were not removed. Moreover, if one or more of these events occurred, then I predicted that abundance of cutthroat trout would increase through time in treatment streams as a result of brook trout removal. If none occurred, then I infer that some other factor besides biotic interactions with brook trout causes cutthroat trout populations to decline (Fausch 1998). In addition to comparing cutthroat trout demographic rates in treatment versus control streams, I also predicted that in control streams rates of recruitment, survival by age class, and immigration of brook trout would be equal to or higher than cutthroat trout, thereby allowing brook trout to successfully invade and persist while forcing cutthroat trout to decline or remain at low abundance. For both species, measuring survival rates by age class, in conjunction with movement, allows understanding the population-level mechanisms of decline and invasion in detail.

Temperature and physical habitat characteristics

Water temperature and physical habitat are critical factors affecting persistence of cutthroat trout populations in the central Rocky Mountains (Harig and Fausch 2002), and may set the context for their response to brook trout invasion. Water temperature was measured (nearest 0.2°C; each 20-72 min) during fall 1998 to fall 2001 by placing a TidBit© thermograph (Onset Computer Corp., Inc., Pocassett, MA) in a deep pool (> 30 cm) in the study reach of each stream. Habitat surveys, adapted from Harig and Fausch (2002), were conducted during fall 2000 to measure physical characteristics such as pool width, number of deep pools, and in-stream structure (e.g., large woody debris) known to influence trout populations (Gowan and Fausch 1996a). Temperature and physical habitat data were subsequently used as covariates to estimate survival and capture probabilities by elevation block.

Trout sampling

Two-pass removal electrofishing was used to obtain annual estimates of trout abundance and recruitment, and to remove brook trout from treatment streams In turn, mark-recapture techniques were used to measure changes in trout survival across years. Streams were sampled annually during 1998 to 2001 at base flow, usually in early August to late September depending on annual flow and temperature. On each day, sections of 200-400 m were enclosed with block nets (5-mm mesh), and were electrofished in an upstream direction using a backpack electrofishing unit (Mark 10, Coffelt Manufacturing Inc., Flagstaff, AZ) operated at 30 Hz, 150 – 450 V pulsed DC. Constant electrofishing effort was applied among habitats and passes.

All trout captured during electrofishing were anesthetized (MS-222), measured (fork length [FL], nearest mm), and weighed (nearest 0.1 g). Trout were assigned to one of three age classes (ages 0, 1, and 2 and older) based on length, using a combination of length-frequency histogram and otolith data (Kennedy et al., *in press*; Peterson and

Fausch, *unpublished data*). All trout returned to streams were marked using a combination of finclips, individual tags, and color batch marks based on age, species, and year, which permitted constructing capture histories of individual fish during the experiment. Age-0 (young-of-the-year) and age-1 trout were given left- and right-pelvic finclips, respectively. Age-2 and older cutthroat trout (i.e., adults; age 2+ hereafter), which were ≥ 85 mm FL, were marked with alpha-numeric coded passive integrated transponder (PIT) tags (Biomark, Inc., Boise, ID) in 1998 or fluorescent visual implant (VI) tags (Northwest Marine Technology, Inc., Shaw Island, WA) during 1999-2001. Use of PIT tags was discontinued because of potential tag loss by spawning females. Instead, I developed a technique for implanting VI tags in the opaque tissue covering the lower (dentary) jawbone of trout, which permitted putting two tags in each fish to prevent loss of capture information if one tag was lost. In control streams, adult brook trout, which were ≥ 110 mm, received dark green Floy Fine Fabric Anchor tags (Floy Tag, Inc., Seattle, WA). The adipose fin was excised from all trout given unique tags to identify subsequent tag loss. Florescent elastomer (Northwest Marine Technology, Inc.) was injected into fin rays or the tissue covering the dentary and maxillary bones to denote the year of initial capture. Recaptured trout that had lost tags were re-tagged, and juvenile trout that grew sufficiently since their previous capture to warrant tagging were also tagged.

Marked trout were held overnight in live baskets placed in deep pools, and released within 25 m of their initial capture location. Brook trout in treatment streams were euthanized with an overdose of anesthetic (MS-222; Animal Care and Use

Committee protocol 98-067A, Colorado State University), preserved in 10% formalin, and transported to the lab for processing.

Estimating abundance and survival

Survival and abundance estimates were calculated for three age classes of each species (age 0, age 1, and age 2+). Trout capture histories were analyzed using maximum-likelihood estimators in program MARK (White and Burnham 1999) using two sets of models. First, data for cutthroat trout and brook trout in control streams were analyzed using Pollock's robust design with Huggins' population estimator. The robust design model is a combination of a demographically open live-recapture model (i.e., Cormak-Jolly-Seber [CJS]) and closed capture-model (Kendall et al. 1995). Survival is estimated across the primary sampling periods (between years), whereas population size is estimated during secondary sampling sessions when the population is effectively closed (during electrofishing surveys). A primary benefit of this model is that the capture probabilities can be estimated from the closed-captures portion of the model, which avoids confounding of survival and capture probabilities in the final sampling period. Thus, under the robust design model three survival estimates are possible for this four-year study (e.g., 1 = 1998-99, 2 = 1999-2000, and 3 = 2000-01), whereas under the CJS model, only two would be possible. Huggins' population estimator (Huggins 1991) is a derived parameter that is calculated outside the maximum-likelihood framework of program MARK, but has better statistical properties than other population estimators when the number of captures is low because it is conditional on only the animals captured.

In this analysis, the robust design model was used to estimate apparent survival (ϕ), abundance (N), and capture probabilities (p). The survival parameter estimated is apparent survival whereby a fish that left the study area and is not at risk of capture is statistically equivalent to a fish that died. Movement and recapture parameters were fixed at zero because movement was explicitly measured (see description of weir captures below) and no recaptures were possible during secondary sampling sessions because I conducted removal electrofishing. For a given species and stream, the estimated abundance of age groups 1 and 2+ during 1999-2001 represents a sum of the estimated abundance of different cohorts derived using a common capture probability. For example, total abundance of age 2+ brook trout in the mid-elevation control stream during 2000 is composed of the sum of the abundances of individuals initially captured as: a) age 2+ in 2000, b) age 1 in 1999, and c) age 0 in 1998. Since abundance of these component groups in 2000 was estimated using a common capture probability, the individual abundance estimates are not independent and covariances among the abundance estimates must be considered to properly estimate the variance of the sum. A large-sample approximation of the covariance between component abundance estimates was derived using the delta method (Seber 1982) as: $\hat{\text{cov}}(\hat{N}_1\hat{N}_2) = \dfrac{\hat{N}_1\hat{N}_2\ \hat{\text{var}}(\hat{p}^*)}{(\hat{p}^*)^2}$, where $\hat{N}_1$ and $\hat{N}_2$ are the abundance estimates and $\hat{p}^*$ is the estimated common capture probability (K. Burnham, Colorado State University, *personal communication*). Thus, the variance of the sum of these estimates becomes the sum of the variance-covariance matrix.

A second model, the generalized removal estimator for closed captures, was used to estimate abundance of brook trout in treatment streams at the time of removal. In addition, in the mid-elevation treatment stream single-pass electrofishing was conducted in early July during 1999 to 2001 to remove brook trout before emergence of age-0 cutthroat trout. This additional removal reinforced the treatment effect in this stream. Additional electrofishing was not done in the high-elevation treatment stream because annual two-pass surveys were conducted in early August as soon as streamflow permitted efficient electrofishing.

Model selection

Data for brook trout and cutthroat trout were analyzed separately, and series of candidate models were fit based on a priori hypotheses about the effects of age (ages classes 0, 1 and 2+), time (year), stream, treatment group (treatment versus control), and elevation (mid versus high) on survival and capture probabilities. Model parameters were also estimated as functions of environmental and biological covariates (e.g., pool density, large woody debris density, water temperature, and competitor density). Covariates for individual trout (e.g., body length) were not used because the data included batch-marked (juvenile) trout as well as individually-tagged (adult) trout. Model structure notation follows Lebreton et al. (1992) where "+" denotes factors which are additive in the logit scale, and "*" represents an interaction.

One or more best approximating models were selected for inference from among candidate models using Akaike's Information Criterion corrected for small-sample bias (AIC_c; Burnham and Anderson 2002). Models were ranked and compared using ΔAIC_c

and AIC_c weights, where ΔAIC_c estimates the relative difference between the top ranked model and each other model, and AIC_c weights measure the weight of evidence in favor of a model given the data. The top ranked model was considered the best model, and when the top model contributed at least 75% of the total AIC_c weight and was at least twice as likely as the next best model, parameter estimates and inferences were based on the single model. However, in cases where the top ranked did not meet this criterion, model averaging was used to make inferences. Model averaging, whereby parameters and associated variances are calculated as a weighted average across models based on AIC_c weights, was used to account for model selection uncertainty when no single model was considered best. Therefore, these parameter estimates are referred to as model-averaged estimates and their associated variances are unconditional because they are not based on a single model (Burnham and Anderson 2002). Modeling strategy for the robust design followed Lebreton et al. (1992), whereby capture probabilities were initially modeled with survival held constant, then the best model structure of capture probabilities was used to model survival. Because brook trout were removed from treatment streams, survival was zero, and only capture probabilities were modeled.

Fish movement

Fish weirs were used to measure movement of trout into and out of study reaches of three streams during 1999 to 2001 (all except East Fork Parachute Creek, a control stream). Weirs consisted of a two-way trap box with side panels (wings hereafter) covered with 6-mm black plastic mesh that funneled trout into the traps (see Gowan and Fausch 1996b for similar design). Trap boxes consisted of a 0.9 long × 0.8 m wide × 0.6

m tall frame of PVC pipe covered with the same plastic mesh, and were divided longitudinally to separate fish moving upstream from those moving down. Velocity refuges (large cobble) were provided for trout in each side. Trap openings were 6 cm wide, and a 20-cm wide board was placed inside the trap box 10 cm from the entrance to obscure the opening from trout already inside the trap. Tests in 1999 showed that trout could exit traps through the opening. Therefore, beginning in 2000 entrances were constricted into a 5- × 8-cm opening and through an angled section of plastic rain gutter fitted with a 10-cm length of flexible nylon stocking, which collapsed after trout passed through it and obscured the exit.

Weirs were placed at the upstream and downstream margins of the study reaches in the three streams, with additional weirs placed inside or outside the study area. Weirs were secured using steel posts, and a 25-cm mesh skirt extending from the bottom of the apparatus was buried in stream gravels to prevent trout from passing beneath the weir. Snorkeling was used to confirm that the weir was closed to all trout > 75 mm FL, which are primarily age-1 and older. Weirs were typically installed when snowmelt runoff subsided in mid June and removed in early October when streams froze. They could be monitored only from summer to fall because sites could not be reached during winter. Weirs were visited every other day, and captured trout were measured and weighed as above and given batch marks to indicate weir location and direction of travel. Fish were marked using various colors of nontoxic Liquitex© acrylic paint (Binney and Smith, Inc., Easton, PA) injected into post-orbital adipose tissue (i.e., adipose eyelid) using a sterile insulin syringe. Adult trout were given the same tags and adipose finclips used during electrofishing if they met the same size criteria described above. After recovery from anesthesia, all cutthroat trout and brook trout in the control stream were released in the direction they were traveling, at least 10 m away from the weir. In treatment streams, brook trout entering the study reach were euthanized to maintain the experimental treatment, but those leaving the reach were released. Weir entrances were closed during electrofishing surveys. Capture data from weirs at the study reach boundaries were analyzed to determine how emigration and immigration of cutthroat trout varied between treatment and control streams. Movement direction by brook trout could be analyzed only in the control stream that had weirs (Indiana Creek), because brook trout were removed in treatment streams and their source populations on one side of the weir were being removed.

Fish diseases

Pathogens and disease in brook trout populations were assayed in 1998 and 2001. Each year, 55 to 65 brook trout were collected from each stream, either during electrofishing removals (treatment streams) or during additional sampling downstream of the study area (≥ 500 m downstream in control streams). Samples were preserved in the field, and transported to laboratory facilities for analysis. Samples collected in 1998 were processed at the Fish Health Laboratory, Colorado Division of Wildlife, Brush, CO, and those from 2001 were analyzed at the Fish Technology Center, US Fish and Wildlife Service, Bozeman, MT, as part of the National Wild Fish Health Survey. Cutthroat trout were not included in the disease testing because they are a species of special concern in Colorado (CRCT Task Force 2001), and their populations might not withstand the sampling necessary to perform statistically valid disease testing. However, if brook trout tested positive for a pathogen or disease thought to be injurious to cutthroat trout, plans called for collecting small numbers of cutthroat trout to determine if these had been transmitted to the native species. Whirling disease (WD) was the primary focus of this testing because of its strong effects on native trout populations in the western US (Nickum 1999).

Results

Trout captures and population structure

A total of 11,241 trout captured during multi-pass electrofishing during 1998 to 2001 was used to estimate survival and abundance. Brook trout (n = 6425 in controls, n = 1983 in treatments) were more abundant that cutthroat trout (n = 2833), representing nearly 75% of the trout captured. An additional 606 brook trout were removed from the mid-elevation treatment stream by additional electrofishing in July during 1999-2001, but these fish were included only after calculating the abundance estimates. Capture probabilities were high ($\bar{p} = 0.68$, range 0.25 – 0.97), and similar for both species ($\bar{p}_{cutthroat} = 0.66$, $\bar{p}_{brook} = 0.70$; Appendix F). Survey lengths were less in 1999 than in the other three years because of expansion of beaver pond habit at one stream made electrofishing unsafe and because of insufficient manpower to complete the most upstream 70 – 200 m in the other streams (Table 1.1). Consequently, trout captured at locations during 1998 that were not resampled in 1999 were excluded from the data to avoid a downward bias in survival estimates. Fish excluded from the 1998 data made up 11.8% of cutthroat trout (range among streams 1.4 – 27.2%) and 12.8% of brook trout (range 3.0 – 32.5%) captured that year, but represent only a small percentage of the entire data set used for estimation (2.5% of 11,241 fish). Abundances are presented as densities to adjust for differences in survey lengths among years.

Trout population structure differed between mid- and higher-elevation streams. All age classes of trout (e.g., ages 0, 1, and 2+) were present in mid-elevation streams each year, but juveniles were often absent in high-elevation streams. Cutthroat trout ages 0 and 1 were never captured in the high treatment stream (Willow Creek), and age-0 cutthroat trout were never captured during electrofishing surveys and age-1 cutthroat were only found in low numbers in the high control (Indiana Creek). Similarly, age-0 and -1 brook trout were rare in the high-elevation control stream.

Juvenile brook trout of a given age were larger than cutthroat trout. Age-0 brook trout averaged 22.3 mm longer than cutthroat trout at the end of their first summer ($\bar{x}_{brook} = 76.3$ mm, $SE = 0.2$ $\bar{x}_{cutthroat} = 54.0$, $SE = 0.4$; $P<0.0001$ by *t*-test), whereas age-1 brook trout had a 45.2-mm size advantage over the same age cutthroat trout ($\bar{x}_{brook} = 126.3$ mm, $SE = 0.5$; $\bar{x}_{cutthroat} = 81.1$, $SE = 0.6$; $P<0.0001$). Adult size differences varied by stream. Brook trout were larger in the mid-elevation treatment and high-elevation control streams (mid TRT: $\bar{x}_{brook} = 164.6$ mm, SE =2.1; $\bar{x}_{cutthroat} = 129.7$, SE =1.4; high CTL: $\bar{x}_{brook} = 233.2$ mm, $SE = 2.6$; $\bar{x}_{cutthroat} = 170.1$, $SE = 1.6$; two-way ANOVA, least-square means test: $P<0.0001$ for both). However, adult cutthroat trout were larger in the high-elevation treatment stream ($\bar{x}_{brook} = 194.6$ mm, $SE = 1.4$; $\bar{x}_{cutthroat} = 234.8$, $SE = 3.1$; $P<0.0001$) and the same size in the mid-elevation control stream ($\bar{x}_{brook} = 184.8$ mm, $SE = 0.8$; $\bar{x}_{cutthroat} = 187.9$, $SE = 2.9$; $P = 0.29$).

Model selection

Cutthroat trout: A series of 29 models were fit to the data to select variables to include in the model of capture probabilities (Appendix A). Apparent survival (ϕ) was held at a full-effects structure (i.e., $\phi_{\text{stream*time*age}}$), and capture probabilities were modeled using variables of fish age, time (year), stream, stream conductivity, and stream width. Because capture probabilities have been reported to vary by size, I also modeled capture probabilities for two size classes based on divisions between age classes across streams (e.g., divided at either 71 mm, which included age-0 trout at mid-elevation streams and age-1 trout at high-elevation streams, or at 100 mm, which included all age-0 and -1 trout at both elevations). The best approximating model structure for capture probabilities was the full two-way effects model ($p_{\text{stream*time, stream*age, age*time}}$), which contributed 53% of the AIC_c weight and was 1.4 times more likely than the next best model ($p_{\text{stream+age*time}}$; AIC_c weight = 0.38).

After selecting a model for capture probabilities, a series of 66 models were fit to the same data to select appropriate variables to model survival (Appendix B). Variables included age, time, stream, trends (T = linear trend in the logit scale), treatment group, elevation stratum, and body size categories divided at 71 mm FL as above. Covariates, included alone or in combination with other factors in models, included: a) temperature effects: mean July temperature, sum of mean daily temperature > 0°C from May through August (summer degree days), and annual degree days; and b) competitor effects: density of same-age or same-size brook trout in a given stream. Model selection indicated that all primary factors (age, time, and stream) affected survival of cutthroat trout. The data supported a complex model structure, and a total of seven models were selected for inference (Table 2.2.A). Models 1 and 2 were considered closely competing models and contributed > 80% of the AIC_c weight, but all models contributing weight were used for inferences (Burnham and Anderson 2002). Model averaging was used to derive all parameter estimates. Models explicitly testing treatment, elevation, or brook trout density effects ranked very low. However, treatment effects were embedded within year and stream factors, so survival differences between treatment and control streams were contrasted by taking simple averages of model-averaged parameter estimates, calculating differences, using the delta method to derive variance estimates (Seber 1982; Burnham et al. 1987), and comparing overlap of confidence intervals.

<u>Brook trout in control streams</u>: A series of 26 models were fit to the data to select a model structure for capture probabilities (Appendix C). Selection of p proceeded with apparent survival held constant (i.e., $\phi_{\bullet}$ = constant over all factors), and included the primary variables of age, time, and stream. The best approximating model structure for capture probabilities was the full two-way effects model ($p_{\text{age*time, time*stream, age*stream.}}$), which contributed > 95% of the AIC_c weight and was over 20 times more likely than the next best model. A series of 41 models were subsequently fit to estimate survival while holding capture probability structure constant across models. Variables and covariates were the same as for cutthroat trout. As for cutthroat trout, model selection indicated that all primary factors (age, time, and stream) affected survival of brook trout (Table 2.2.B). In contrast to cutthroat trout, a single model for survival of brook trout in control streams ($\phi_{\text{stream*time, stream*age, age*time}}$) was nearly six times more likely than the next best model, so this single model was used for inference. Brook trout survival was compared to cutthroat

trout with the same method used to compare cutthroat trout survival across treatment groups (see *Model selection*, Cutthroat trout).

Brook trout in treatment streams: A series of 14 models using primary factors (age, stream, and time) were fit to select a model structure for capture probabilities for abundance estimates (Table 2.3). Ten models had some degree of support (i.e., AIC_c weight > 0), but age was clearly the single most important factor predicting capture probability and appeared in all 10 models. Model averaging was used to derive parameter estimates based on the top 10 models.

Trout survival

Age-0 cutthroat trout in the mid-elevation control stream survived at a lower rate than age-0 cutthroat trout in the mid-elevation treatment stream, and at a lower rate than age-0 brook trout in the mid-elevation control stream (Figure 2.2.A, Table 2.4). Age-0 cutthroat trout survival in the mid-elevation treatment stream was 12 times greater on average than in the mid-elevation control stream. Survival of age-0 brook trout was about 10 times higher than cutthroat trout in the mid-elevation control stream, although survival rate declined for both species. Only two survival estimates for age-0 cutthroat trout were possible in the mid-elevation treatment stream because this age class was inadvertently not marked in 1998. No estimates of age-0 survival were possible for either species at high-elevation sites because either few or no age-0 trout were produced or they emerged in late fall after surveys were completed.

Age-1 cutthroat trout in the mid-elevation control stream survived at a much lower rate than age-1 cutthroat trout in the mid-elevation treatment stream from 2000 to 2001, but at a similar rate to age-1 brook trout in the mid-elevation control stream across all years (Figure 2.2.B). In contrast to age-0 trout, survival of age-1 cutthroat trout and brook trout was not significantly different in the control streams (Table 2.4). Both species survived at similar rates that decreased as density increased (see *Trout abundance*). In the high-elevation control stream, low abundance of age-1 trout resulted in large confidence intervals for survival estimates, making comparison difficult (Figure 2.2.C), and no age-1 cutthroat trout were captured in the high-elevation treatment stream.

Adult cutthroat trout survived at similar rates in treatment and control streams, and survived at a similar rate to adult brook trout in control streams (Figures 2.2.D and 2.2.E; median $\hat{\phi} = 0.44$ for adult trout). Adult survival of both species remained relatively constant over time in three streams, but declined in the mid-elevation control stream as trout density increased. Overall, adult cutthroat trout survival was greater in high- than in mid-elevation streams, probably due to greater trout longevity in populations at cold, high-elevation sites (Kennedy et al. *in press*).

Trout abundance

Electrofishing removal was effective at reducing recruitment and abundance of juvenile brook trout in treatment streams, especially at the mid-elevation site, but adult brook trout were more difficult to control. Brook trout recruitment was reduced to very low levels after two consecutive years of removals in both treatment streams, and remained so in the mid-elevation treatment stream (Figures 2.3.A and 2.3.B). Although some recruitment was expected in treatment streams because adult brook trout may have immigrated and spawned after removal treatments each year, the increase in brook trout recruitment in the high-elevation treatment stream during 2001 was unexpected. Warm water temperatures during fall 2000 and spring-summer 2001 probably caused high overwinter egg survival, earlier fry emergence, and higher fry survival.

Relatively high abundance of adult brook trout in both treatment streams each year indicated that substantial immigration occurred between late fall, after electrofishing removal was completed and the weirs were removed, and the following summer when weirs were reinstalled. Adult brook trout density in the high-elevation treatment stream was reduced to about 40% of its initial level during 1999 through 2001 (Figure 2.3.F), but was not markedly altered in the mid-elevation treatment stream (Figure 2.3.E). In fact, adult brook trout density in the latter increased during 1999-2001 if fish captured during additional electrofishing are added to the two-pass abundance estimate.

Age-0 cutthroat trout abundance generally increased over time in the mid-elevation treatment stream, but the same age class declined in the mid-elevation control stream and was much less abundant than age-0 brook trout (Figures 2.3.A and 2.4.A). In the mid-elevation streams, the mean difference in density of age-0 cutthroat trout was greater during 2000 and 2001 compared to 1998 and 1999, indicating a significant treatment effect on density (one-tailed *t*-test: $t = 4.55$, df = 2, $P = 0.02$).

Age-1 cutthroat trout abundance in the mid-elevation treatment stream increased in 2001 and was greater than in the mid-elevation control stream in all years, where abundance declined (Figure 2.4.B). Age-1 cutthroat trout were much less abundant than age-1 brook trout in the mid-elevation control stream, but more abundant in the high-elevation control stream (Figures 2.3.D and 2.4.D). In the mid-elevation streams, the difference in density of age-1 cutthroat trout was greater during 2001 than in 1998 through 2000 (one-tailed *t*-test: $t = 6.51$, df = 2, $P = 0.01$). In contrast, in the high-elevation streams, age-1 cutthroat trout were absent (treatment) or present in low numbers (control), so no such comparisons were possible (Figure 2.4.C).

Abundance of adult cutthroat trout did not increase in treatment streams, and declined in all but the high-elevation control stream (Figures 2.4.D and 2.4.E). Adult brook trout were much more abundant than adult cutthroat trout in the mid-elevation control stream, but not in the high elevation control stream (Figures 2.3.E, 2.3.F, 2.4.E, and 2.4.F).

Cutthroat trout survival related to competitor density

Survival of juvenile cutthroat trout was inversely related to density of brook trout, the only other fish competitor present in these streams. Brook trout density varied widely among streams (Figure 2.5), so survival of cutthroat trout of a given age class was plotted against the estimated density of the same age or size class of brook trout during the interval over which survival was estimated. Graphs revealed a negative relationship between survival of age-0 and age-1 cutthroat trout and brook trout density, but no such relationship for age-2+ cutthroat trout.

Movement through weirs

A total of 965 trout were captured in weirs located at the margins of study areas in three streams from June through October of 1999 through 2001 (Figure 2.6). Trout as small as 45 mm FL were captured, but most were >75 mm. Over 70% of all trout were captured in the mid-elevation treatment stream, where weirs were operated longer each year (range 100 – 123 d) than in the high-elevation sites (TRT 62 – 74 d, CTL 69 – 98 d), because streamflow permitted earlier installation. Brook trout (*n* = 647) were captured more frequently than cutthroat trout (*n* = 318).

Cutthroat trout showed a tendency toward net emigration during summers, but this tendency was apparently not influenced by brook trout removal. Logistic regression (SAS Version 8.2, SAS Inc., Cary, NC) was used to estimate the proportion of cutthroat trout moving into or out of the study segments. Five models were fit to the data to determine the influence of year and treatment group (brook trout removed or not) on emigration and immigration. Models with intercept only and intercept plus treatment group accounted for over 85% of the AIC_c weight. Estimates averaged using these two models showed that 58% of cutthroat trout emigrated during summer (95% CL: control stream 51-64%, treatment streams 53-65%), whereas approximately 42% immigrated (95% CL: control stream 36-49%, treatment streams 35-47%). However, of 76 individually-tagged cutthroat trout that emigrated through weirs during 1999-2001, 22% returned to the study area the same year, 21% were present in the study area the following year, and about 3% did both.

In contrast to cutthroat trout, many more brook trout attempted to immigrate into the study reach than leave it (Figure 2.6). Statistical comparison of movement direction in treatment streams, however, is not valid because all immigrants (*n* = 500) were euthanized to maintain the treatment. Nonetheless, logistic regression analysis of captures in the high-elevation control stream (*n* = 26) using two models (intercept only and intercept plus year) indicated that brook trout had a tendency to immigrate in at least one year. Model averaging estimated that 66-85% of brook trout were immigrants during 1999 to 2001, but the immigrant estimate (85%) was significantly different from the emigrant estimate (15%) only in 2001 (95% CL: immigrants 57-95%, emigrants 5-43%), but overall sample size was small.

Fish diseases

I could find no evidence that brook trout affected cutthroat trout via transmission of diseases or parasites. Tests for whirling disease indicated brook trout were not infected with either the hard spore stage (1998 – Pepsin-Trypsin assay) or the DNA (2001 – nested polymerase chain reaction [PCR] assay) of *Myxobolus cerebralis*, the parasite causing the disease. Cutthroat trout were not assayed because tests on brook trout were negative, and no clinical signs of whirling disease were ever encountered in the thousands of cutthroat trout captured. Brook trout in all streams tested positive for *Renibacterium salmoninarum*, which causes bacterial kidney disease in salmonids, during 2001 (US Fish and Wildlife Service, ELISA assay), but not in 1998 (Colorado Division of Wildlife, PCR assay). However, PCR performed by USFWS was not able to confirm the presence of *R. salmoninarum* DNA in the 2001 samples. Separate samples of brook trout from Little Muddy Creek in 1998 were analyzed by both laboratories, and gave conflicting results for bacterial kidney disease. Presence of *R. salmoninarum* is common among wild trout, but clinical symptoms and mortality are rare (K. Peters, US Fish and Wildlife Service, Bozeman, MT, *personal communication*), so it is not likely that bacterial kidney disease was affecting cutthroat trout in study streams.

Discussion

Age-specific biotic interactions as a mechanism causing replacement of cutthroat trout

Results from this four-year field experiment provide new insight into the decades-long controversy about how nonnative brook trout replace native cutthroat trout in streams of the western US. My data are consistent with the hypothesis that biotic interactions with brook trout suppressed cutthroat trout, particularly in the first two years of life (Figure 2.7). In addition, the data demonstrate that brook trout are adept invaders, capable of sustaining or rapidly increasing their abundance. However, abiotic factors that varied by elevation influenced the demographics of both trout species. Here I discuss how these results relate to my initial predictions about cutthroat trout population response to brook trout removal and the overall hypothesis that biotic interactions are responsible for replacement of cutthroat trout by brook trout?

First, the experiment supported the prediction that removing brook trout would increase recruitment of age-0 cutthroat trout, and that brook trout cause the decline of cutthroat trout populations by depressing recruitment. Recruitment of cutthroat trout depended on elevation, however, and increases were observed only in the mid-elevation treatment stream. In contrast, cutthroat trout recruitment in high-elevation streams was low or absent, and removal of brook trout did not ameliorate recruitment failures in the high-elevation treatment stream. Spawning habitat was available because brook trout recruited in the study segment of this stream and age-0 cutthroat were present in low numbers in a warmer reach more than 2 km downstream. Thus, abiotic factors, primarily cold summer water temperatures, appear to limit cutthroat trout recruitment in high-elevation streams of the central Rocky Mountains (Harig et al. 2000; Harig and Fausch 2002).

Second, as predicted, cutthroat trout survival increased after brook trout were removed, thus demonstrating that brook trout reduce survival of cutthroat trout, but this effect varied by age class. Survival of age-0 and age-1 cutthroat trout in the mid-elevation treatment stream was > 10 times and 2 times greater on average, respectively, compared to that the mid-elevation control stream, but survival of adult cutthroat trout did not change in response to brook trout removal at either elevation. Moreover, age-0 and age-1, but not age-2+, cutthroat trout survival was inversely related to brook trout density (Figure 2.5). These results indicate that brook trout invasion imposes a population bottleneck (Elliot 1994) at the juvenile life stage of cutthroat trout by reducing their survival, which contributes to the overall population decline. This mechanism could not be detected in high-elevation streams, however, because abiotic factors apparently caused recruitment failures in cutthroat trout. In these high-elevation streams, cutthroat trout sympatric with brook trout, or existing in allopatry upstream from brook trout, are probably senescent populations with a low chance of long-term persistence. However, adult cutthroat trout survival is higher than in mid-elevation streams (Figures 2.2.D and 2.2.E; Table 2.4) and trout in cold habitats tend to live longer (Jonsson et al. 1991; Downs et al. 1997; Kruse et al. 1997), so these populations may decline slowly for many years before vanishing.

Third, greater age-0 cutthroat trout recruitment and survival in the treatment versus control streams at mid-elevation led to greater age-1 abundance in the final year (2001), but latent brook trout reproduction caused lag effects in detecting these increases for juveniles and precluded detecting increases for adults. Consecutive years of removal and weir operation were necessary to reduce brook trout reproduction to very low levels because adults immigrated into the study area after weirs were removed and spawned. As a result, relatively high densities of age-0 brook trout were produced during 1998 and 1999 in the mid-elevation treatment stream, so recruitment by cutthroat trout did not increase until the third and fourth years (2000 and 2001). Consequently, I did not detect an increase in adult cutthroat trout abundance in treatment versus control streams at mid-elevation because more time would have been required to measure the entry of these large cohorts, caused by brook trout removal, into the adult population.

Fourth, the experiment confirmed the prediction that brook trout survive at higher rates than cutthroat trout in the mid-elevation control stream, but only for age-0 trout, supporting the hypothesis that higher survival by one or more age classes of brook trout can lead to successful invasion and replacement of cutthroat trout. Age-0 brook trout survival was 10 times higher on average than that of age-0 cutthroat trout in the mid-elevation control stream, but no differences in survival were detected for age-1 trout of either species in this stream, or for adults in streams at either elevation (Figure 2.2, Table 2.4). Strong year classes (i.e., large cohorts) of age-0 brook trout during 1999 and 2000 in the mid-elevation control stream may have caused density-dependent declines in all ages of both trout species in the stream. However, survival differences between age-0 trout of the two species remained consistent as density increased five-fold, indicating an invasion effect of brook trout on cutthroat trout irrespective of overall trout density.

Fifth, my data did not confirm the prediction that emigration by cutthroat trout would decrease where brook trout were removed. Cutthroat trout showed a slight tendency to emigrate during summer, but there was no difference in emigration rates between treatment and control streams. Therefore, I reasoned that in the absence of a source of immigrants, cutthroat trout would reduce their emigration rates from reaches where brook trout were removed, but this did not happen because emigration rates were similar across streams. Moreover, emigration was only temporary for some fish, suggesting weirs operated from summer through fall may have measured only a portion of the annual movement of cutthroat trout in these streams. More thorough monitoring using telemetry would be necessary to define these patterns (e.g., Schmetterling 2001; Schrank 2002). Overall, the data indicate that presence of brook trout did not affect summer movement of cutthroat trout, which were mostly adult fish.

In contrast, the data show the importance of high brook trout immigration rates for supplementing and sustaining their invasion. Net immigration by brook trout was measured in all three streams and in every year weirs were operated. However, results in treatment streams must be interpreted cautiously because electrofishing removals in the study reach reduced the supply of emigrants. Brook trout captured immigrating through weirs made up a substantial proportion of the abundance of brook trout already present in the study reach (mean = 0.41, $SE = 0.12$, $n = 9$). In fact, electrofishing data indicated that immigrants replaced either the total (mid-elevation treatment) or 40% (high-elevation control) of the adult brook trout abundance in the 8 months between weir removal in the fall and installation the following summer. This population turnover caused by immigration has been observed for brook trout in other Colorado streams (Gowan and Fausch 1996a, 1996b), and is clearly an important factor in invasion success in the region. For example, despite low recruitment or survival of age-0 brook trout in the high-elevation streams in my study, immigration of adult brook trout sustained the invasion in at least one stream. Moreover, although brook trout recruited and survived at least as well as cutthroat trout in mid-elevation streams, this immigration accelerated the invasion in the treatment stream, where the entire starting population was replaced by immigration each year.

Sixth, disease assays failed to show that brook trout introduced debilitating or fatal parasites or diseases, so this was not a mechanism by which they reduce cutthroat trout survival and abundance. Brook trout samples from all streams tested negative for whirling disease in 1998 and 2001, and none of the thousands of cutthroat trout observed during this study exhibited any clinical signs of parasitic infestation or disease.

Competition and predation are believed to be the individual-level mechanisms behind replacement of cutthroat trout by brook trout in western US streams (Griffith 1988). Numerous individual-level studies have attempted to measure competition between these two species, but with varying success (Chapter 1). Studies focusing on adult cutthroat trout found no evidence that brook trout were superior competitors (Griffith 1972; Cummings 1987), unless cutthroat trout faced a numerical disadvantage (Schroeter 1998). However, juvenile cutthroat trout interacting with brook trout shifted to energetically less favorable positions (Cummings 1987), were behaviorally subordinate (Griffith 1972; Novinger 2000), grew less and had depressed lipid reserves (Thomas 1996), and survived at a lower rate than when in allopatry (Novinger 2000). Most of these studies mimicked the size advantage juvenile brook trout maintain over cutthroat trout during their first one or two years of life. In contrast, results of size-matched trials using age-1 and older trout depended on temperature, whereby brook trout dominated cutthroat trout 20°C but not at 10°C (DeStaso and Rahel 1994). The population-level results from my study show that brook trout affect cutthroat trout survival in the first two years of life, and thus increase the relevance of individual-level experiments of competition and predation that used juvenile age classes of cutthroat trout. The cumulative evidence indicates that age- (or size-) specific biotic interactions (i.e., competition or predation) are mechanisms by which brook trout replace cutthroat trout.

Management implications

My results demonstrate that brook trout are effective invaders of headwater streams in the central Rocky Mountains. Brook trout recruited and survived as well or better than native cutthroat trout, immigrated rapidly and even sustained invasion by immigration alone, have increased longevity in some habitats that buffers against recruitment failures, and ultimately had large effects on the vulnerable juvenile life stages of cutthroat trout, resulting in population declines and often extirpation.

How can this information be used by managers to counteract effects of brook trout invasion on native trout? Given the ability of brook trout to invade and harm sensitive cutthroat trout populations, the highest priority is to prevent brook trout introductions. However, managers are typically confronted with ongoing invasions and must take appropriate steps to mitigate their effects. Complete eradication of brook trout above a barrier to brook trout immigration would be ideal, and this experiment demonstrated that recruitment and survival of cutthroat trout will increase where brook trout are removed. Long-term, large-scale electrofishing removals were successful in nearly eliminating nonnative trout and increasing abundance of native brook trout in the southern Appalachian Mountains (Moore et al. 1986; Kulp and Moore 2000), and cutthroat trout in Montana (Shepard et al., *in press*). Unfortunately, total removal of nonnative trout is labor intensive and often impossible if stream habitats are even moderately complex. Despite this, selective removal strategies can permit persistence of cutthroat trout even if total brook trout removal is not possible. For example, my data indicate that at least two consecutive years of removing over 90% of the estimated brook trout population (as was possible in both treatment streams) should permit a large cohort of cutthroat trout to survive from age 0 to age 2, after which they would be affected little by biotic interactions with brook trout. At least two within-year removals would also be required to produce the intended result (Thompson and Rahel 1996; Kulp and Moore 2000). For central Rocky Mountain streams, the first removal should target age-0 brook trout in early summer so they will not interact with the later-emerging age-0 cutthroat trout, and the second removal in early fall should target adult brook trout that might spawn and produce offspring that would interact with young cutthroat trout the following summer. Two removals per year for two consecutive years should probably be repeated every three years to increase the probability of cutthroat trout persistence despite biotic interactions with brook trout. Ultimately, constant vigilance and careful planning are necessary for effective conservation of native cutthroat trout populations confronted with invasion by nonnative brook trout.

A conceptual model of brook trout invasion

The results of this study can be integrated with those from individual-level competition experiments (Novinger 2000), an empirical model for cutthroat trout persistence (Harig and Fausch 2002), and empirical and population projection models for brook trout in the Rocky Mountains (Adams 1999), to develop a conceptual model for brook trout invasions in cold versus warm montane streams supporting native cutthroat trout (Figure 2.8). After adult brook trout arrive via immigration, recruitment is relatively high and constant in warm streams, but low and more variable in cold streams reflecting interannual climate variation (Figure 2.8.C), so adult brook trout abundance increases more slowly in cold streams because fewer young fish survive to adulthood. As the invasion progresses, however, adult abundance in the cold stream increases at a greater rate because brook trout live longer there (Kennedy et al, *in press;* Figure 2.8.A). Invasion by brook trout causes cutthroat trout recruitment to decline in cold and warm streams through biotic interactions (e.g., competition – DeStaso and Rahel 1994; predation – Novinger 2000). This virtually eliminates recruitment in cold streams where it may be naturally sporadic (Harig et al. 2000), and causes lower and more variable recruitment in warmer streams because brook trout invasion reduces juvenile (age-0 to age-1) survival (Figure 2.8.D). Recruitment failures ultimately cause adult cutthroat trout to decline, which occurs faster in warmer streams, due to their shorter presumed life span than in colder streams where they live longer. However, these fish may be the "living dead" (Rieman and Dunham 2000), because birth rate is lower than death rate and the population declines rapidly toward extinction as it senesces (Figure 2.8.B). Thus, status of isolated cutthroat trout populations should not be judged exclusively on presence of adults.

Value of experiments on demography of invasions

This study demonstrates that it will be difficult to determine the mechanisms underpinning success of invaders and impacts on native species without detailed population-level experiments. The brook trout – cutthroat trout dilemma, like that of interactions between native and Argentine ants (Hollway 1999) or between bullfrog (*Rana catesbeiana*) and native ranid frogs in the western US (Kiesecker et al. 2001), is an example of invasions where the pattern of replacement was well known, but the underlying mechanisms were not (Lodge 1993a). In addition, many organisms have complicated life cycles where vital rates vary by age or stage (Gotelli 2001), and in many vertebrates certain life stages are highly mobile. For such organisms, detailed demographic data – such as recruitment, survival by age class, emigration, and immigration – of native species in the presence and absence of an invader will be required to determine at which life stages biotic interactions with invaders produce the greatest impact. For example, if I had measured only abundance or survival of adult cutthroat trout in response to four years of brook trout removal, I would have concluded that brook trout had no effect (Figures 2.2 and 2.3) and some other factor caused declines in cutthroat trout populations. Furthermore, measuring demographic rates in field experiments permits focusing subsequent laboratory studies of individual-level mechanisms on life stages where impacts are known to be greatest and strengthens the inference to patterns observed in the field. My data indicate that further studies should focus on the youngest age classes of cutthroat trout to determine the relative importance of competition and predation on changes in survival, and to identify which age classes of brook trout have the greatest influence.

Experiments on invading populations and host communities are rare, but the few done are instructive (e.g., Miller et al. 2002). Population-level manipulations of invasions have focused primarily on weeds (Shea and Kelly 1998; Dayton and Primack 1999; McEvoy and Coombs 1999), and have successfully identified life stages of invasive species to target for biocontrol. However, similar approaches have seldom been used for mobile organisms, and experiments with mobile, stage-structured organisms have been primarily at the individual-level. For example, individual-level experiments successfully predicted the effects of bullfrog (*Rana catesbeiana*) invasion on native frogs (Kiesecker and Blaustein 1997; Kupferberg 1997), but larger-scale enclosures were required to isolate the mechanisms (Kupferberg 1997; Kiesecker and Blaustein 1998). Population-level experiments with stream fish invasions will be difficult because of their ranging behavior, age- or size structure, and longevity (Behnke 1992; Schlosser and Angermeier 1995) require large scales to encompass (Fausch et al. 2002), but such large-scale studies are necessary to measure and understand impacts (Parker et al. 1999).

Bottlenecks caused by biotic interactions at juvenile life stages are hypothesized to have large effects on dynamics of size- or stage-structured populations (Werner and Gilliam 1984; Persson 1988; De Roos and Persson 2001), and should alter invasion dynamics. The results showed that biotic interactions with brook trout are responsible for decreased survival of age-0 and age-1 cutthroat trout, which may produce the bottleneck leading to declines in cutthroat trout populations. Similarly, simulation modeling of brook trout populations subject to invasion by rainbow trout in the Appalachian

Mountains (US) showed that these populations are also sensitive to variation in juvenile survival rates (Marschall and Crowder 1996; Clark and Rose 1997).

Immigration by brook trout may provide the progagule pressure (i.e., number of dispersers) necessary to ensure successful invasion when conditions are favorable for recruitment and can also sustain invasions in sink habitats unsuitable for brook trout recruitment. Brook trout are highly mobile and tend to move upstream during summer in western US mountain streams (Gowan and Fausch 1996a; Adams et al. 2000). Immigration was capable of replacing 40-100% of the adult population removed from treatment streams within about eight months (Figure 2.3). Downstream-directed invasions are also common where brook trout have been introduced into headwater lakes (Adams et al. 2001). Ultimately, propagule pressure is positively correlated to invasion success and impacts (Kolar and Lodge 2001), so high immigration rates by brook trout undoubtedly contribute to their widespread invasions and frequent replacement of native cutthroat trout in the western US.

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Table 2.1. Physical characteristics of the four study streams in north-central Colorado during 1998 through 2001.

						Pools per 100 m ‡			Mean temperature (°C)‖		
Stream	Category†	Median LAT(N)/ LON(W)	Elevation range (m)	Segment length (m)	Mean bankfull width (m)	Deep	Shallow	LWD per 100 m §	May	July	Conductivity (µS)
E. Fk. Parachute	Mid CTL	39°34'50" 107°55'31"	2542 – 2560	700-800	1.6	0.38	0.375	0.3	6.3	12.4	460
Little Muddy	Mid TRT	39°56'59, 106°02'46"	2658 – 2694	877-944	3.1	2.51	4.33	24.4	3.3	12.7	101
Indiana	High CTL	39°25'38", 106°59'44"	3194 – 3246	950-1100	3.2	1.36	1.60	1.8	1.3	6.6	174
Willow	High TRT	40°28'12", 105°46'48"	3188 – 3219	1002-1200	2.3	0.75	1.83	0.0	0.1	6.9	17

† Category – elevational blocks: Mid-elevation (Mid) = 2500 – 2700 m, high-elevation (High) = 3150 – 3250 m elevation; treatment groups: treatment (TRT) = brook trout removal, control (CTL) = unmanipulated.

Table 2.1. Concluded.

‡ Pools per 100 m – Deep pools were defined as those with ≥ 30 cm residual depth (cf. Harig & Fausch 2002; residual depth = maximum depth – maximum tail crest depth at the downstream hydraulic control forming the pool) during baseflow in 2000 based on the median residual depth of all pools in all streams. Shallow pools were those with residual depth between 18 and 29 cm.

§ Large Woody Debris (LWD) – woody debris pieces ≥ 15 cm diameter and ≥ 3 m long at least partially in or suspended over the bankfull channel.

|| Thermographs were not deployed until fall 1998, so summer 1998 temperatures were not available.

Table 2.2. Models used for inference of apparent survival (ϕ) and abundance for (A) cutthroat trout in all streams and (B) brook trout in control (CTL) streams under Pollock's robust design with Huggins' population estimator. For cutthroat trout, model averaging was used to estimate parameters used for inference.

Group	Model	Hypothesized model structure†	K	AIC$_c$	ΔAIC$_c$	w_i	Deviance	Description of survival probabilities
A. Cutthroat trout	1	$\phi_{\text{age*t*stream}}$	55	5282.78	0.00	0.478	18827.6	Age effect depends on time and stream (full 3-way model)
	2	$\phi_{\text{age*t, t*stream, age*stream}}$	53	5283.52	0.74	0.330	18832.5	Age effect varies by time; stream effect varies by time; age effect varies by stream (full 2-way model)
	3	$\phi_{\text{t*stream, age*stream}}$	48	5285.84	3.06	0.103	18845.3	Stream effect varies by time; stream effect varies by age
	4	ϕ JUVENILES: age*t*stream, ADULTS: stream	44	5286.97	4.19	0.059	18854.7	Juveniles (ages 0 and 1) vary by time and stream; adults (age-2+) vary only by stream
	5	$\phi_{\text{age*t*stream}}$ $p_{\text{age*t*stream}}$ (global model)	62	5288.94	6.16	0.022	18819.1	Global model: full 3-way model for both survival and capture probabilities

Table 2.2. Concluded.

	6	$\phi_{\text{age*t, t*stream}}$	47	5290.92	8.14	0.008	18852.4	Age effect varies by time; stream effect varies by time
	7	ϕ JUVENILES: age*t*stream, ADULTS: t	43	5304.02	21.24	0.00001	18873.8	Juveniles vary by time and stream; adults vary by time
B. Brook trout (CTL)	1	$\phi_{\text{age*stream, t*stream, age*t}}$	32	11747.44	0.00	0.819‡	66013.8	Age effect varies by time; time effect varies by stream; age effect varies by stream (full 2-way model)

Notes: Factors are time (t = year), stream, and age (ages 0, 1, and 2+) effects. Asterisks (*) denotes interactions between factors. Abundance estimates for all models differed by time, age, and stream (i.e., age × stream × time). Movement (γ' and γ'') and recapture parameters (c) were fixed to zero. Akaike's Information Criterion corrected for small sample size (AIC$_c$) based on the log likelihood and number of parameters (K) was used to select models for inference. The difference in AIC$_c$ between the highest-ranking and subsequent models (ΔAIC$_c$), and AIC$_c$ weights (w_i) provide an index of relative support for each model. Deviance is defined as the difference in –2Log(Likelihood model|data) of the current model and –2Log(Likelihood model|data) of the saturated model. The saturated model is the model with the number of parameters equal to the sample size.

† Capture probabilities for both trout species were based on the model: $p_{\text{age*t, t*stream, age*stream}}$ except for cutthroat trout model 5, where the global model (time*stream*age) was used for both survival and capture probabilities.

‡ Model 1 was almost six times more likely than the next best model, so a single model was used for inference.

Table 2.3. Models used for inference about abundance of brook trout in control (CTL) streams under a closed captures model. Model averaging was used to account for model uncertainty and to calculate parameter estimates.

Model	Hypothesized model structure	K	AICc	ΔAICc	w_i	Deviance	Description of survival probabilities
1	p_{age}	26	-12765.38	0.0	0.453	98.1	Age effect
2	$p_{stream+age}$	27	-12764.46	0.92	0.286	97.0	Constant (additive) stream effect on age
3	$p_{stream*age}$	29	-12762.66	2.72	0.116	94.7	Age effect varies by stream
4	p_{t+age}	29	-12761.19	4.19	0.056	96.2	Constant time effect on age
5	$p_{stream*age+t}$	31	-12760.16	5.22	0.033	93.1	Age effect varies by stream; constant time effect
6	$p_{stream+t+age}$	30	-12759.00	5.39	0.031	95.3	Stream, time, and age effects all constant (additive)
7	$p_{stream*t+age}$	33	-12758.50	6.88	0.015	90.7	Stream effect varies by time, constant age effect
8	p_{t*age}	35	-12756.70	8.64	0.006	88.3	Age effect varies by time

Table 2.3. Concluded.

9	$p_{\text{stream*t, stream*age}}$	35	-12756.08	9.30	0.004	89.0	Stream effect varies by both time and age
10	$p_{\text{stream*t*age}}$	46	-12748.00	16.39	0.0001	73.3	Age effect varies by time and stream (full 3-way model)

Notes: Factors and model-selection criteria are as in Table 2.2. Abundance estimates for all models differed by time, age, and stream (i.e., age × stream × time)

Table 2.4. Mean values and differences in apparent survival of trout in four study streams in northern Colorado during 1998 to 2001.

	Means (*SE*)					
Age	Treatment group (cutthroat)		Elevation block (cutthroat)		Species in control streams	
	TRT	CTL	Mid	High	Brook	Cutthroat
Age 0	0.318 (0.0438)†	0.0247 (0.0077)†	0.142 (0.0181)	‖	0.235 (0.0107)#	0.0247 (0.0077)#
Age 1	0.421 (0.0357)‡	0.227 (0.0462)‡	0.324 (0.0292)	‖	0.281 (0.0135)#	0.227 (0.0462)#
Age 2+	0.468 (0.0309)§	0.435 (0.0293)§	0.356 (0.0277)	0.547 (0.0324)	0.418 (0.027)††	0.435 (0.0293)††
	Differences (95% CI)					
	TRT – CTL		Mid – High		Brook – Cutthroat	
Age 0	0.294 (0.207, 0.381)†		‖		0.21 (0.185, 0.236)#	
Age 1	0.193 (0.0791, 0.308)‡		‖		0.0542 (-0.0401, 0.1484)#	
Age 2+	0.0333 (-0.0502, 0.117)§		-0.191 (-0.275, -0.108)¶		-0.0202 (-0.0984, 0.0579)††	

Table 2.4. Concluded.

Notes: Mean survival was averaged across years using model-averaged values (cutthroat trout) or values from a single model (brook trout). CTL = control stream, TRT = treatment stream (i.e., brook trout removed). Variances of means for maximum-likelihood estimators were calculated using the delta method (Seber 1982) where $\hat{\text{v}}\text{ar}(\hat{\bar{\phi}}) = \frac{\sum_{i=1,j=1}^{n} \hat{\text{c}}\text{ov}(\hat{\phi}_{ij})}{n^2}$ (e.g., Burnham et al. 1987) and covariances were included for within-stream means. Variances of differences were calculated by the delta method as $\hat{\text{v}}\text{ar}(\hat{\phi}_1 - \hat{\phi}_2) = \hat{\text{v}}\text{ar}(\hat{\phi}_1) + \hat{\text{v}}\text{ar}(\hat{\phi}_2)$, and covariances were zero because the means were independent.

† Values are mean of mid-elevation TRT ($n = 2$) and mean of mid-elevation CTL ($n = 3$).

‡ Values are mean of mid-elevation TRT ($n = 3$) and mean of mid-elevation CTL ($n = 3$).

§ Values are mean of mid-elevation and high-elevation TRT ($n = 6$) and mean of mid-elevation & high-elevation CTL ($n = 6$).

|| No estimate was made due to no or sparse data.

¶ Values are mean of mid-elevation TRT & CTL ($n = 6$) and mean of high-elevation TRT & CTL ($n = 6$)

Values are mean of mid-elevation CTL brook trout ($n = 3$) and mean of mid-elevation CTL cutthroat trout ($n = 3$).

†† Values are mean of brook trout in mid- & high-elevation CTL (n=6) and mean of cutthroat trout in mid- and high-elevation CTL ($n = 6$).

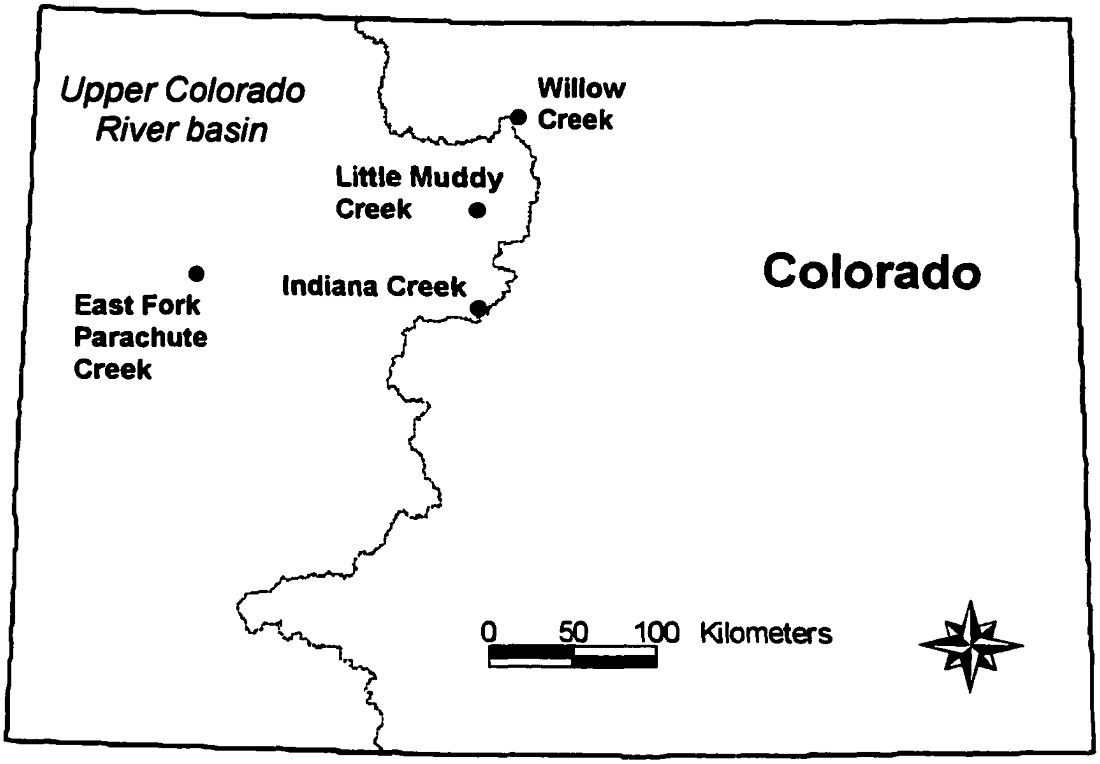


Figure 2.1. Locations of four streams in Colorado where effects of brook trout invasions on cutthroat trout were studied during 1998 to 2001. Little Muddy (2676 m elevation) and Willow creeks (3203 m) were treatment streams where brook trout were annually removed. East Fork Parachute (2551 m) and Indiana creeks (3220 m) were control streams where brook trout were not removed.

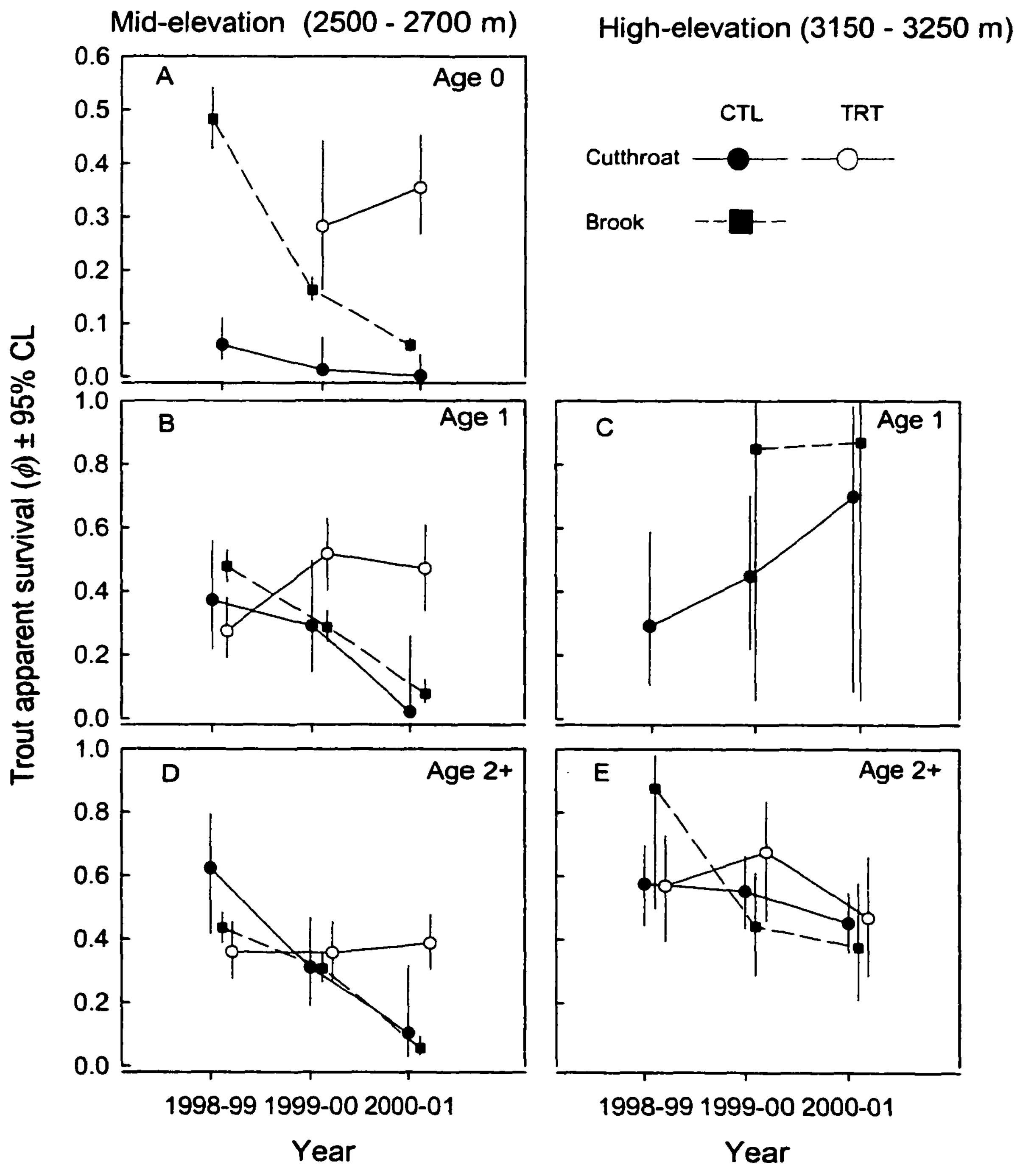


Figure 2.2. Apparent survival of cutthroat trout and brook trout in study streams during 1998 through 2001. CTL = control stream, TRT = treatment stream where brook trout were removed, age 2+ = trout age 2 and older, no age-0 cutthroat trout were captured or marked in high- elevation streams, and no estimates were possible for brook trout in treatment streams.

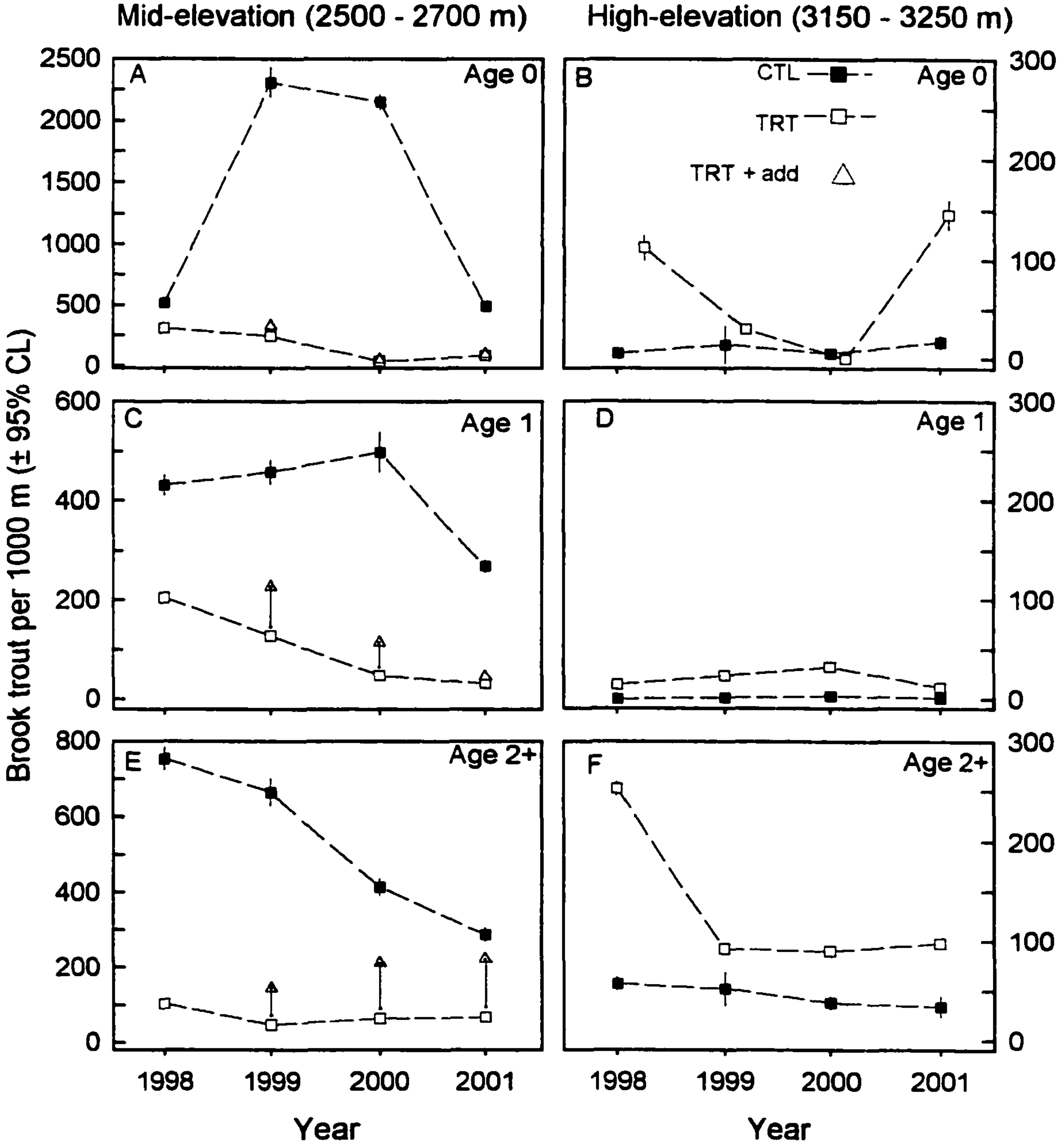


Figure 2.3. Density of brook trout in study streams during 1998 through 2001. Abbreviations are as in Figure 2.2. The age-1 estimates in the high-elevation control stream (panel D) are the actual number captured because of low numbers. Scale of *y*-axes differ between mid- and high-elevation streams. Open triangles on stalks above density estimates in the mid-elevation treatment stream (TRT + add) include the additional brook trout removed during July electrofishing.

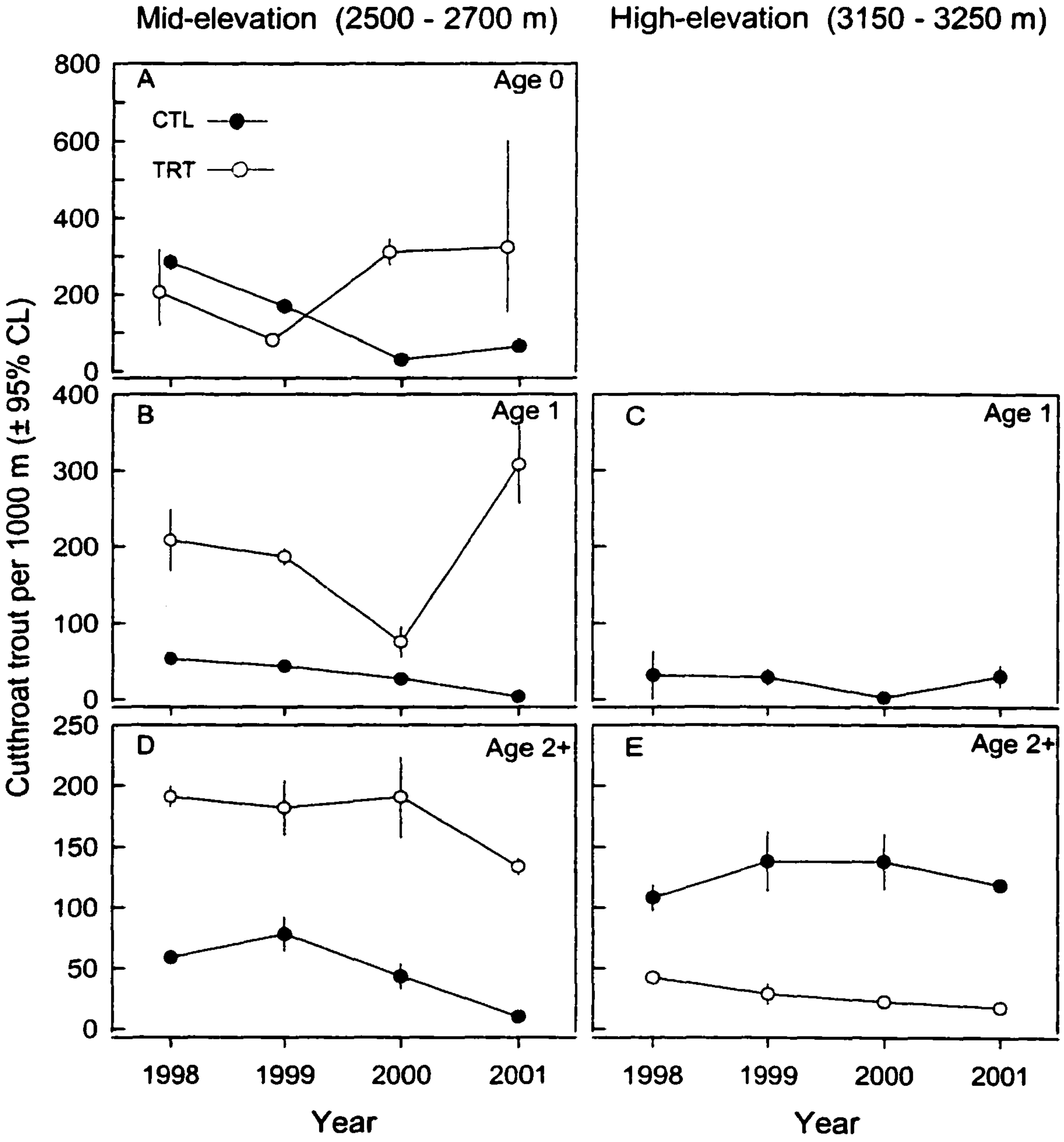


Figure 2.4. Density of cutthroat trout in study streams during 1998 through 2001. CTL = control stream, TRT = treatment stream where brook trout were removed, age 2+ = trout age 2 and older, and no age-0 cutthroat trout were captured or marked in high elevation streams.

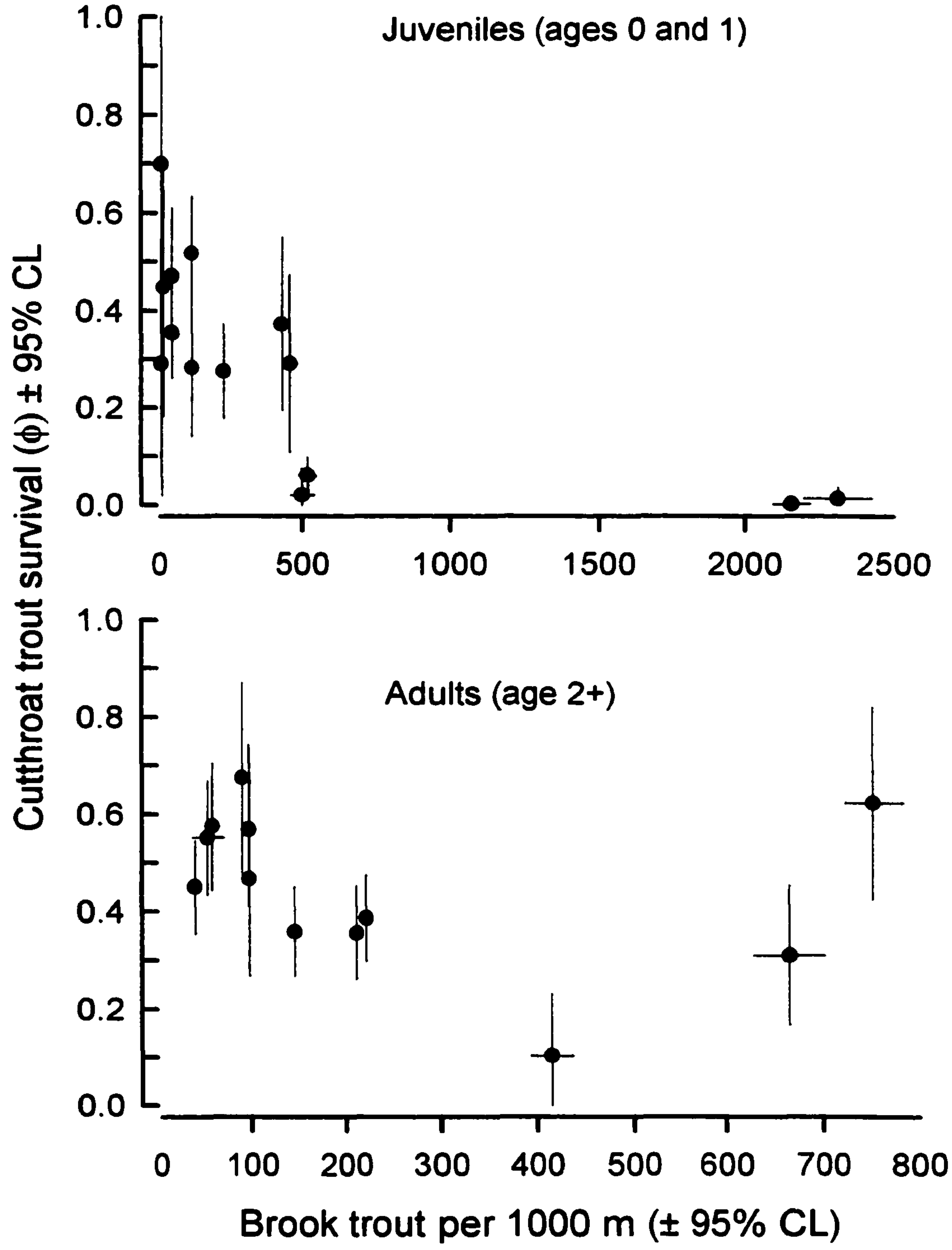


Figure 2.5. Survival of cutthroat trout during 1998 through 2001 at different densities of nonnative brook trout. Brook trout densities were matched to cutthroat trout survival by age or size class during the appropriate time interval. For example, in control streams age-0 brook trout density in fall 1998 was paired with age-0 cutthroat trout survival during fall 1998 to fall 1999.

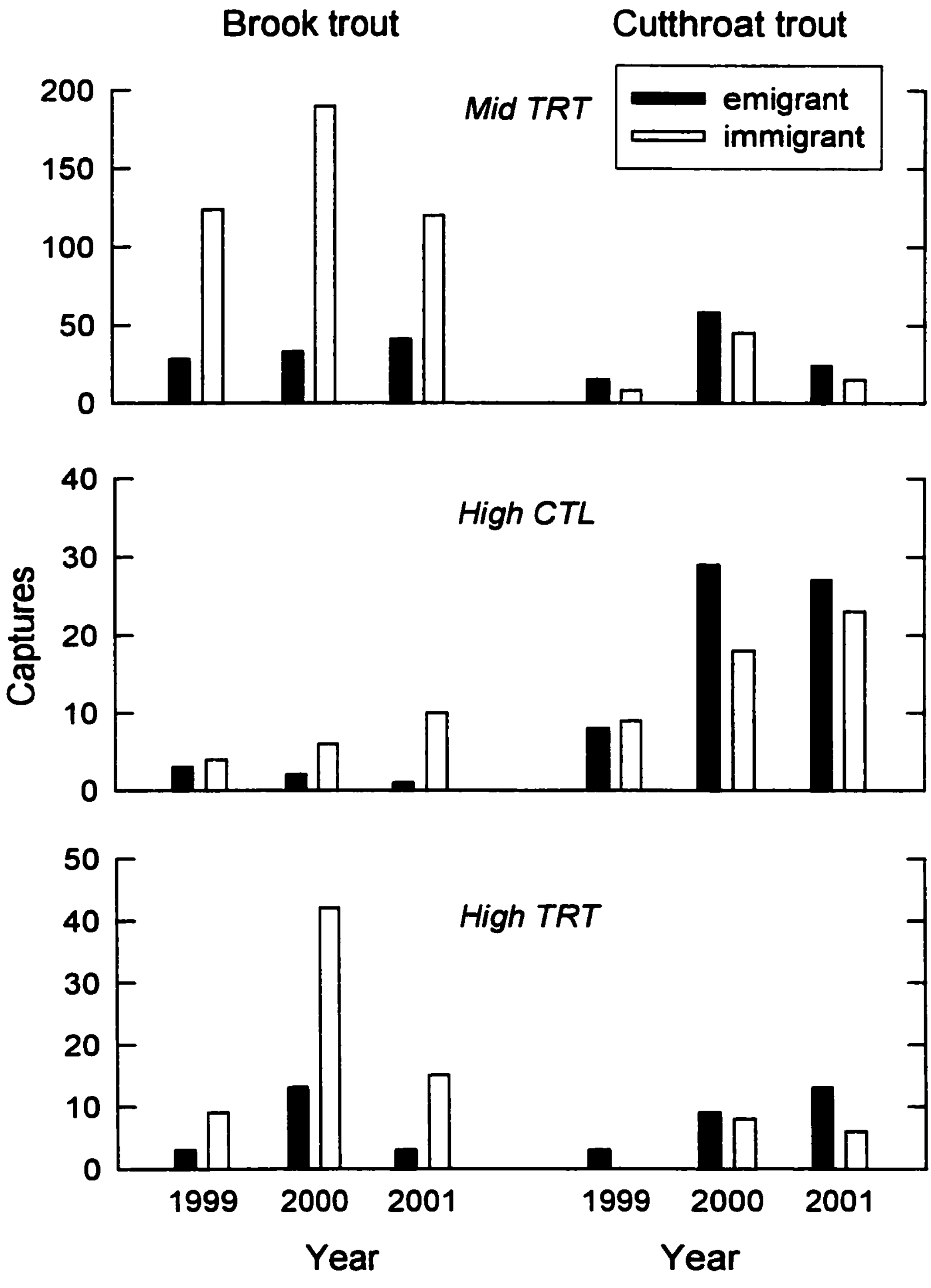


Figure 2.6. Trout movement in three study streams during June through September of 1999 through 2001. Values are captures at two-way weirs of trout entering (immigrant) or leaving (emigrant) the study reaches. Abbreviations are as in Figures 3.2 through 3.4. Immigrant brook trout in treatment streams were removed to maintain the treatment, but emigrant brook trout were allowed to emigrate.

Figure 2.7. Demography of brook trout invasion and effects on cutthroat trout in four Colorado streams. Conceptual diagram depicts the life stages of cutthroat trout and brook trout (e.g., eggs, age-0, etc.), and transitions between stages (e.g., spawning, recruitment, and survival) or movement (e.g., immigration and emigration) that are the mechanisms causing changes in abundance of trout. Biotic interactions with brook trout affect cutthroat trout most strongly at the younger life stages, with the relative effects indicated by the thickness of the arrow. Recruitment of both species is apparently depressed or eliminated by low summer water temperatures in high-elevation streams. In addition, biotic affects from brook trout may interact with low temperatures to suppress recruitment of cutthroat trout in colder, high-elevation streams. Cutthroat trout tended to emigrate from study segments during summer, but this emigration may be part of an annual movement pattern and thus be only temporary emigration. In contrast, brook trout immigrated into study segments at high rates from source populations downstream.

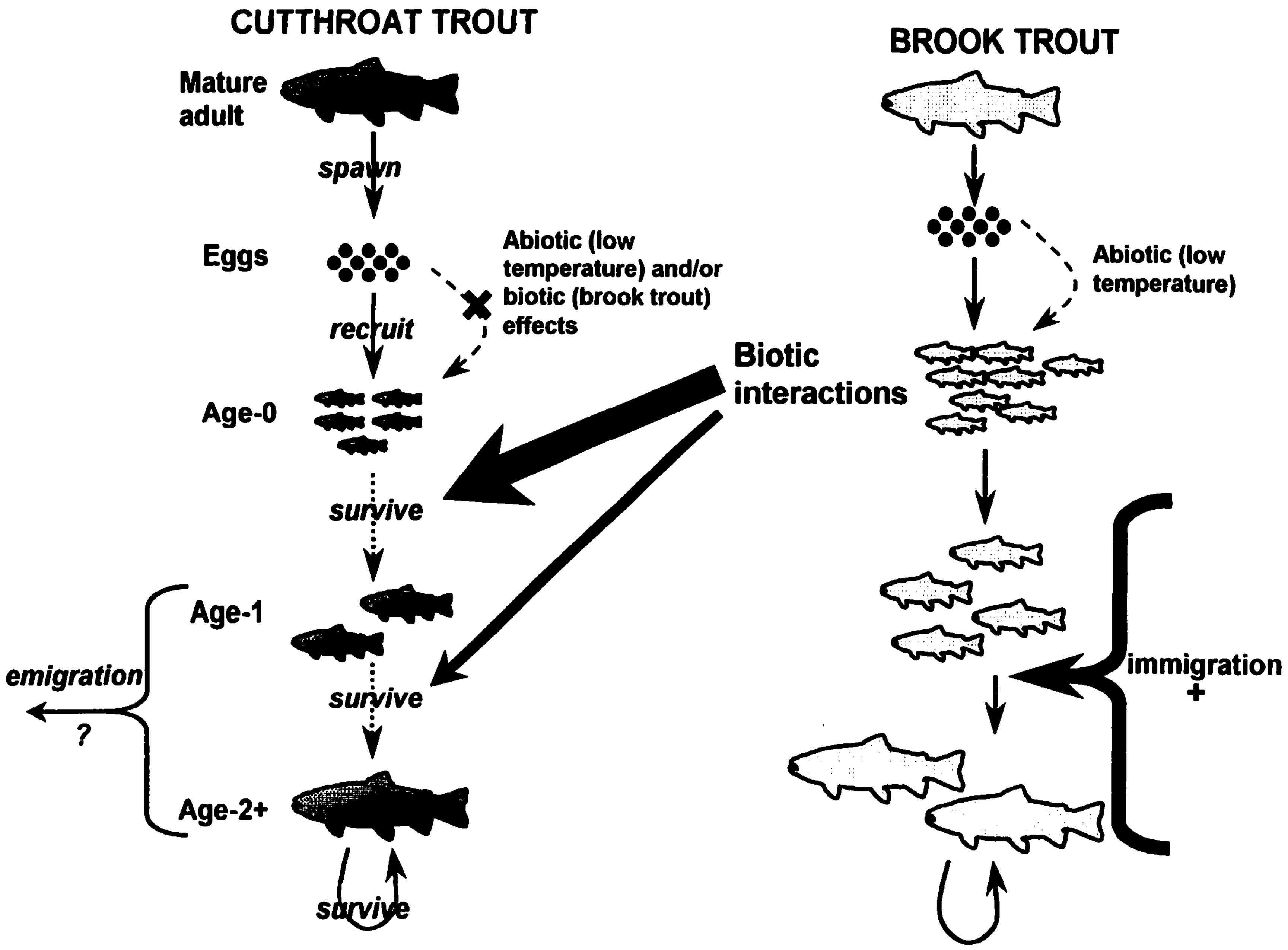
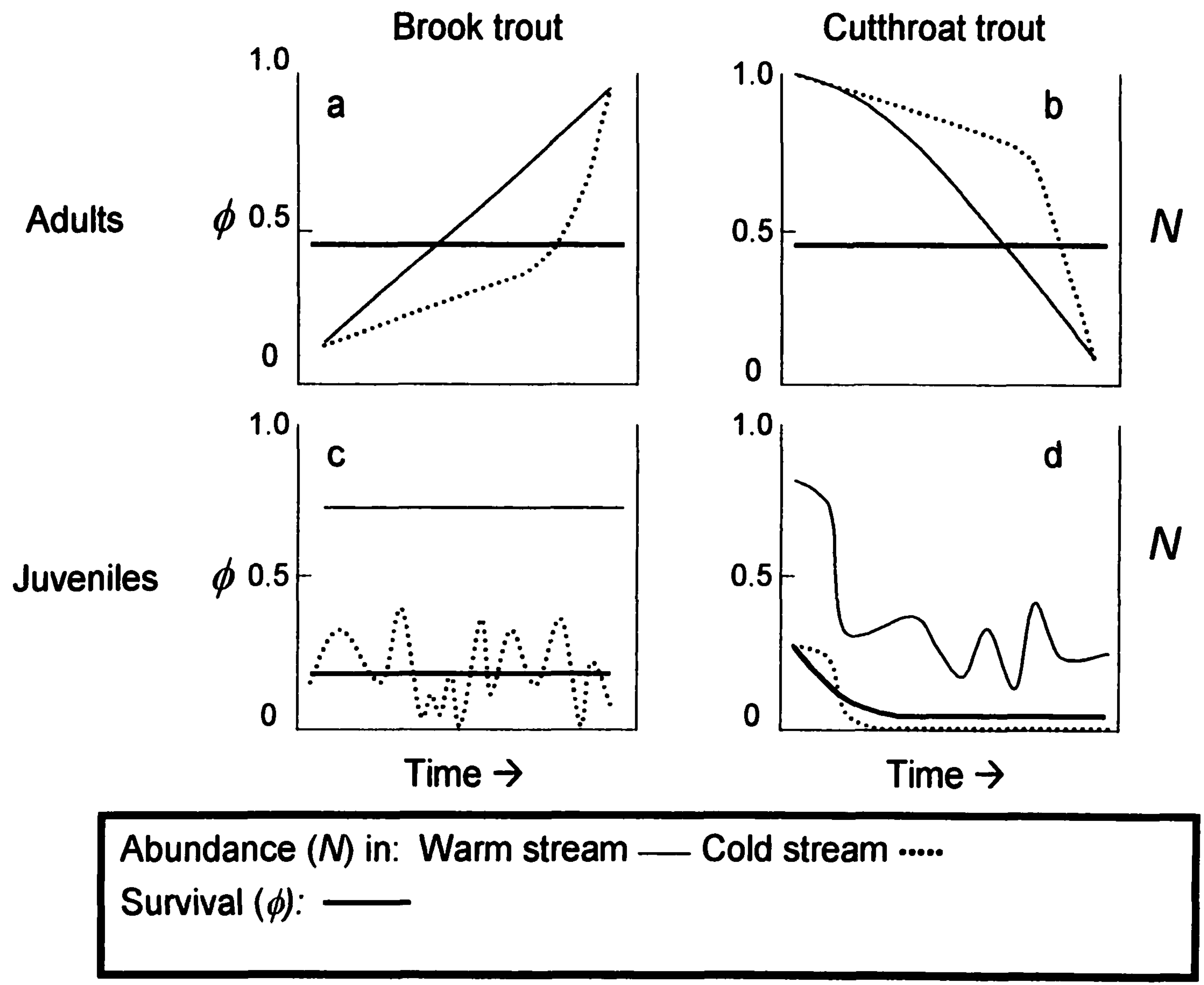

CUTTHROAT TROUT
Mature adult
spawn
Eggs
Abiotic (low temperature) and/or biotic (brook trout) effects
recruit
Age-0
survive
Age-1
emigration
?
survive
Age-2+
survive
BROOK TROUT
Abiotic (low temperature)
Biotic interactions
immigration
+

Figure 2.8. Conceptual model of the demography of a brook trout invasion into small Rocky Mountain streams inhabited by cutthroat trout. Model shows trends in survival (ϕ – solid lines, left vertical axis) and abundance (N – dashed lines, right vertical axis) as the invasion progresses through time, for warm streams at mid elevation and cold streams at high elevation. Each panel (a-d) has one plot for survival, but two for abundance. Juvenile abundance represents recruitment, defined as the number of age-0 trout surviving to early fall, and juvenile survival means survival from age-0 to age-1 from one fall to the next. The projections are based on empirical data from the experiment whereby: a) brook trout strongly reduce survival of juvenile cutthroat trout but not survival of adult cutthroat trout, b) juvenile trout survive at lower rates than adults, c) adult trout survival is higher in cold streams because of greater longevity, and d) brook trout have a downstream source population supplying immigrants whereas cutthroat trout do not.


Brook trout
Cutthroat trout
Adults
Juveniles
ϕ 0.5
1.0
0
a
b
c
d
N
Time →
Time →
Abundance (N) in: Warm stream —— Cold stream •••••
Survival (ϕ): ——

CHAPTER THREE: DISPERSAL OF BROOK TROUT PROMOTES INVASION SUCCESS AND REPLACEMENT OF CUTTHROAT TROUT

Abstract

Dispersal is a key process determining the success, rate, and effects of biological invasions. To understand how dispersal influences the processes by which invading nonnative brook trout replace native cutthroat trout, I studied trout movement in three mountain streams in Colorado during 1999 to 2001. Over 3500 trout were marked and recaptured at weirs and during electrofishing both within and downstream of stream segments used for a concurrent experiment on the population ecology of the invasion. Nearly 80% of brook trout captured at weirs were moving upstream, whereas almost 65% of cutthroat trout captured at weirs were moving downstream. Brook trout movements peaked in early summer at the end of snowmelt runoff, and again in fall during spawning. Brook trout immigration rates from downstream source populations were high, and invaders could repopulate experimental segments where they were removed within one summer (Little Muddy Creek) or by the next year (Willow Creek). Invading brook trout were typically mature adults, with a tendency to be larger than the general population in high-elevation streams, and smaller in the moderate-elevation stream, but all trout were in similar condition regardless of stream. Brook trout immigrated from a range of distances, with local movement (within 250 m) more common, but some individuals moved >1-2 km within a summer. Brook trout invasions appear to be driven by two simultaneous

processes: a wave of local movement that exerts biotic pressure on the downstream limit of the cutthroat trout population, and jump dispersers moving upstream beyond the invasion front that facilitate rapid colonization and population spread.

Introduction

Invasions are a major factor in the imperilment, extinction, and homogenization of aquatic fauna (Miller et al. 1989; Rahel 2000). Salmonid fishes have been widely introduced, and the invasions that often result are known to produce large ecological effects from the genetic to ecosystem levels (Kreuger and May 1991; Allan and Flecker 1993). For example, introduction and subsequent invasion by brook trout (*Salvelinus fontinalis*) in the western US is believed to be a primary factor in population declines of native species of inland cutthroat trout (*Oncorhynchus clarki*), and brook trout tend to replace cutthroat trout where they co-occur (Griffith 1988; Fausch 1989; Young 1995).

Movement by invading salmonids has not been well studied in comparison to other aspects of their invasions. Description of the pattern of replacement observed in natural populations has been followed by individual-level studies of competition between native and nonnative species (Chapter 1). However, movement is a critical component of the life history and population dynamics of salmonids (Northcote 1997), and so is likely to be a factor influencing invasion dynamics. Although ranging behavior to seek suitable habitat or feeding conditions outside the home range (sensu Dingle 1996) is a key determinant of invasion success and rate of spread, movements of invading salmonids are poorly understood and have only recently received attention (e.g., Adams et al. 2000, 2001).

Detailed studies of movement by invading salmonids are warranted because invasion dynamics are sensitive to age-, size-, or stage-structured differences in dispersal (Neubert and Caswell 2000; Fagan et al. 2002). Stream salmonids have age-structured populations, so an accurate assessment of the demography of a salmonid invasion must account for age- or size-specific differences in movement, and their relative contributions to the rate of population spread. Particular components of stream salmonid populations are thought to exhibit more frequent ranging behavior than others (Gowan et al. 1994; Fausch and Young 1995; Gowan and Fausch 1996), providing the potential for rapid, far-ranging colonization of new habitats.

Movement in isolated populations of native salmonids subjected to nonnative invasions also has rarely been considered. Many populations of native cutthroat trout in streams are isolated in headwater reaches because of fragmentation and loss of downstream habitat, impassible barriers, or nonnative species (Behnke 1992; Harig et al. 2000). Inland salmonid species historically included migratory (e.g., fluvial or adfluvial) life history types (Northcote 1997), but these components are thought to have been lost from, or are now maladaptive for, isolated populations (e.g., Young 1996). However, even resident populations can exhibit ranging behavior to meet life-history requirements (Fausch and Young 1995), although it is not known how such behavior is influenced by the presence of nonnative salmonids.

In this study I measured characteristics of movement by nonnative brook trout invading moderate and high-elevation headwater streams inhabited by native Colorado River cutthroat trout (*O. c. pleuriticus*). To understand how movement influences invasion dynamics, I measured the timing, direction, distance, and rate of movement by brook trout in an ongoing invasion. I characterize the age classes of brook trout populations that contribute differentially to the success of such invasions, and also describe how movement of cutthroat trout may contribute to the observed pattern of replacement.

Methods

Study sites

Trout movement was measured in Little Muddy, Indiana, and Willow creeks in northern Colorado during 1999 to 2001 (Table 3.1; Figures 3.1 – 3.3; also see Figure 2.1). Sites were small, first- or second-order montane streams with baseflow $<0.05 m^3 \cdot s^{-1}$. Habitat alternated between 1-2% gradient meadow reaches with willow (*Salix* sp.), and 2-6% gradient forested reaches with mixed stands of lodgepole pine (*Pinus contorta*), subalpine fir (*Abies lasioicarpa*), Englemann spruce (*Picea engelmannii*), and aspen (*Pinus temuloides*). Streams had sympatric populations of brook trout and Colorado River cutthroat trout, but only Indiana Creek had a reache upstream of the study area where cutthroat trout were allopatric. All other streams were completely invaded by brook trout. However, brook trout abundances were reduced in 877 – 1200-m long segments (hereafter, study segments) of Little Muddy and Willow creeks during 1998 to 2001 as part of a removal experiment to test mechanisms by which brook trout replace cutthroat trout (Chapter 2). Removal methods are described below.

Predictions

Based on previous studies demonstrating widespread trout movement and ranging behavior in streams (e.g., Gowan et al. 1994; Rodríguez 2002), I made a series of predictions about movements by trout in study streams. These predictions generated subsequent expectations as to how such movement would influence the processes by which brook trout invade small, headwater streams inhabited by cutthroat trout. First, I predicted that brook trout would exhibit seasonal variation in movement, with peaks in early summer during elevated stream discharge (i.e., snowmelt runoff) and in fall during spawning (Flick and Webster 1975; Gowan and Fausch 1996). Second, I predicted that brook trout would tend to move upstream in summer (Flick and Webster 1975; Gowan and Fausch 1996), whereas cutthroat trout would show no tendency to move in a particular direction (Young 1996). Third, I predicted that adult brook trout would move more frequently than juveniles (Gowan and Fausch 1996). If so, these adults would likely be sexually mature and capable of reproducing and establishing populations. Fourth, I predicted that trout moving during summer would be longer, but in poorer condition than individuals in the general population (Gowan and Fausch 1996). Fifth, I predicted that brook trout would move rapidly upstream, from a variety of distances downstream (Gowan and Fausch 1996). Consequently, if these predictions held I expected that invading brook trout would be primarily upstream-moving adults arriving from a variety of distances, and within-season movement rates would be high enough to promote rapid colonization and invasion.

Weirs

To measure timing and direction of trout movement and to characterize the age composition and body condition of moving trout, I operated two-way fish weirs in three streams during summer to late fall from 1999 to 2001 (Table 3.2). Each stream had three or four weirs, one each at the upstream and downstream margins of the study segment, and additional weirs either within this segment or downstream (Figures 3.1 – 3.3). Weirs consisted of a two-way trap box with side panels (wings hereafter) covered with 6-mm black plastic mesh that funneled trout into the traps (see Gowan and Fausch 1996 for similar design). Trap boxes consisted of a 0.9 long × 0.8 m wide × 0.6 m tall frame of PVC pipe covered with the same plastic mesh, and were divided longitudinally to separate fish moving upstream from those moving down. Large cobble and plywood wedges provided velocity refuges for trout in each side. Trap openings were 6 cm wide, and a 20-cm wide board was placed inside the trap box 10 cm from the entrance to obscure the opening from trout already inside the trap. Tests in 1999 showed that trout could exit traps through the opening (Peterson and Fausch, *unpublished data*). Therefore, beginning in 2000 entrances were constricted into a 5- × 8-cm opening and through an angled section of plastic rain gutter fitted with a 10-cm length of flexible nylon stocking, which collapsed after trout passed through it and obscured the exit. Weirs were secured using steel posts, and a 25-cm mesh skirt extending from the bottom of the apparatus was buried in stream gravels to prevent trout from passing beneath the weir. Snorkeling was used to confirm that the weir was closed to all trout >75 mm fork length (FL). Weirs were installed from mid June to late July, depending on when high flow from melting snow receded, and removed in early October (see Table 3.2). Weirs could be monitored only during summer to fall because sites could not be reached during winter.

Weirs were visited every second day, and captured trout were anesthetized (MS-222), measured (FL, nearest mm), and weighed (nearest 0.1 g). Trout were assigned to one of three age classes (i.e., ages 0, 1, and 2 and older) based on length, using a combination of length-frequency histograms and otolith data (Kennedy et al., *in press*). Brook trout entering the study segments in Little Muddy and Willow creeks were euthanized with an overdose of anesthetic as part of the removal experiment. Ub in all other cases trout of both species received batch marks to indicate weir location and direction of travel, including brook trout leaving study segments of Little Muddy and Willow creeks. Fish were marked using various colors of nontoxic Liquitex© acrylic paint (Binney and Smith, Inc., Easton, PA) injected into post-orbital adipose tissue (i.e., adipose eyelid) using a sterile insulin syringe. Adult brook trout (age 2 and older, hereafter age 2+), which were ≥110 mm FL, received dark green Floy Fine Fabric Anchor tags (Floy Tag, Inc., Seattle, WA), and adult cutthroat trout, which were ≥85 mm FL, were tagged using two fluorescent visual implant (VI) tags (Northwest Marine Technology, Inc., Shaw Island, WA). The adipose fin was excised from all trout given unique tags to identify subsequent tag loss. After recovery from anesthesia, trout were released in the direction they were traveling, at least 10 m away from the weir. Stream stage was recorded from a staff gauge on each day weirs were checked, and discharge was estimated using a rating curve calibrated for each stream each year.

Downstream marking of brook trout

To characterize the origin of invading brook trout and to detect longer-distance movements, I marked brook trout downstream and outside of the study segments (hereafter, downstream marking). Brook trout invasions were directed upstream in all streams, so source populations only existed downstream of the study segments. Batches of approximately 40 – 120 brook trout of all age classes were captured, marked, and released at distances 0, 250, 500, 1000, and 2000 m-downstream from the study segment during 1999 to 2001 (Table 3.2; Figures 3.1 – 3.3). Downstream marking was conducted in each stream in each year (except Willow Creek in 1999), but not all locations at 0 and 500 m were sampled each year and the 2000 m site in Indiana Creek could not be sampled because the stream was bordered by private property. Brook trout were captured by one-pass backpack electrofishing (Mark 10, Coffelt Manufacturing, Inc., formerly of Flagstaff, AZ, settings: 30 Hz, 150 – 450 V pulsed DC) in reaches at least 100 m in length with a block net (5-mm mesh) placed at the top of the reach. Brook trout captured were measured and tagged as above, and all fish received florescent elastomer (Northwest Marine Technology, Inc.) injected into rays of the dorsal or caudal fins to indicate year and location of capture. Trout were held overnight in live baskets placed in deep pools, then released at the capture location.

Annual electrofishing surveys

As part of the brook trout removal experiment, annual two-pass depletion electrofishing was conducted in the study segments of all streams during baseflow (Table

3.2). The electrofishing technique was similar to that used for downstream marking, except trout populations were enclosed by block nets at upstream and downstream margins. Cutthroat trout in all streams and brook trout in Indiana Creek were counted, marked as above (see Chapter 2 for details), and released into their 50-m section of capture, whereas brook trout captured in the study segments of Little Muddy and Willow creeks were euthanized. Weirs inside and at the margins of the study segments were closed during electrofishing.

Analysis

Marked trout were recaptured at weirs, during annual electrofishing surveys of the study segment, or during downstream marking. These sampling methods encompassed a total distance of 2877 to 3325 m per stream. I analyzed the timing of movement both graphically, in relation to date, and analytically, in relation to discharge. The relationship between the number of trout captured at weirs and stream discharge was explored using Pearson correlation on log-transformed data, by stream and year ($n=9$ analyses for each species). Confidence intervals for correlations were calculated by transforming coefficients by the Fisher Z-transformation, calculating confidence intervals on the z-values, then back transforming the endpoints (Zar 1996). Correlations were considered statistically significant if confidence intervals did not overlap zero.

Direction of trout movement through weirs was estimated by logistic regression. Stream and year were primary factors, and log-transformed fork length was used as a covariate. In addition, treatment group (e.g., brook trout removal stream or not) was used as a class variable for cutthroat trout. Weir type (confounded or unconfounded) was used as an additional class variable for brook trout, whereby confounded weirs were those located adjacent to stream reaches where brook trout were being removed in Little Muddy and Willow creeks, and unconfounded weirs were those weirs downstream from removal reaches (Little Muddy and Willow creeks) or in a stream where brook trout were not removed (Indiana Creek). An information-theoretic (IT) approach to model selection was used, whereby AIC weights were used to assess the relative likelihood of competing models (Burnham and Anderson 2002). Importance of individual factors was determined by cumulative AIC weights, defined as the sum of the AIC weights of all models containing that factor. The proportions of trout moving a given direction were estimated using model averaging. Brook trout captured at weirs were assigned to age classes based on length-frequency histograms and otoliths to identify specific demographic contributed to the invasion.

Lengths of marked trout in the general population that subsequently moved through weirs were compared to those that did not using analysis of variance (ANOVA – general linear models) or covariance (ANCOVA) and information-theoretic model selection. Lengths were log-transformed, and stream, year, and treatment group (cutthroat trout only) were factors. For brook trout, the general populations was defined as trout caught and individually tagged during downstream marking in Little Muddy and Willow creeks because brook trout were repeatedly removed from study segments, whereas in Indiana Creek trout marked during annual electrofishing and downstream marking data were pooled. For cutthroat trout, the general population was those fish individually-tagged inside the study segments or during downstream marking. Only individually-tagged trout, generally age-1 and older, were used for these analyses because they moved more frequently than age-0 trout (see below) and individual identification was necessary so that trout recaptured at weirs could be separated from those that did not when between-group comparisons were being made.

Fish condition of trout recaptured moving through weirs was also compared to those that did not (i.e., the general population) using analysis of covariance of the same marked trout as for length comparisons. In a typical ANCOVA, length-mass regression lines for each group are fit to the data to first test for differences in slopes (i.e., growth rates) among groups. If slopes are similar (i.e., group × length interaction not significant), one can estimate differences in body condition among treatment groups by comparing intercepts (cf. Riley and Fausch; Gowan and Fausch 1996). In contrast, I used an information-theoretic approach to this analysis. Preliminary model selection for both species indicated that the relationship between length and mass (both log-transformed) depended on stream (or treatment group) and year and their interactions, so data were analyzed separately for each stream in each year ($n = 7$ analyses for brook trout and $n = 9$ analyses for cutthroat trout). Three models were fit each analysis, whereby mass was a function of: a) group, length, and their interaction (interaction model); b) group and length (group model); and c) length only (length only model). Model averaging across these three models was used to estimate the mass of trout that moved through weirs versus those that did not (general population), and simple differences were calculated to determine if trout in one group were in better condition than those in the other.

Immigration of downstream-marked brook trout into study segments was used to detect long-distance movements in each stream, and data from all weirs, annual electrofishing, and downstream marking were combined to estimate total and net movement of brook trout. Movement distances were estimated to within 25 m, because annual electrofishing was conducted in 50-m reaches and trout were returned to the middle of these reaches after marking (see Chapter 2 for details). To measure the potential for brook trout to quickly colonize new habitats, I estimated within-season movement rates of brook trout during 2000 to 2001 using combined data from downstream marking and weirs. Data from 1999 were not analyzed because downstream marking was done relatively late in the summer (Table 3.2), and none of these fish, or fish marked at weirs, were recaptured within the 1999 recapture season. Total and net movement patterns were described, but not statistically analyzed as with other data because of potential bias because some locations were not sampled in every year and recaptures would be expected to increase through time because more marked fish were available. In contrast, the relationship between upstream movement rates were modeled as a function of stream, year, and size of brook trout using general linear models (ANOVA) and cumulative AIC weights, because these data were less subject to the biases affecting the total and net movement frequency data. All statistical analyses were performed with SAS (Proc Genmod, Proc Mixed, and Proc Logistic; Version 8.2, SAS Institute, Inc., Cary, NC).

Results

Timing and direction of trout movement through weirs

I captured 1726 trout at weirs in three streams during 1999 to 2001, but numbers captured varied by species, year, and stream (Figures 3.1 – 3.6). Over twice as many brook trout (*n* = 1220) were captured than cutthroat trout (*n* = 506), and more trout of both species were captured in 2000 than other years. Captures of both species at weirs were highest in the stream with the greatest trout densities (Little Muddy Creek: see Chapter 2).

Movement was more frequent in early summer and late fall, associated with higher discharge, particularly in Little Muddy and Indiana creeks (Figures 3.4 – 3.6). Movement of brook trout was positively correlated with discharge in Little Muddy Creek during 2000 and 2001 ($r = 0.65$, 95% CL 0.48 to 0.78; and $r = 0.60$, 0.41 to 0.74), but negatively correlated in Indiana Creek in 2001 ($r = -0.30$, -0.53 to -0.04). In contrast, cutthroat trout movement was positively correlated with discharge every year in Little Muddy Creek ($r_{1999} = 0.33$; 95% CL 0.04 to 0.56; $r_{2000} = 0.73$, 0.58 to 0.83; and $r_{2001} = 0.50$, 0.28 to 0.67), and two of three years in Indiana Creek ($r_{1999} = 0.40$, 0.09 to 0.64 and $r_{2000} = 0.37$, 0.09 to 0.59), but was negatively correlated with discharge in Indiana Creek during 2001 ($r = -0.33$, -0.55 to -0.08).

Brook trout tended to move upstream during summers, in all streams and in most years, regardless of whether or not weirs were adjacent to brook trout removal reaches (Figure 3.7). Logistic regression using 24 a priori models indicated that stream, year, length, weir type, stream × year interaction, and year × length interaction were important factors (cumulative AIC weights all >0.99). The proportion of brook trout moving a given direction for each stream × year × weir type combination (at the mean length for each year) was estimated by model averaging over the top two models that contributed 99% of the total AIC weight (Table 3.3). Brook trout moved upstream more often than downstream every year in Little Muddy Creek (70-98% estimated moving upstream), two of three years in Willow Creek (69-83%), and one year in Indiana Creek (91%). These values estimate the number of brook trout captured at weirs that were moving upstream, and do not make inference as to what proportion of the entire brook trout populations in these streams moved a given direction.

In contrast, cutthroat trout moved downstream more often than upstream in two of three summers (Figure 3.8). Results from 23 models indicated that year (cumulative AIC weight >0.99) and length (0.52) were important factors. Estimates for the proportion of cutthroat trout moving a given direction each year were made by model averaging over 11 models (see Table 3.3 for top five models). During 2000 and 2001, an estimated 63% and 82% of cutthroat trout captured at weirs were moving downstream, respectively.

Characteristics of trout moving through weirs

Trout of both species captured at weirs during summer were predominantly age 1 or age 2+ (Figure 3.9). In Little Muddy and Indiana creeks a small percentage of trout captured at weirs were age 0 (2-6.5%). Age 0 trout were underrepresented in weir captures in relation to their abundance for both species in Little Muddy Creek and for brook trout in Indiana and Willow creeks (cf. Chapter 2).

Lengths of brook trout recaptured moving through weirs were statistically similar to those in the general population in all cases (Figure 3.10), though there was a tendency for brook trout moving though weirs to be smaller than the general population in Little Muddy Creek, and longer in Willow and Indiana creeks. Cumulative AIC weights for all single and two-way factors from 19 ANOVA models were all at least 0.99, indicating that the group effect for brook trout varied by stream and year. These effects are evident in the difference between Little Muddy compared to Willow and Indiana creeks, and the downward trend in length across years for all streams. In comparison, cutthroat trout moving through weirs tended to be larger than cutthroat trout in the general population in Little Muddy and Indiana Creeks, but the 2001 estimates for Little Muddy Creek were the only comparison where 95% confidence intervals did not overlap. Cumulative AIC weights from 19 ANOVA models indicated that cutthroat trout length depended on stream (weight = 1.0), group (0.99), and year (0.52), but not on the two- (0.17 to 0.41) and three-way interactions (<0.01), indicating that group and stream effects were consistent across years.

Fish condition

There was no evidence to suggest any biologically-meaningful differences in body condition between brook trout recaptured at weirs or in the general population (Table 3.4). On average, brook trout in the general population were heavier in Little Muddy Creek (AIC weight for group 0.59-0.69), but the absolute and relative effect sizes were small. Similarly, condition of cutthroat trout captured at weirs and in the general population was similar except for two cases. In one of these, the absolute difference was less than 1 gram (Little Muddy Creek in 2000), but in the other, cutthroat trout in the general population averaged 28 g heavier than those captured at weirs (Willow Creek in 2001).

Population turnover

Summer immigration by brook trout was substantial from 1999 to 2001, particularly in Little Muddy Creek. The numbers of brook trout captured and removed during 100 – 123 d of summer trapping at weirs on the margins of the study segment in Little Muddy Creek was 38 – 66% of the estimated combined abundance of age-1 and age-2+ brook trout within the segment during annual electrofishing and an additional removal each July (Figure 3.12). Adult (age-2+) brook trout immigration averaged 19% of the estimated abundance in other streams.

Movement distances and rates

Recaptures of brook trout marked downstream of the study segments showed that they had immigrated from up to 2 km away, but local immigration from within 250 m was most common (Figures 3.13 – 3.15). A total of 1872 brook trout were marked and released during downstream marking in the three streams, which resulted in 405 recaptures of 368 individual fish encountered at weirs, during downstream marking, or inside the study area during annual electrofishing surveys. Recapture rates were 19 – 28% among streams. The proportions recaptured inside the study area could not be compared among streams because sampling effort and locations varied, but movement was detected more frequently in Little Muddy Creek than in Indiana or Willow creeks. There were sufficient recapture data for downstream marking in Little Muddy Creek to fit a logistic regression model that predicted the proportion of brook trout invading the study segment from different distances (intercept and distance, $P<0.0001$). Batch marks of brook trout captured at 500 m downstream in 1999 quickly faded, so these data were excluded. The model predicts that 15% of brook trout at 250 m, 6% at 1000 m, and 2% at 2000 m would move upstream and enter the study segment.

Recaptures throughout the stream of these marked brook trout showed that the modal frequencies of total and net distances moved was ≤50 m, but substantial numbers of fish moved hundreds to thousands of meters (maximum value ≥ 2500 m; Figures 3.14 and 3.15). For example, 54% of recaptured brook trout in Little Muddy Creek, 38% in Willow Creek, and 11% in Indiana Creek were estimated to have moved more than 50 m. Movement beyond 50 m was more common for brook trout in Little Muddy Creek than for other streams, and most individuals that did move were ultimately recaptured upstream from their original capture location (Figure 3.15).

Median rates of upstream movement by brook trout captured within a summer during 2000 or 2001 were higher in Little Muddy Creek (16.7 $m \bullet d^{-1}$) than in Indiana (9.0 $m \bullet d^{-1}$ in 2001) or Willow creeks (11.5 and 12.5 $m \bullet d^{-1}$ in 2000 and 2001; see Figure 3.16). However, in Little Muddy Creek the median rate of upstream movement was twice as high in 2000 as in 2001 (33.3 versus 16.7 $m \bullet d^{-1}$). Cumulative AIC weights from 18 models indicated that movement rates depended on length (cumulative weight = 0.99), year (0.91), and stream (0.61), but the length effect did not depend on stream or year (weights for all two-way interactions < 0.4). The top-ranked model, in which movement rate was a function of year and length, suggested that there was a negative relationship between movement rate and size (i.e., negative regression coefficient for length whose 95% confidence interval did not include 0). However, there was considerable uncertainty about this relationship because this model accounted for only 22% of the total AIC weight. For all streams in all years, only seven brook trout were recaptured moving downstream within a season (range 4 – 150 m) so these data were not analyzed.

Discussion

Movement of brook trout and cutthroat trout in headwater streams

The results from three streams in Colorado demonstrated that brook trout were quite mobile even in small headwater habitats, and that the demography of these far-ranging, rapidly moving immigrants makes them potent invaders. Here I address which of the predictions made at the outset about trout movement and brook trout invasion were supported by the data. First, my data confirmed the prediction that brook trout movement would show seasonal peaks, during early summer and early fall. Although brook trout were captured at weirs throughout the summer trapping seasons, most were caught during mid June to mid July or in late September. Movement peaks were related to hydrologic conditions because many brook trout moved through weirs during high discharge caused by snowmelt runoff or localized thunderstorms, though the relationship was most consistent in the stream with the highest brook trout density. Similar to brook trout, cutthroat trout movement also tended to coincide with increased discharge. I assumed that increased movement by brook trout during fall was associated with spawning as others have found (Flick and Webster 1975; Gowan and Fausch 1996; Bélanager and Rodríguez 2001), because most brook trout captured at weirs during this time were ripe, extruding milt or eggs.

Second, I confirmed the prediction that brook trout tend to move upstream during summer, but in contrast to my initial prediction I found that cutthroat trout moved downstream more often than upstream. Brook trout tended to move upstream both within and between seasons, which promoted invasion of headwater habitats inhabited by cutthroat trout. Even after accounting for potential bias caused by the removal experiment, I still found a majority of brook trout (>60-90% depending on stream) were moving upstream when captured at weirs. Similar tendencies for upstream movement were found for brook trout in streams in Idaho (Adams et al. 2000), Colorado (Riley et al. 1992; Gowan and Fausch 1996), and New York (Flick and Webster 1975). Net movement by brook trout was also upstream, although brook trout captured within, or attempting to enter, the study segments of Little Muddy and Willow creeks were removed and never had the opportunity to return to their original location. Nonetheless, these upstream-moving individuals would be expected to settle if they encountered suitable habitat (Gowan and Fausch 1996, 2002), and interact with cutthroat trout at least temporarily. Although this upstream-directed movement pattern appears to be common among salmonids (Hughes 1998), the mechanisms responsible for it are not clear and remain to be tested. Possible hypotheses include homing of fish displaced earlier in their life cycles (Hunt 1965), recruitment of certain ages or life stages to upstream stream reaches (Hughes 1999), olfactory clues from conspecifics or natal habitat (Bélanager and Rodríguez 2001), ranging behavior to seek suitable habitat (Gowan and Fausch 2002), or dispersal of surplus production from source habitats (Adams 1999).

In contrast to brook trout, I found that least 60% of cutthroat trout captured at weirs tended to be moving downstream in two of three summers. Fluvial cutthroat trout can move dozens of kilometers after descending from headwater or tributary streams following spawning whether brook trout were present in the system (Schmetterling 2001) or not (Schrank 2002). However, Hilderbrand and Kershner (2000) found s that four times as many cutthroat trout sympatric with brook trout moved upstream than downstream through weirs in Utah and Idaho, and Young (1996) found no directional bias for radio-tagged cutthroat trout in a Wyoming stream where brook trout were not present. These different results may be caused by the timing of sampling, as well its spatial and temporal extent, or variation in measurement techniques (e.g., weirs, telemetry, or electrofishing), or habitat size and connectivity. Alternatively, presence of nonnative trout like brook trout may affect movement patterns of cutthroat trout, but specific data testing these potential effects are lacking (but see Hilderbrand 1998), particularly for small headwater streams that are the final stronghold for threatened cutthroat trout like those I studied.

Third, I substantiated the prediction that adult brook trout move more frequently than juveniles and constitute the majority of immigrants and invaders. Brook trout captured at weirs in Indiana and Willow creeks were almost exclusively large adults (age 2+), and brook trout moving in Little Muddy Creek were primarily age-1 and age-2+ individuals larger than 100 mm. Larger trout have greater swimming ability and may be able to ascend higher, steeper barriers than smaller individuals (Thompson and Rahel 1998; Adams et al. 2000), or move longer distances (Young 1994; Schrank 2002). Fecundity increases with body size, so larger, mature adults would be expected to have the highest reproductive potential, and thus the greatest probability of establishing a new population. Most of the brook trout moving through weirs were indeed mature adults, but even a proportion of age-1 individuals were reproductively mature in Little Muddy Creek. Using median sizes of invading brook trout in Little Muddy Creek (111 – 125 mm), a logistic regression model predicts that 15-70% of males and up to 20% of females at these lengths would be mature (Kennedy et al., *in press*).

Fourth, differences between moving trout and the general population did not strongly support the prediction that moving trout would be larger and in poorer condition than the general population. However, in the high-elevation streams, the tendency (i.e., a trend was apparent, but not statistically significant) for trout captured at weirs to be larger than the general population was generally consistent with the hypothesis that larger, dominant stream-dwelling trout tended to search for suitable habitat and better foraging locations during summer as stream flow, habitat area, and invertebrate drift decline (Gowan and Fausch 2002). However, these fish were not necessarily in poorer condition than the general population, and so were not necessarily competitively inferior. For example, Kahler et al. 2001 found that juvenile anadromous salmonids that moved grew more quickly that those that did not. Feeding locations for stream salmonids are determined by size-mediated dominance hierarchies (Fausch 1984; Nakano 1995), so large, dominant brook trout immigrate into native cutthroat trout habitat, biotic interactions would be expected (Griffith 1988). Even if these brook trout did not settle and reproduce (e.g., Adams et al. 2000), they may competitively displace smaller cutthroat trout during the summer and affect their growth or survival rates (Novinger 2000). In contrast, immigrant brook trout in Little Muddy Creek, which was warmer than the other streams, were smaller that the general population, and may represent surplus production from a source population (e.g., Pulliam 1988) or subdominant individuals searching for open habitat.

Fifth, the data show that brook moved rapidly upstream from a variety of distances downstream. Summer immigration alone comprised up to two-thirds of the existing population in Little Muddy creek (Figure 3.16), and between-summer immigration completely repopulated depleted stream segments where brook trout were removed (see Chapter 2). Population turnover by brook trout had both local (Rodríguez 2002) and far-ranging components (Gowan and Fausch 1996). Based on recaptures of marked individuals, local (≤ 250 m) movements by brook trout were most common, but long-distance movements up to 2 km were detected within a summer. Moreover, between 70-80% of brook trout tagged at weirs and during downstream marking were never recaptured, so movement was likely more common than I measured and probably occurred outside the detection limits of this study (e.g., Gowan and Fausch 1996). Clearly, brook trout move to and from a range of distances, so a simple dichotomous categorization of individuals as mobile or sedentary is unlikely to capture the complexity of such behavior and its implications for the population ecology of the invasion (Gowan et al. 1994; Gowan and Fausch 1996; Hilderbrand and Kershner 2000; Schrank 2002).

Trout movement: implications for invasion

The combination of high immigration rates, a tendency to move upstream, and the inclination to move during elevated discharge make brook trout effective invaders of streams inhabited by native cutthroat trout. In headwater streams like I studied in Colorado, brook trout often have a source population downstream which can provide a supply of potential immigrants, whereas cutthroat trout populations are generally isolated (Fausch 1989; Behnke 1992), thus brook trout have a numerical advantage. Regardless of the proximate mechanism, the apparent propensity toward upstream-directed movement by brook trout creates an inherent bias toward invading upstream reaches that are typically the last stronghold for native cutthroat trout (Young 1995; Fausch and

Young 1995). Pulses of brook trout movement were observed during elevated discharge caused by snowmelt runoff and summer storms, so brook trout dispersing at these times may be able to pass barriers that would normally block their movements under base-flow conditions (Thompson and Rahel 1998; Adams et al. 2000). Stream reaches where brook trout were removed over four consecutive years were repopulated between late fall and the following summer in every case (e.g., Little Muddy Creek).

In comparison, if cutthroat trout consistently exhibit downstream-directed movement as I measured in this study, such behavior may have negative consequences for their populations. For example, downstream emigration would increase the probability that cutthroat trout would encounter high-density brook trout reaches, and if these cutthroat trout subsequently spawned in downstream reaches, their offspring would be particularly vulnerable to biotic interactions with brook trout (Chapter 2). However, I measured trout movement only during one-third of the year, so I likely captured only a portion of overall movement dynamics. Even though cutthroat trout captured at weirs tended to move downstream during summer, there is some evidence to suggest seasonal movement patterns. About 20% of the individually-tagged cutthroat trout that left the study area during one summer had returned by the following summer (Chapter 2).

Dispersal ability is typically influenced by size or age, so demography of dispersing brook trout is likely to have profound effects on the invasion (Fagan et al. 2002). Immigrant brook trout tended to be adults (Gowan and Fausch 1996; Adams et al. 2000), in similar condition to the general population. Swimming ability, position in dominance hierarchies, and fecundity are both positively correlated with size in stream-dwelling trout (Fausch 1984; Moyle and Cech 2000). Thus, results suggest that in high-elevation streams I studied, invading brook trout were those components of the population with the potential to range into new habitats, defend profitable feeding positions, and reproduce; whereas in moderate-elevation streams, invaders represented surplus production from downstream habitats than can numerically swamp cutthroat trout populations, and may nonetheless be mature (e.g., Kennedy et al., *in press*). In addition, the progeny of these brook trout invaders have a competitive advantage over young cutthroat trout (Griffith 1972; DeStaso and Rahel 1994; Novinger 2000), which can translate into lower survival rates and population declines (Chapter 2). Thus, brook trout appear to have flexible life histories (Kennedy et al., *in press*), which make then potent invaders in some western US streams.

Characteristics of brook trout dispersal also likely promotes rapid invasion, and far-ranging elements of the dispersal continuum (i.e., the range of distances from and to which trout move; sensu Schrank 2002) may contribute disproportionately to invasion spread. Local movement at the invasion front was quite common, and exerted considerable biotic pressure on cutthroat trout, facilitating rapid recolonization in streams where brook trout were removed. However, processes such as competition, reproduction, or environmental fluctuation occurring downstream of the invasion front can be critical proximate mechanisms causing dispersal or ranging behavior that influences invasion speed. Brook trout can move upstream many kilometers within a summer (Riley et al. 1992; Gowan and Fausch 1996), and the frequency distribution of recaptures from brook trout marked at various distances outside the study area appears to be leptokurtic, especially in the moderate-elevation stream (Figures 3.14 and 3.15; cf. Skalski and Gilliam 2000). Both theoretical (Kot et al. 1996; Lewis 1997) and empirical (e.g., Suarez et al. 2001) evidence indicates that these long-distance movers facilitate rapid invasion via jump dispersal.

It has been suggested that brook trout may be exceptionally mobile compared to other stream-dwelling salmonids (Rodríguez 2002), and it may be just this property that makes them capable invaders. Taken together, flexible life history and rapid dispersal to many distances from downstream source populations, and flexible life history make brook trout forceful invaders of headwater streams inhabited by threatened or endangered cutthroat trout.

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Table 3.1. Location and habitat characteristics of three study streams in northern Colorado during 1999 to 2001.

Stream	Location (Latitude, Longitude)	Length of study segment (m) †	Elevation range (m)	Mean July water temperature (°C)	Bankfull width range (m)
Little Muddy Creek	39°56’59, 106°02’46”	877	2658 – 2694	12.7	2.5 – 3.8
Indiana Creek	39°25’38”, 106°59’44”	950 – 1090	3194 – 3246	6.6	2.9 – 3.8
Willow Creek	40°28’12”, 105°46’48”	1002 – 1200	3188 – 3219	6.9	2.1 – 2.6

† Length of study segment varied among years in two streams because of habitat changes caused by beaver (Indiana Creek) and logistic constraints (Willow Creek).

Table 3.2. Dates of weir operation, downstream marking, and annual electrofishing surveys during 1999 to 2001.

			Unconfounded weirs §		
Stream	Year	Weirs (number of days) †	(total weirs)	Downstream marking	Electrofishing survey
Little Muddy	1999	6/24 - 10/1 (100)	0 (3)	8/5 – 8/6	9/10 – 9/13
	2000	6/16 - 10/16 (123) ‡	1 (4)	6/8 – 6/9, 7/12 – 7/13	9/21 – 9/24
	2001	6/10 - 10/4 (117) ‡	1 (4)	6/10, 6/16, 6/26	9/18 – 9/21
Indiana	1999	7/21 - 9/27 (69)	3 (3)	8/3 – 8/4	8/17 – 8/19
	2000	6/29 - 10/4 (98)	3 (3)	7/14 – 7/15	8/14 – 8/18
	2001	6/29 - 10/3 (97)	3 (3)	7/3, 7/5	8/13 – 8/15
Willow	1999	7/30 - 9/29 (62)	1 (3)	‖	9/17 – 9/20
	2000	7/23 - 10/3 (73)	1 (3)	8/1 – 8/3	9/17 – 9/20
	2001	7/20 - 10/1 (74)	1 (3)	7/17 – 7/18	9/17 – 9/20

† Weirs could not be operated during winter or early spring because sites were inaccessible or discharge was too high.

‡ Three weirs were used in all streams, except four weirs were used in Little Muddy Creek during 2000 and 2001.

Table 3.2. Concluded.

§ Unconfounded weirs are those where movement direction of brook trout was not biased by removing them from the study segments., whereas no cutthroat trout were removed, so data from all weirs were used.

‖ Downstream marking was not conducted in Willow Creek in 1999.

Table 3.3. Results of logistic regression to estimate the proportion of brook trout and cutthroat trout moving upstream versus downstream through weirs during 1999 – 2001. Only the top 2-11 models for each species are presented from a total of 24 (brook trout) and 23 (cutthroat trout) a priori models. Trout used in this analysis include both new captures and recaptures.

Model predicting movement direction	-2 Log $\mathcal{L}$ ‡	K	AIC$_c$ ‡	ΔAIC$_c$	w_i
Brook trout (n=1220)					
$\beta_0 + \beta_1$(stream) + β_3(year) + β_4(weir type) + β_5(length) + β_6(stream × year) + β_7(year × length) + ε	1134.95	12	1159.21	0	0.78
$\beta_0 + \beta_1$(stream) + β_3(year) + β_4(weir type) + β_5(length) + β_6(stream × year) + β_7(year × length) + β_8(stream × length) + β_9(stream × year × length) + ε	1129.36	16	1161.81	2.6	0.21
Cutthroat trout (n=506)					
$\beta_0 + \beta_1$(year) + ε	637.59	3	643.63	0	0.24
$\beta_0 + \beta_1$(year) + β_2(length) + β_3(year × length) + ε	627.83	8	644.12	0.49	0.18
$\beta_0 + \beta_1$ (group) + β_2(year) + ε	636.78	4	644.85	1.22	0.13
$\beta_0 + \beta_1$(year) + β_2(length) + ε	637.11	4	645.18	1.55	0.11

Table 3.3. Concluded.

$\beta_0 + \beta_1(\text{stream}) + \beta_2(\text{year}) + \varepsilon$	635.52	5	645.64	2.01	0.09
$\beta_0 + \beta_1(\text{group}) + \beta_2(\text{year}) + \beta_3(\text{length}) + \varepsilon$	635.53	5	645.65	2.01	0.09
$\beta_0 + \beta_1(\text{group}) + \beta_2(\text{year}) + \beta_3(\text{length}) + \beta_4(\text{group} \times \text{year}) + \beta_5(\text{group} \times \text{length}) + \varepsilon$	627.69	9	646.05	2.42	0.08
$\beta_0 + \beta_1(\text{stream}) + \beta_2(\text{year}) + \beta_3(\text{length}) + \varepsilon$	635.14	6	647.31	3.67	0.04
$\beta_0 + \beta_1(\text{group}) + \beta_2(\text{year}) + \beta_3(\text{group} \times \text{year}) + \varepsilon$	636.26	6	648.42	4.79	0.02
$\beta_0 + \beta_1(\text{group}) + \beta_2(\text{year}) + \beta_3(\text{length}) + \beta_4(\text{group} \times \text{year}) + \varepsilon$	635.06	7	649.28	5.65	0.01
$\beta_0 + \beta_1(\text{stream}) + \beta_2(\text{year}) + \beta_3(\text{length}) + \beta_4(\text{stream}\times\text{year}) + \beta_5(\text{year} \times \text{length}) + \varepsilon$	625.02	12	649.65	6.02	0.01

Notes: Factors in models include: year (1999 – 2001), stream (Little Muddy, Indiana, and Willow creeks), length (log-transformed fork length), group (cutthroat trout only: treatment group – Little Muddy and Willow creeks where brook trout were removed versus control group where they were not removed – Indiana Creek), weir type (brook trout only: confounded weir - weir potentially confounded by removing brook trout in adjacent stream reaches versus unconfounded weir – weir not influenced by removal experiment). β-terms preceding factors indicate regression coefficients, with β_0 = intercept term, and ε = error term.

† Akaike's Information Criterion corrected for small sample sizes (AIC$_c$) based on the log likelihood ($\mathcal{L}$) and number of parameters (K) was used to select models for inference. The difference in AIC$_c$ between the highest-ranking and subsequent models (ΔAIC$_c$), and AIC$_c$ weights (w_i) provide an index of relative support for each model. Cumulative AIC weights, defined as the sum of the w for models including a given factor, were used to determine factors predicting movement direction.

Table 3.4. Results of analysis of covariance (ANCOVA) comparing body condition of trout caught at weirs with those in the general population.

		Sample size †			Model weights ‡			Difference in body mass (General – weir) §	
Stream	Year	General population	Weir captures	Size range (mm)	Interaction	Group	Intercept	Absolute (g, *SE*)	Relative (%)
				Brook trout					
Little Muddy	2000	155	42	103 – 200	0.31	0.59	0.10	0.8 (0.37)	3.0
	2001	147	32	86 – 210	0.31	0.69	0.00	2.3 (0.45)	8.9
Willow	2000	113	5	78 – 244	0.42	0.42	0.16	11.1 (5.9)	17.4
	2001	137	10	108 – 243	0.13	0.38	0.49	-3.5 (4.3)	-6.9
Indiana	1999	142	2	115 – 330	-	-	-	-	-
	2000	205	5	105 – 300	0.11	0.25	0.64	2.9 (16.0)	2.8
	2001	300	7	110 – 351	0.28	0.29	0.43	-1.6 (2.3)	-2.6

Table 3.4. Continued.

				Cutthroat trout					
Little Muddy	1999	145	6	81 – 220	0.09	0.25	0.66	0.2 (0.66)	0.9
	2000	134	30	82 – 211	0.42	0.57	0.01	0.9 (0.30)	5.2
	2001	182	16	82 – 200	0.99	0.00	0.01	-	-
Willow	1999	22	1	95 – 286	-	-	-	-	-
	2000	24	5	119 – 308	0.41	0.17	0.42	3.7 (7.3)	2.4
	2001	19	10	125 – 301	0.27	0.73	0.00	28.0 (6.5)	20.6
Indiana	1999	120	9	78 – 273	0.08	0.24	0.68	0.1 (1.2)	0.11
	2000	133	18	87 – 280	0.18	0.42	0.42	1.1 (1.1)	1.9
	2001	212	14	89 – 289	0.40	0.25	0.35	2.7 (1.9)	5.0

† The general population was defined as trout captured during electrofishing in the study segment or at downstream marking sites that received individual tags and were generally age-1 and older. Weir recaptures were trout from the general population that were subsequently recaptured at weirs.

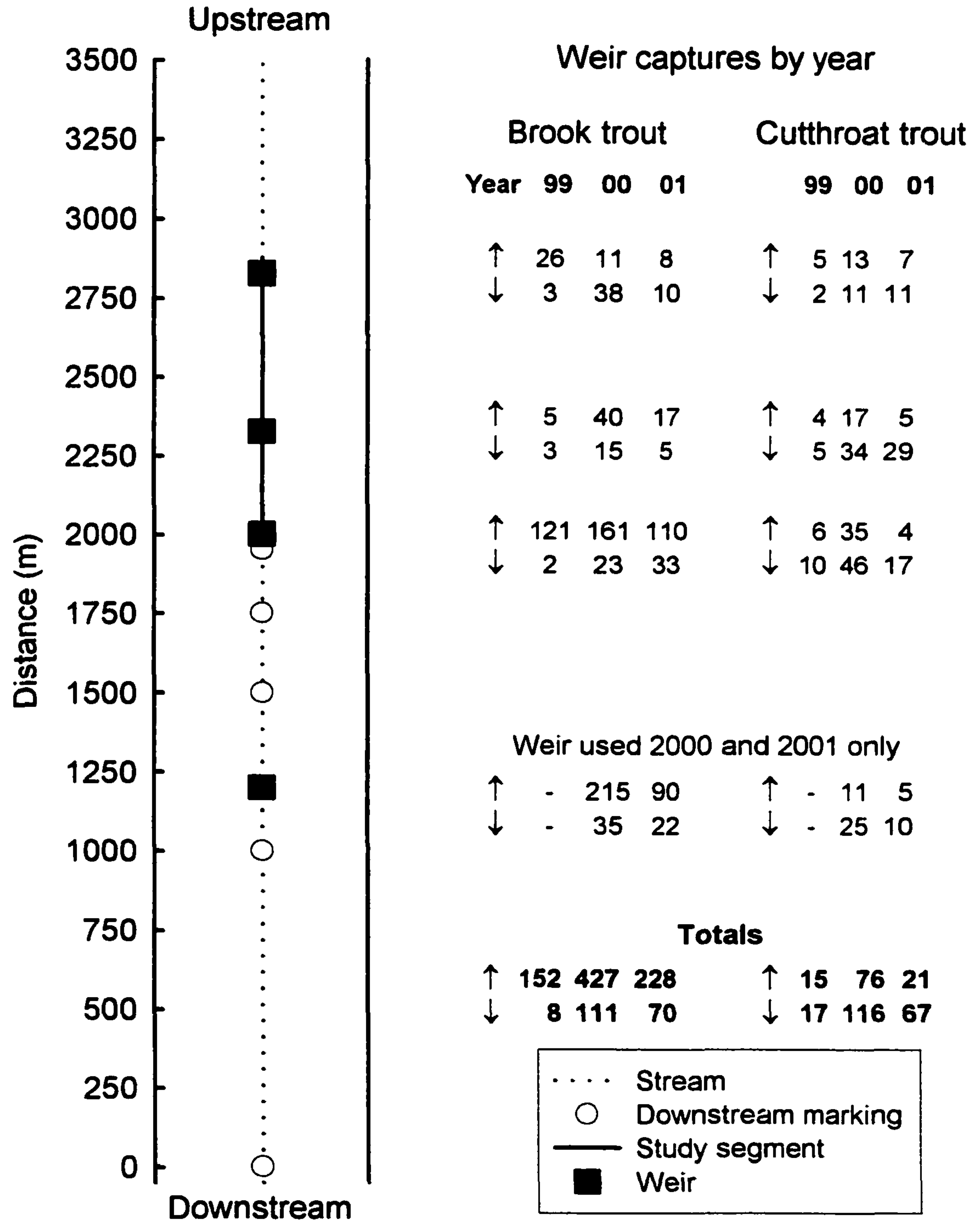
Table 3.4. Concluded.

‡ Model weights were the AIC weights of the three models under analysis of covariance. The interaction model [body weight = $\beta_0 + \beta_1(\text{group}) + \beta_2(\text{length}) + \beta_3(\text{group} \times \text{length}) + \varepsilon$] tests whether the two groups are growing at similar rates. The group model [body weight = $\beta_0 + \beta_1(\text{group}) + \beta_2(\text{length}) + \varepsilon$] tests whether the intercepts (or heights of the lines) are similar, that is whether there is a difference in condition between groups. The intercept only model [body weight = $\beta_0 + \beta_1(\text{length}) + \varepsilon$] tests whether length is related to weight (i.e., no group effect).

§ Differences were calculated as the difference in the model-averaged estimates of weight at the mean fork length for a given group, stream, and year.

Figure 3.1. Sampling locations and weir captures for Little Muddy Creek from 1999 to 2001. Numbers of trout captured moving upstream (↑) or downstream (↓) are listed to the right of the weir where they were captured. The two-way weirs were operated only during summer to early fall. The study segment was the location of an intensive mark-recapture study to estimate trout survival (see Chapter 2), and downstream marking locations were sites where brook trout were marked and released to estimate distance and rate of movement.

Little Muddy Creek



Weir captures by year

	Brook trout			Cutthroat trout		
Year	**99**	**00**	**01**	**99**	**00**	**01**
↑	26	11	8	5	13	7
↓	3	38	10	2	11	11
↑	5	40	17	4	17	5
↓	3	15	5	5	34	29
↑	121	161	110	6	35	4
↓	2	23	33	10	46	17
Weir used 2000 and 2001 only						
↑	-	215	90	-	11	5
↓	-	35	22	-	25	10
Totals						
↑	**152**	**427**	**228**	**15**	**76**	**21**
↓	**8**	**111**	**70**	**17**	**116**	**67**

Figure 3.2. Sampling locations and weir captures for Willow Creek from 1999 to 2001. Numbers of trout captured moving upstream (↑) or downstream (↓) are listed to the right of the weir where they were captured. Sampling locations are as described in Figure 3.1.

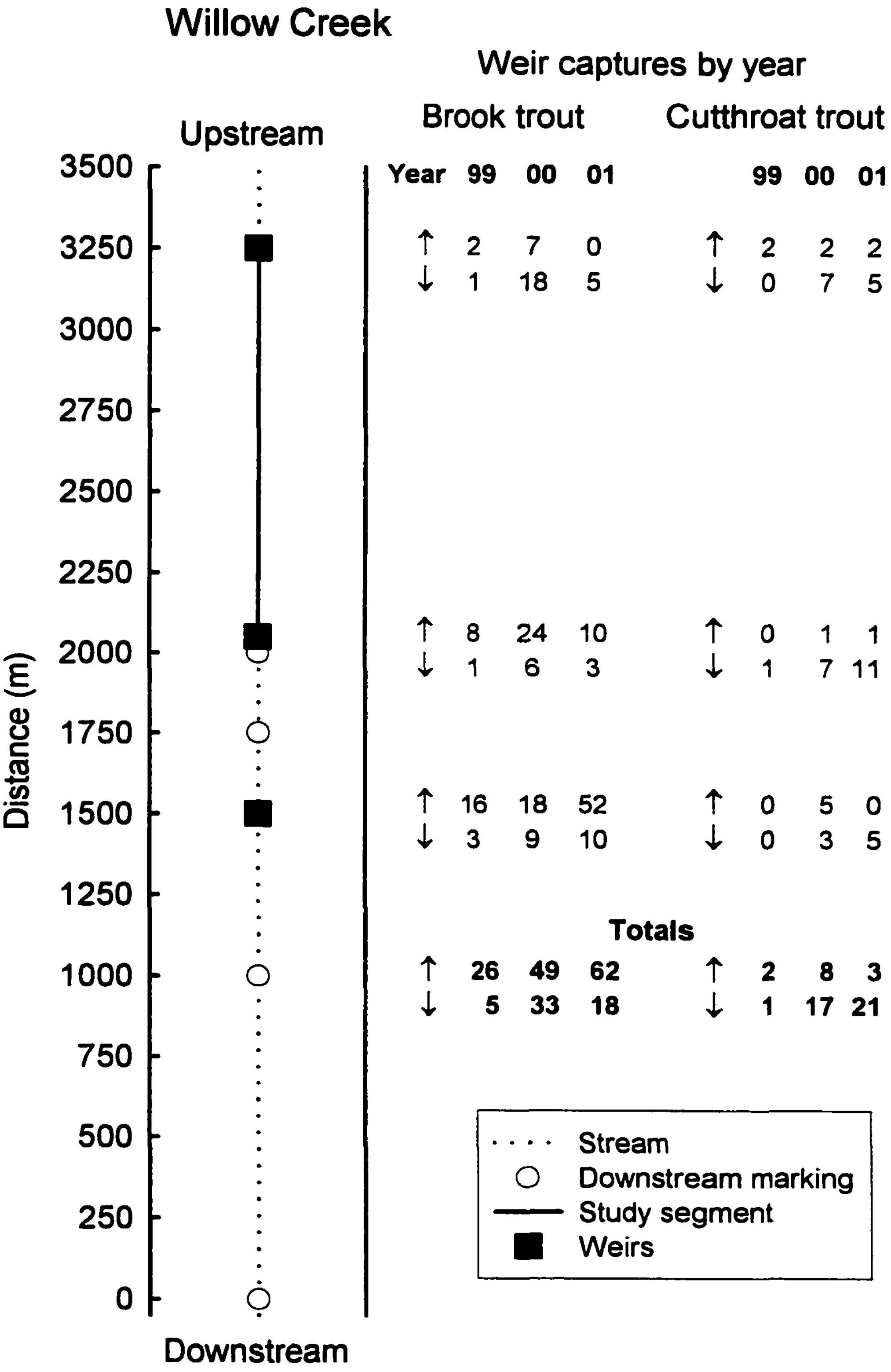
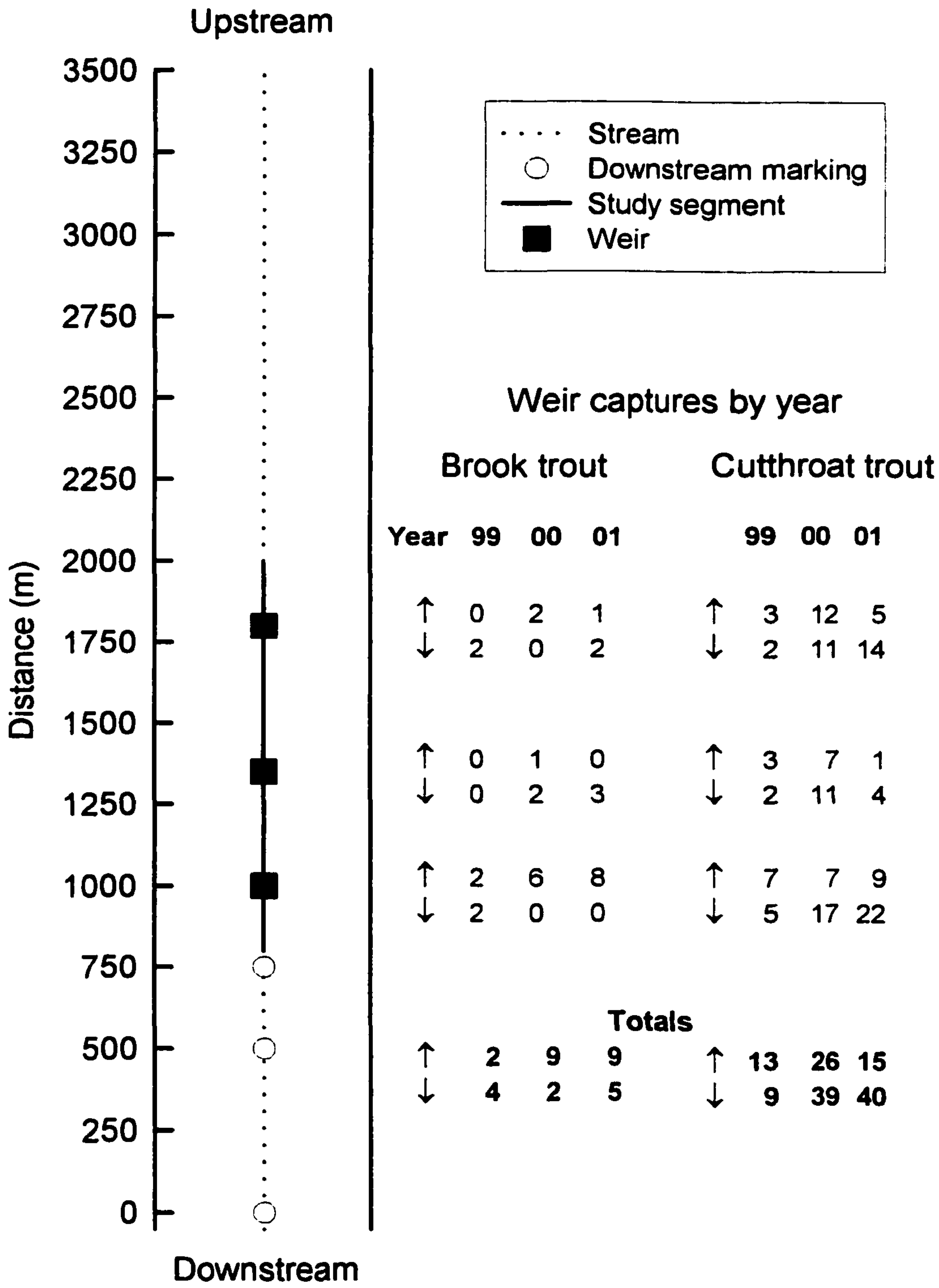

Willow Creek
Weir captures by year
Upstream
Brook trout
Cutthroat trout
Year 99 00 01
99 00 01
3500
3250
3000
2750
2500
2250
2000
1750
1500
1250
1000
750
500
250
0
Distance (m)
↑ 2 7 0
↓ 1 18 5
↑ 2 2 2
↓ 0 7 5
↑ 8 24 10
↓ 1 6 3
↑ 0 1 1
↓ 1 7 11
↑ 16 18 52
↓ 3 9 10
↑ 0 5 0
↓ 0 3 5
Totals
↑ 26 49 62
↓ 5 33 18
↑ 2 8 3
↓ 1 17 21
Stream
Downstream marking
Study segment
Weirs
Downstream

Figure 3.3. Sampling locations and weir captures for Indiana Creek from 1999 to 2001. Numbers of trout captured moving upstream (↑) or downstream (↓) are listed to the right of the weir where they were captured. Sampling locations as are described in Figure 3.1.

Indiana Creek



Weir captures by year

	Brook trout				Cutthroat trout		
Year	**99**	**00**	**01**		**99**	**00**	**01**
↑	0	2	1	↑	3	12	5
↓	2	0	2	↓	2	11	14
↑	0	1	0	↑	3	7	1
↓	0	2	3	↓	2	11	4
↑	2	6	8	↑	7	7	9
↓	2	0	0	↓	5	17	22
			Totals				
↑	**2**	**9**	**9**	↑	**13**	**26**	**15**
↓	**4**	**2**	**5**	↓	**9**	**39**	**40**

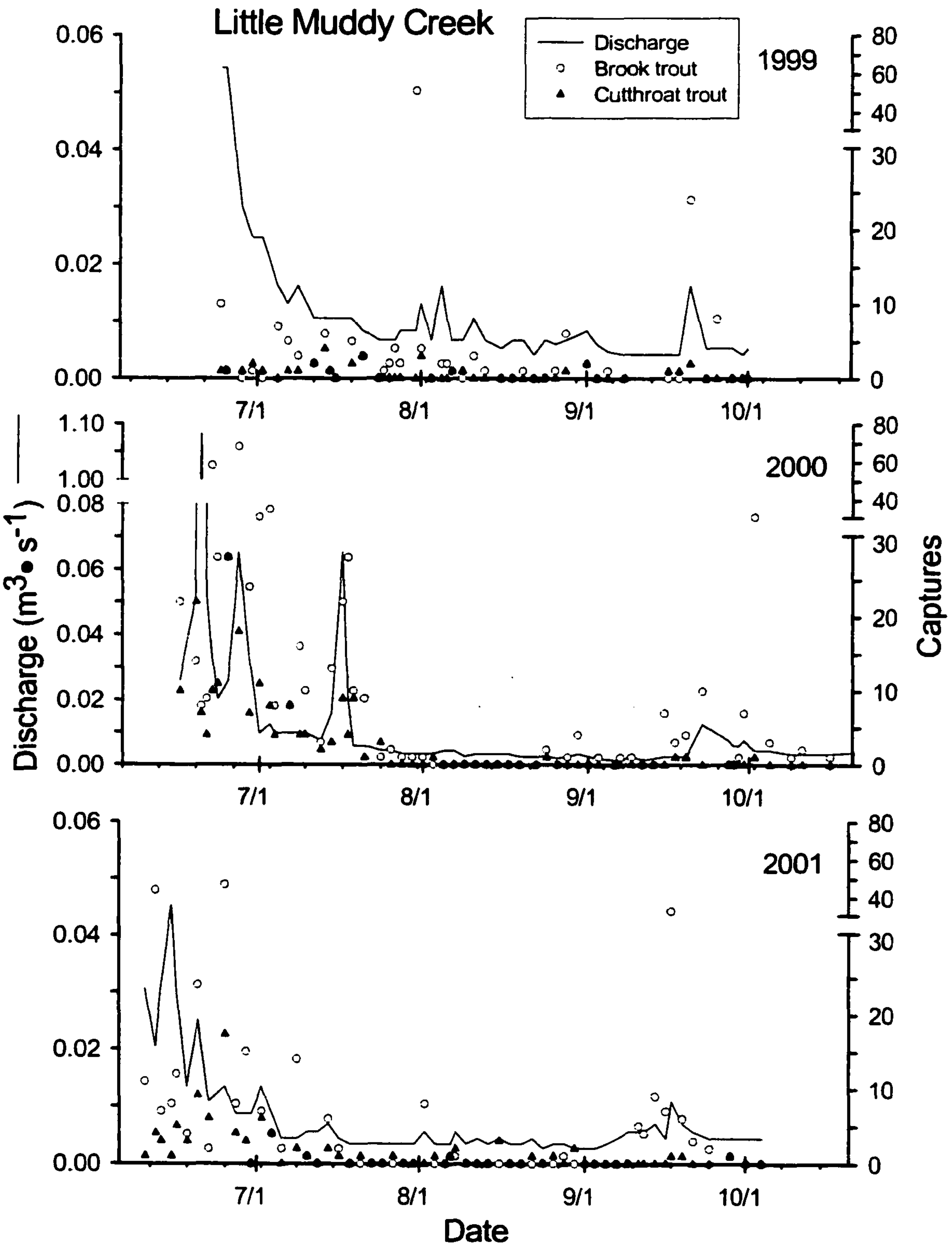


Figure 3.4. Number of brook trout and cutthroat trout captured at all weirs, and stream discharge in Little Muddy Creek during summer to late fall in 1999 to 2001.

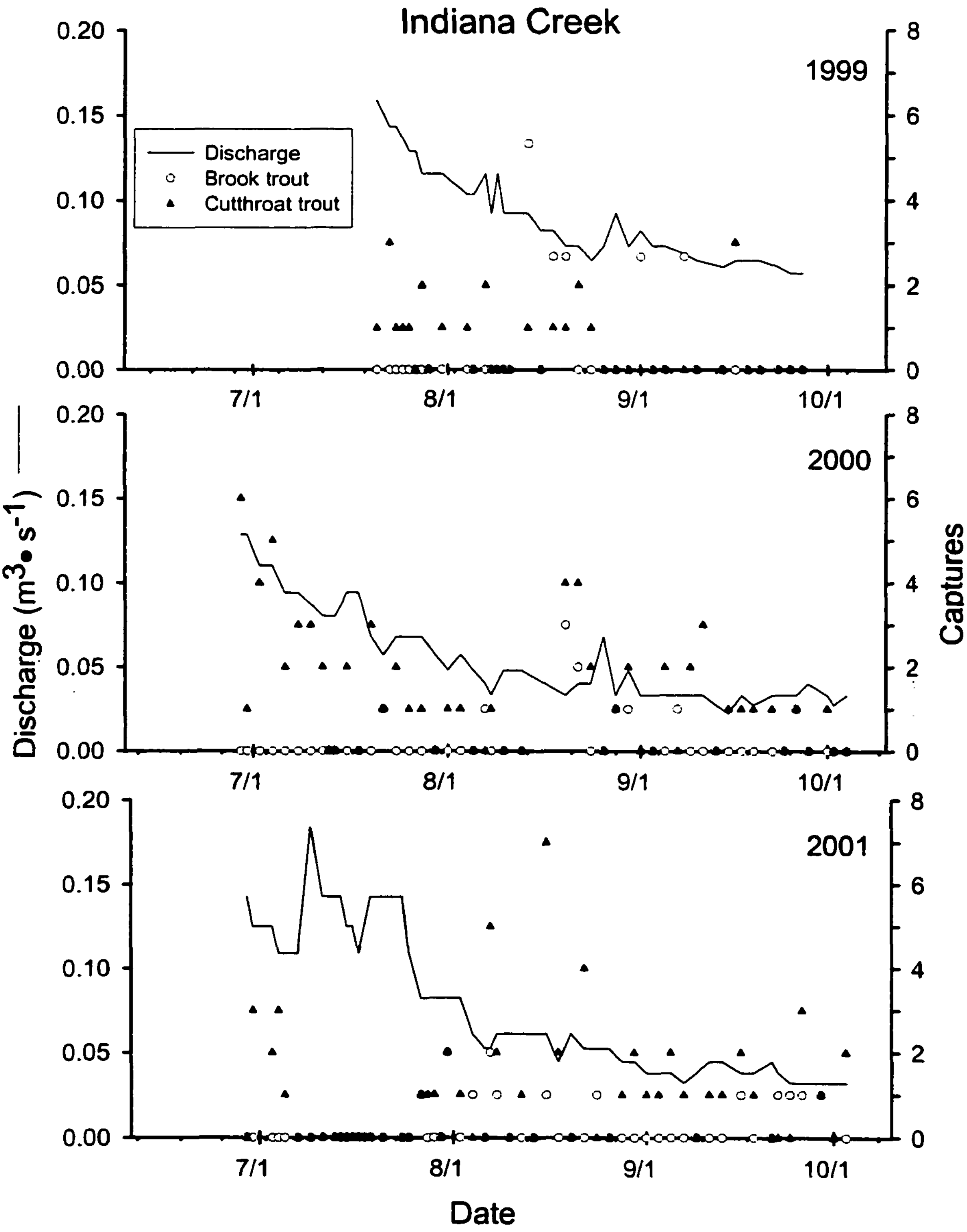


Figure 3.5. Number of brook trout and cutthroat trout captured at all weirs, and stream discharge in Indiana Creek during summer to late fall in 1999 to 2001.

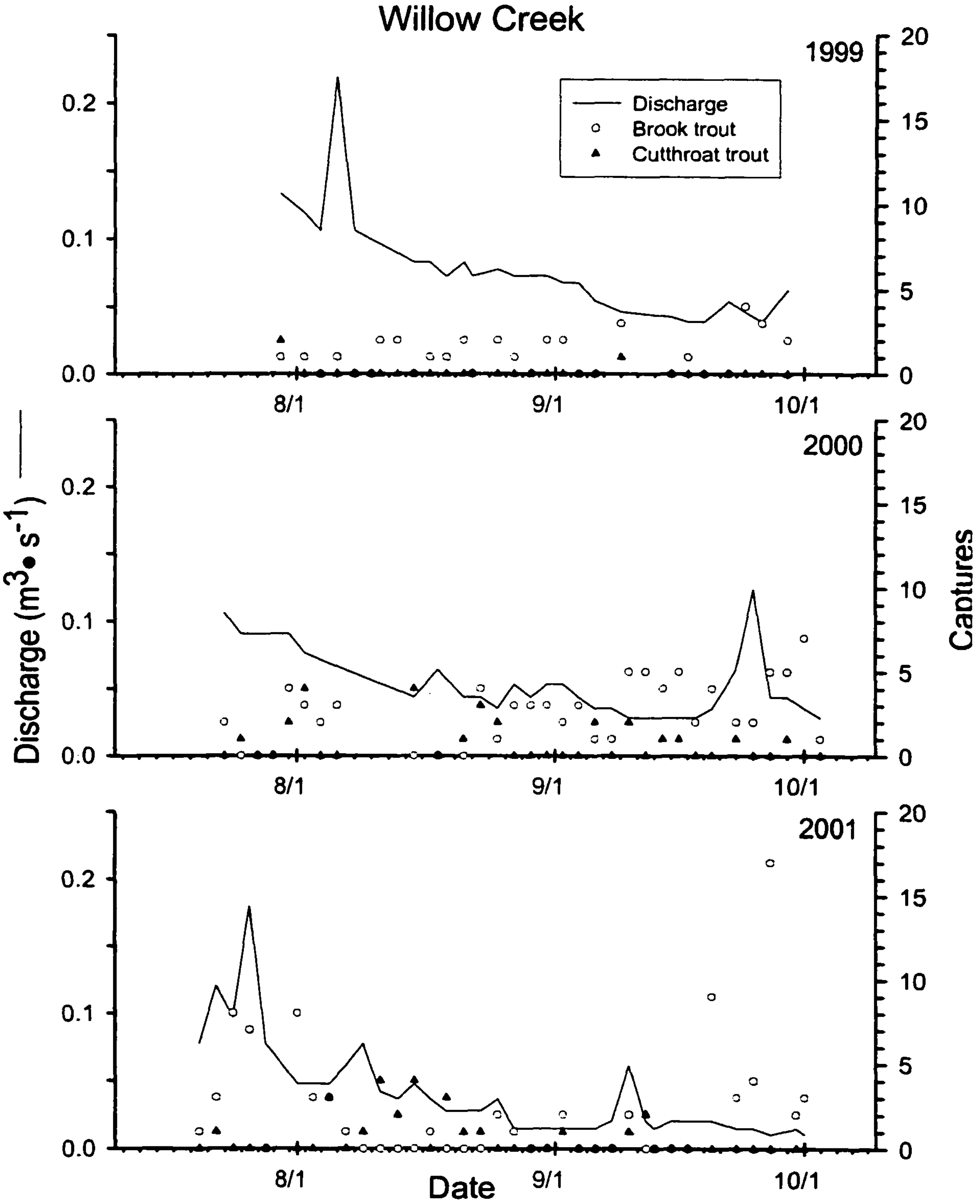
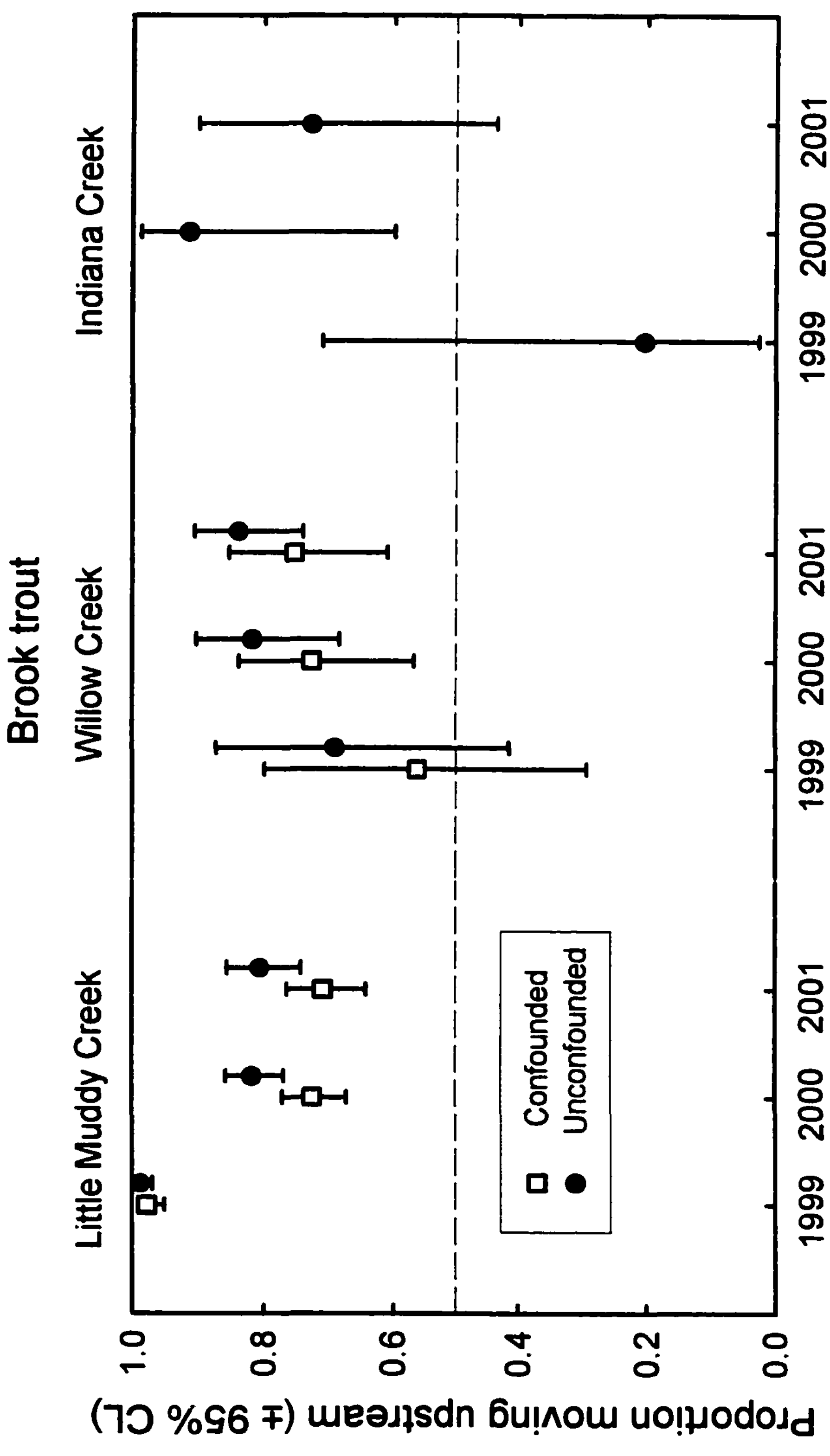


Figure 3.6. Number of brook trout and cutthroat trout captured at all weirs, and stream discharge in Willow Creek during summer to late fall in 1999 to 2001.

Figure 3.7. Proportion of brook trout moving upstream through weirs in Little Muddy, Willow, and Indiana creeks during summer to late fall in 1999 to 2001 as estimated by logistic regression. Confounded estimates are based on brook trout captured at weirs adjacent to study segments in Little Muddy and Willow creeks where brook trout were being removed by electrofishing (Figures 3.1 and 3.3), and brook trout attempting to enter the study areas were being euthanized (see Chapter 2). Thus, tests of movement direction through these weirs was potentially confounded by the population manipulation. In contrast, unconfounded estimates are based on brook trout captured at weirs downstream from the study segments in Little Muddy and Willow creeks and at all locations in Indiana Creek (Figure 3.2). Confidence intervals that do not intersect the horizontal dashed line (proportion = 0.5) indicate that brook trout had a tendency to move upstream.


Brook trout
Little Muddy Creek
Willow Creek
Indiana Creek
Proportion moving upstream (± 95% CL)
1.0
0.8
0.6
0.4
0.2
0.0
1999
2000
2001
Year
□ Confounded
● Unconfounded

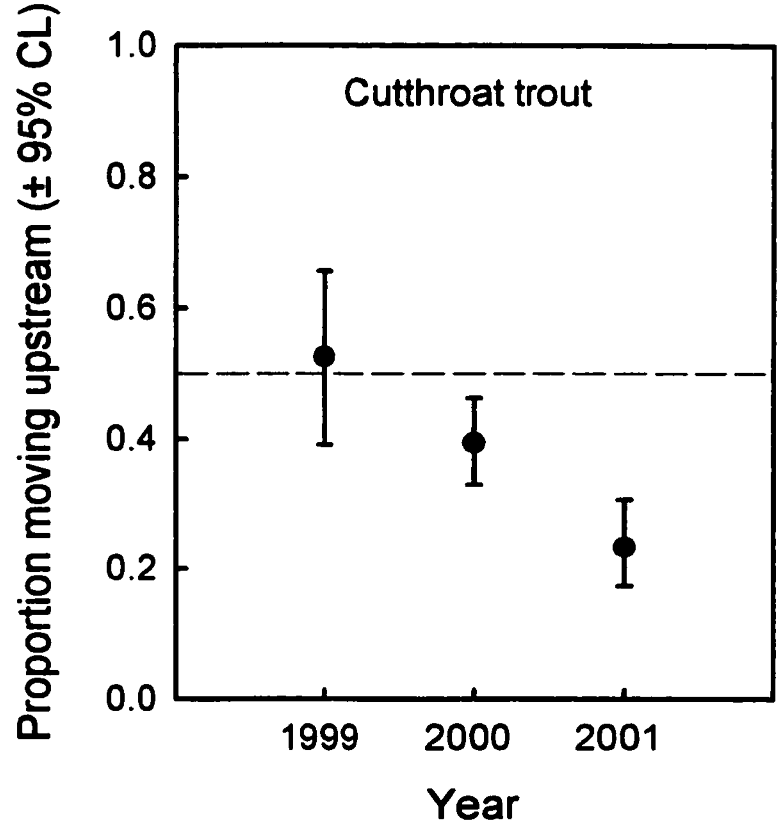
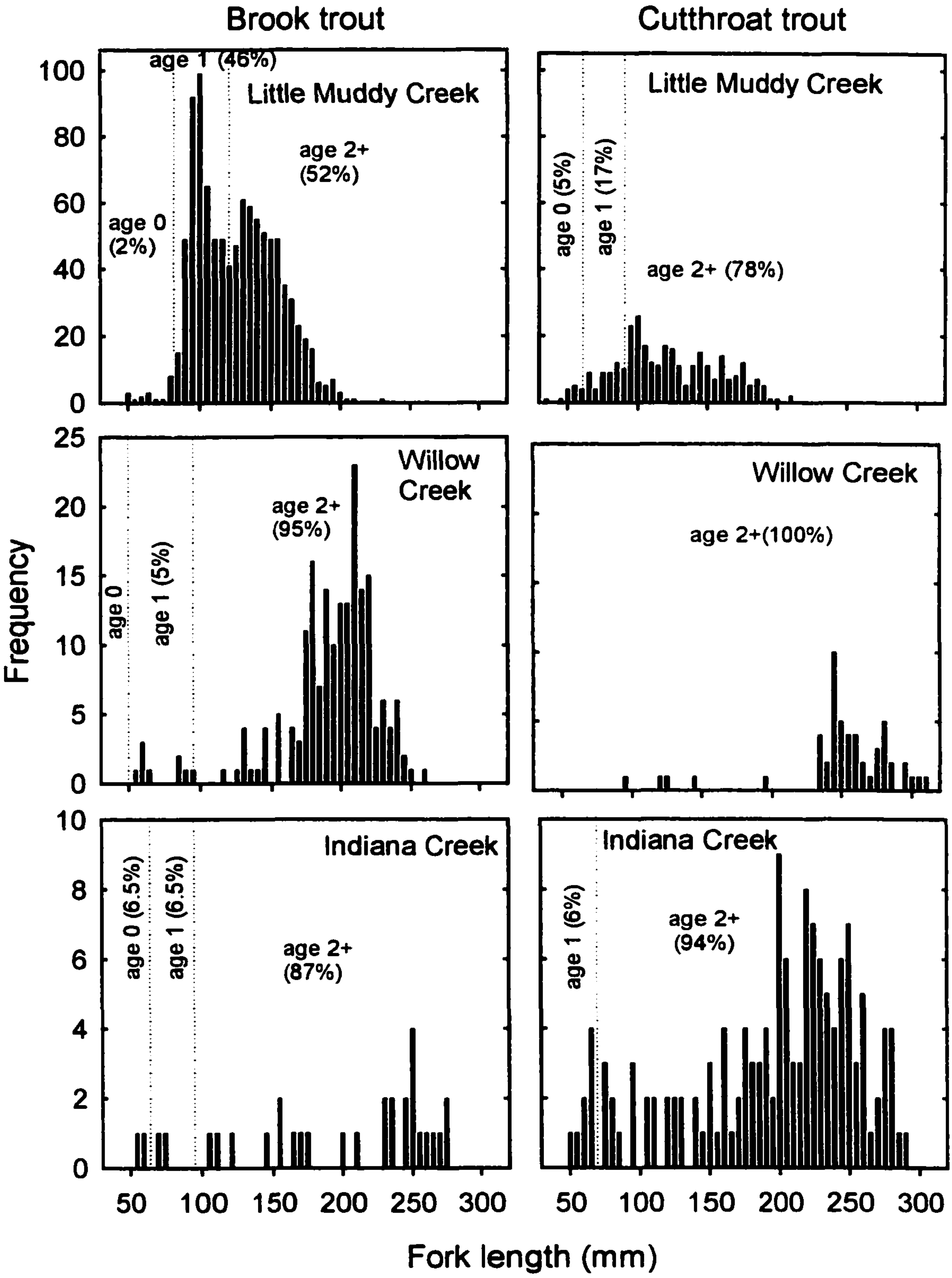


Figure 3.8. Proportion of cutthroat trout moving upstream through weirs in Little Muddy, Willow, and Indiana creeks during summer to late fall in 1999 to 2001 as estimated by logistic regression. Confidence intervals that do not intersect the horizontal dashed line (proportion = 0.5) indicate that brook trout had a tendency to move downstream.

Figure 3.9. Length frequency histogram of trout captured at weirs from 1999 to 2001 in Little Muddy, Willow, and Indiana creeks. Bars are in 5 mm increments and represent the sum of captures over three years. Vertical dashed lines separate age classes, and numbers in parentheses are percentage captured by age class. Only age-2 and older (age 2+) cutthroat trout and age-1 and older brook trout were captured at weirs in Willow Creek, and only age-1 and cutthroat trout were captured in Indiana Creek.


Brook trout
Cutthroat trout
Little Muddy Creek
age 1 (46%)
age 0 (2%)
age 2+ (52%)
age 0 (5%)
age 1 (17%)
age 2+ (78%)
Willow Creek
age 0
age 1 (5%)
age 2+ (95%)
age 2+(100%)
Indiana Creek
age 0 (6.5%)
age 1 (6.5%)
age 2+ (87%)
age 1 (6%)
age 2+ (94%)
Frequency
0
20
40
60
80
100
0
5
10
15
20
25
0
2
4
6
8
10
50
100
150
200
250
300
Fork length (mm)

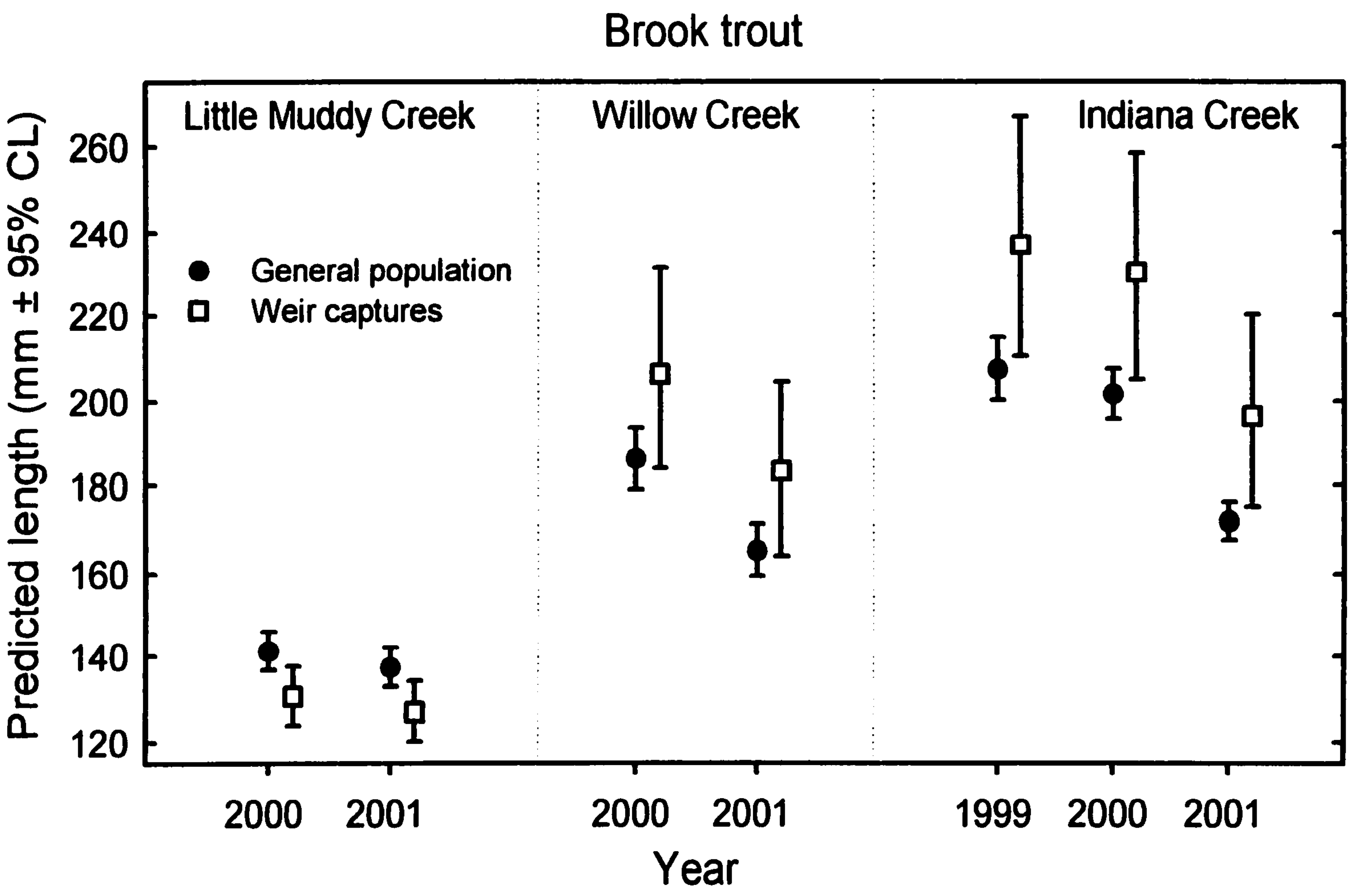


Figure 3.10. Predicted sizes of brook trout captured at weirs and in the general population in Little Muddy, Willow, and Indiana creeks from 1999 to 2001. Data are for individually-tagged brook trout (generally >100 mm fork length) originally marked inside the study area or during downstream marking and either subsequently recaptured at a weir or not.

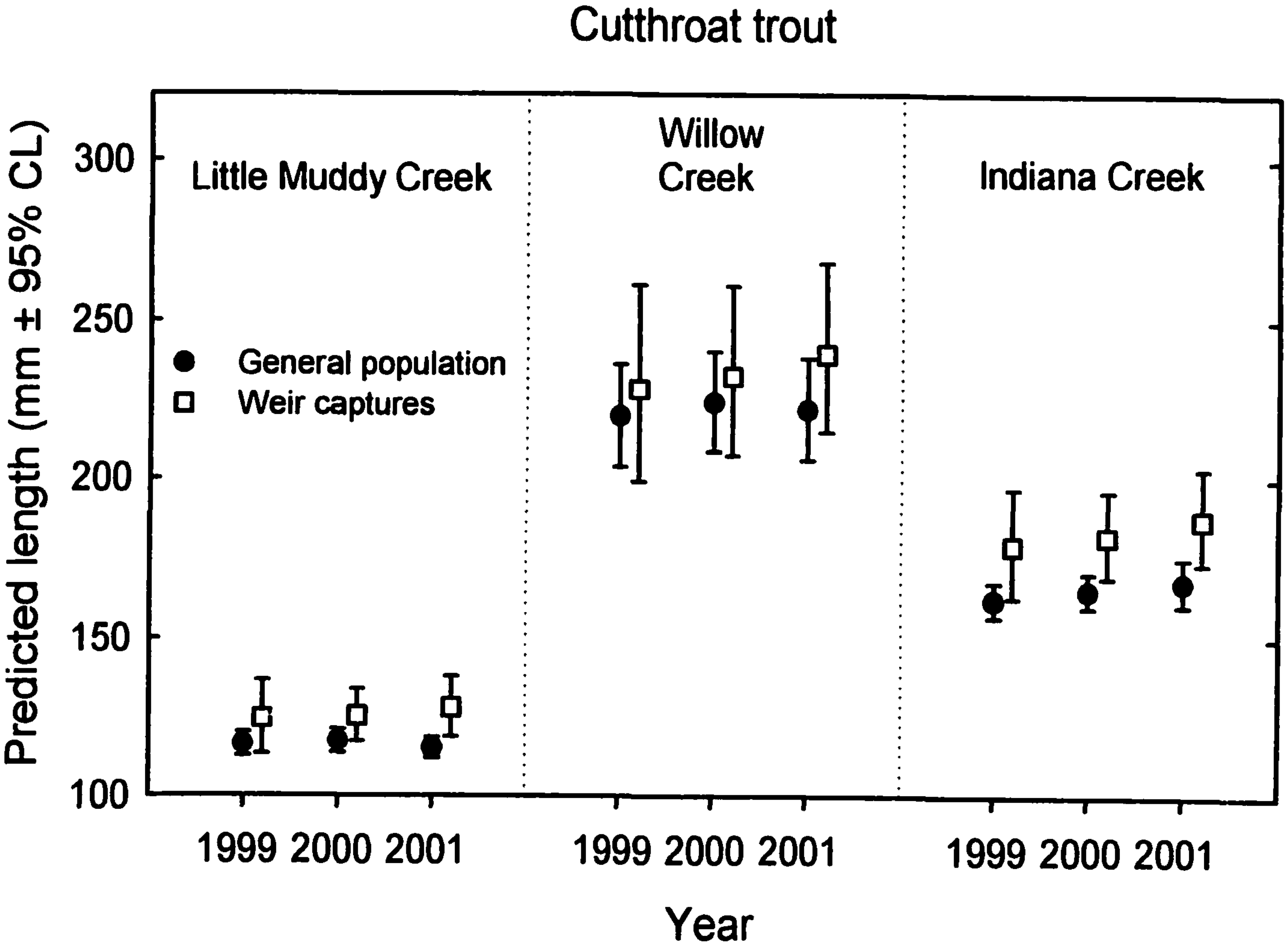


Figure 3.11. Predicted sizes of cutthroat trout captured at weirs and in the general population in Little Muddy, Willow, and Indiana Creeks from 1999 to 2001. Data are for individually-tagged brook trout (generally >85 mm fork length) originally marked inside the study area or during downstream marking and subsequently either recaptured at a weir or not.

Figure 3.12. Number of brook trout immigrants during summer compared to the estimated brook trout abundance in the study segments in Little Muddy, Indiana, and Willow creeks. Abundance is only compared for the age class or classes in each stream that make up nearly all the immigrants. Numbers above bars for weir captures are the percentage of the estimated abundance in the study segment. Data are from weirs located only on the upstream and downstream margins of the study segment, and abundance estimates are from Chapter 2.

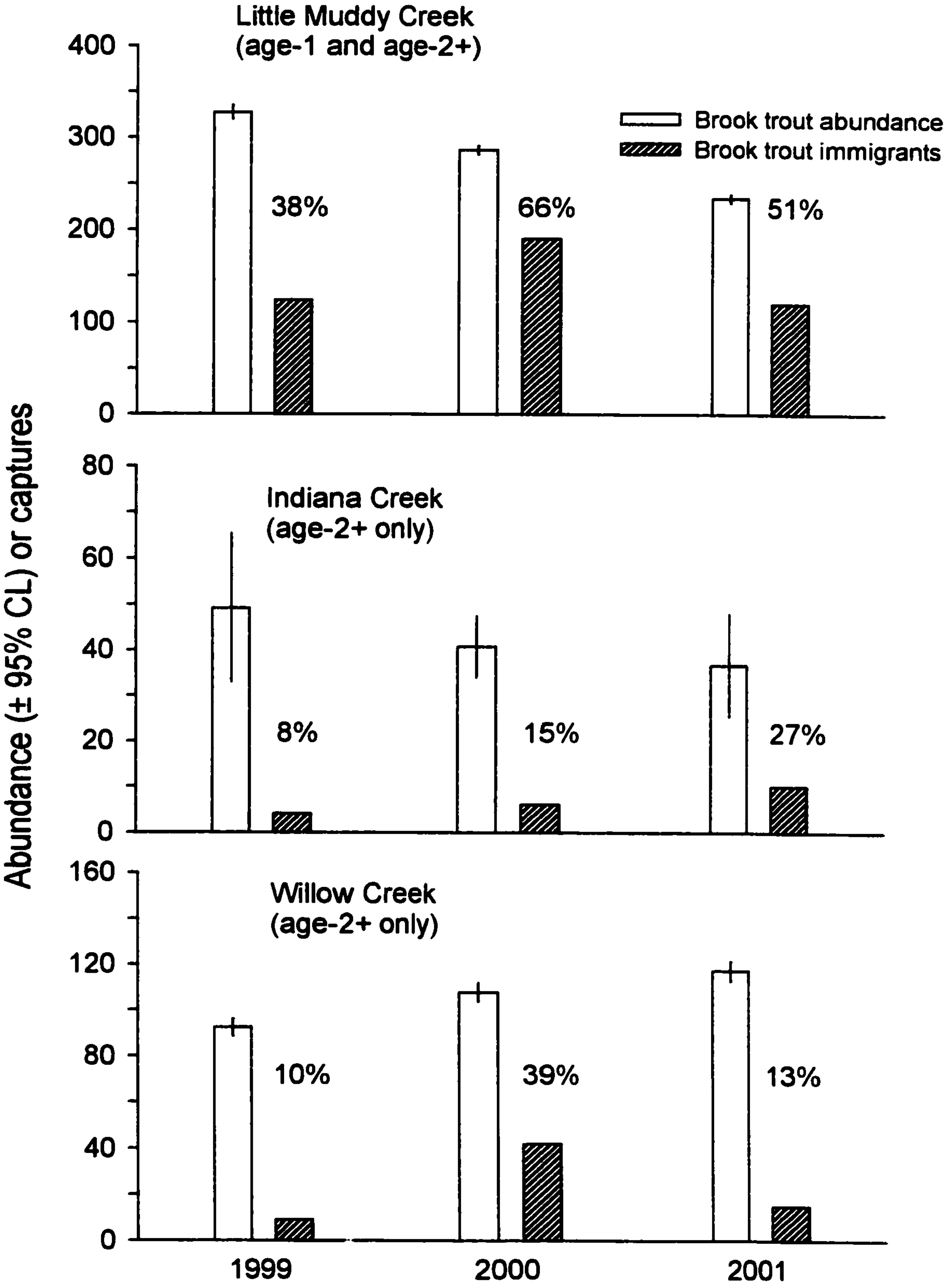

Little Muddy Creek
(age-1 and age-2+)
Brook trout abundance
Brook trout immigrants
38%
66%
51%
400
300
200
100
0
Abundance (± 95% CL) or captures
80
60
40
20
0
Indiana Creek
(age-2+ only)
8%
15%
27%
160
120
80
40
0
Willow Creek
(age-2+ only)
10%
39%
13%
1999
2000
2001

Figure 3.13. Proportion of brook trout recaptured inside or entering the study segments of Little Muddy, Indiana, and Willow creeks that were originally marked downstream. Trout were marked during summer 1999 to 2001, and recaptured during any year at weirs, during downstream marking, or during annual electrofishing surveys of the study segments. Numbers of live releases for each year and location are given above each bar. No downstream marking was done in Willow Creek during 1999. The dashed line in the panel for Little Muddy Creek shows predicted values of the proportion recaptured as a function of distance (m) downstream, estimated from a logistic regression averaged over year of release: $p(recapture) = \frac{\exp(-1.3476 - 0.00143 * \text{Distance})}{1 + \exp(-1.3476 - 0.00143 * \text{Distance})}$. The 500 m location in 1999 was excluded from the logistic regression analysis because of batch mark failure.

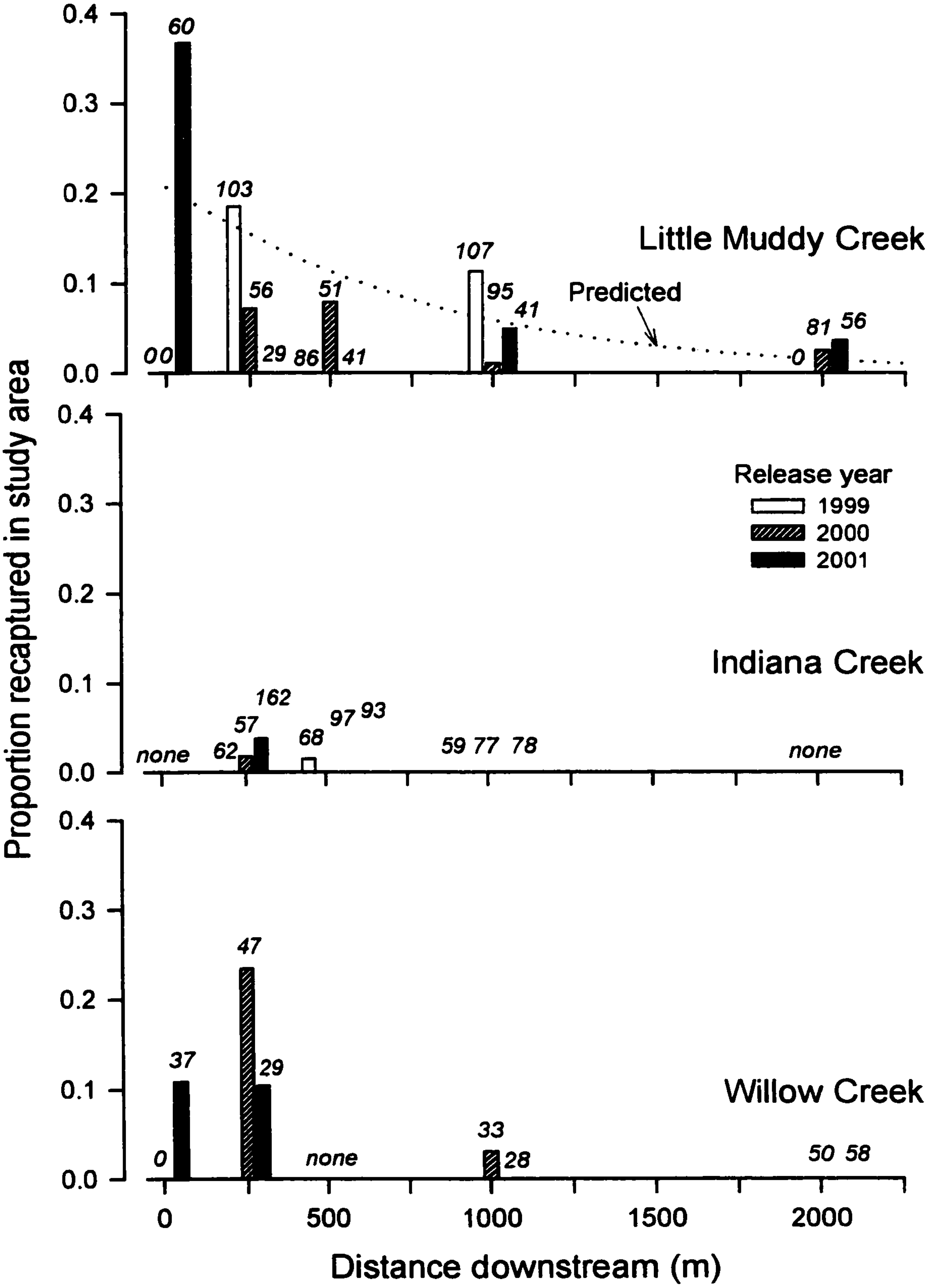

Proportion recaptured in study area
0.4
0.3
0.2
0.1
0.0
Little Muddy Creek
60
103
107
56
51
95
41
0 0
29
86
41
Predicted
81
56
0
Release year
1999
2000
2001
Indiana Creek
162
57
62
68
97
93
59 77 78
none
none
Willow Creek
47
37
29
0
none
33
28
50 58
0
500
1000
1500
2000
Distance downstream (m)

Figure 3.14. Frequency of total distances moved by brook trout marked downstream in Little Muddy, Indiana, and Willow creeks during 1999 to 2001. Total distance was the sum of absolute distances between all pairs of capture locations, which included recaptures at weirs, during downstream marking, or during annual electrofishing surveys in study segments. Distance bins are 50-m increments, so the first (left-most) bar includes fish that moved an estimated 0 to 49.9 m.

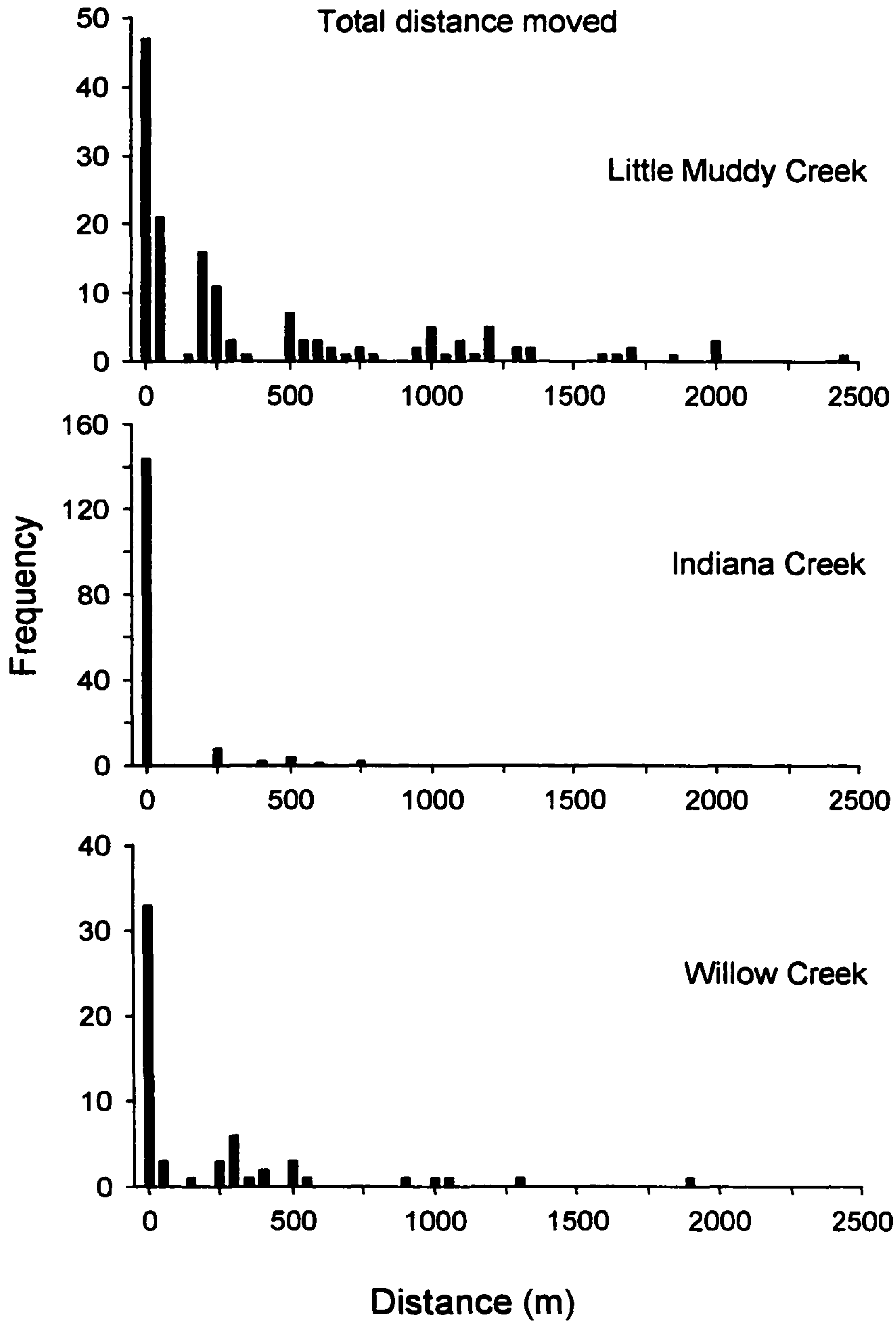
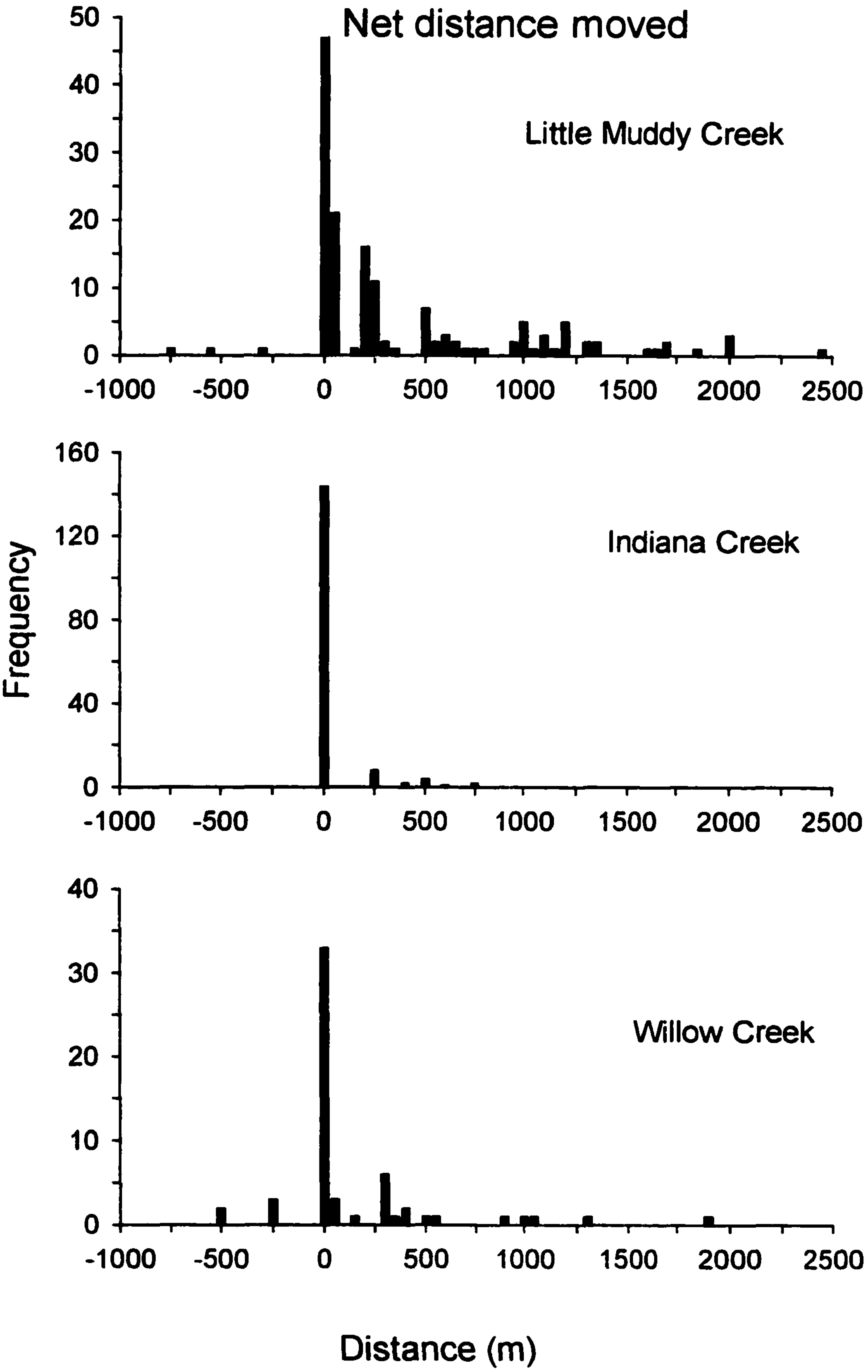

Total distance moved
Little Muddy Creek
Indiana Creek
Willow Creek
Frequency
Distance (m)
50
40
30
20
10
0
160
120
80
40
0
40
30
20
10
0
0
500
1000
1500
2000
2500

Figure 3.15. Frequency of net distances moved by brook trout marked downstream in Little Muddy, Indiana, and Willow creeks during 1999 to 2001. Net distance was between initial and final recapture locations, so negative values indicate trout that moved downstream. Recapture methods and bin distance ranges are as in Figure 3.13.


Net distance moved
Little Muddy Creek
Indiana Creek
Willow Creek
Frequency
Distance (m)
50
40
30
20
10
0
160
120
80
40
-1000
-500
0
500
1000
1500
2000
2500

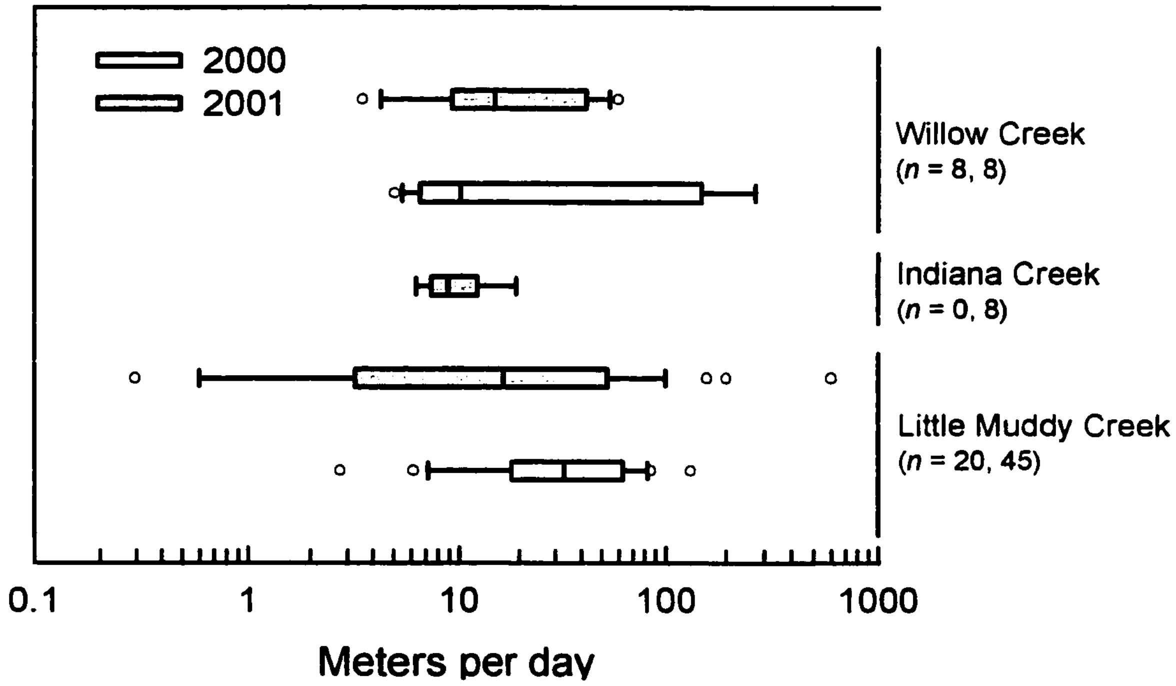


Figure 3.16. Rate of upstream movement by brook trout recaptured within a year during 2000 to 2001 in Little Muddy, Indiana, and Willow creeks. Box plots show the 5th, 25th, 50th (median), 75th, and 95th percentiles of the movement distribution, and outliers are open circles. Sample sizes for 2000 and 2001 are given next to each plot.

APPENDIX A: MODEL SELECTION RESULTS FOR CAPTURE PROBABILITIES OF CUTTHROAT TROUT

Appendix A. Model selection for cutthroat trout capture probabilities ($\hat{p}^*$) in four streams under the robust design with Huggins' population estimator. Selection proceeded with apparent survival ($\hat{\phi}$) held at full effects (stream × age × time), and movement parameters (γ' and γ'') and recapture parameter (c) were fixed to zero. The most-supported model structure for $\hat{p}^*$ was subsequently used to model apparent survival. Hypothesized models are organized by factors containing: A – main effects of time (t), age class (age), and stream; B – body size effects (including main effects); C – environmental covariates (including main and body size effects). The most supported model (i.e., $p_{\text{age*t, t*stream, age*stream}}$) had 1.4 times more support than the second best model, and was used to model apparent survival.

Hypothesized model structure	AIC$_c$	ΔAIC$_c$	w_i	K	Deviance	Description of capture probabilities
$p_{\text{age*t, t*stream, age*stream}}$	5282.78	0.00	0.532	55	18827.62	Full two-way model
$p_{\text{stream+age*t}}$	5283.44	0.66	0.383	42	18855.30	Age effect varies by time with constant stream effect
$p_{\text{t*age, age*WIDTH}}$	5288.06	5.28	0.038	45	18853.71	Age effect varies by time and stream width
$p_{\text{age*t*stream (global)}}$	5288.94	6.16	0.024	62	18819.11	Full three-way model
$p_{\text{age*t, age*stream}}$	5289.06	6.28	0.023	47	18850.56	Age effect varies by both time and stream
p_{age}	5350.24	67.46	0.0	29	18948.84	Age effect
p_{t}	5346.37	63.59	0.0	30	18942.92	Time effect
$p_{\text{age+time}}$	5343.07	60.29	0.0	33	18933.47	Constant (additive) effect of time on age

Appendix A. Continued.

$p_{\text{age*t}}$	5305.76	22.98	0.0	38	18885.88	Age effect varies by time
$p_{\text{age+stream}}$	5330.13	47.35	0.0	33	18920.53	Age effect has constant stream effect
$p_{\text{age*stream}}$	5331.05	48.28	0.0	35	18917.35	Age effect varies by stream
$p_{\text{stream+age+t}}$	5323.71	40.93	0.0	37	18905.88	Stream, age, and time effects additive (constant)
$p_{\text{stream*t+age}}$	5308.45	25.67	0.0	45	18874.10	Stream varies over time with constant age effect
$p_{\text{stream*age+t}}$	5330.40	47.62	0.0	42	18902.26	Stream effect varies by age, constant time effect
$p_{\text{t*stream, age*stream}}$	5315.59	32.81	0.0	51	18868.78	Effect of stream varies by both time and stream
$p_{\le >\text{100mm}}$	5345.66	62.88	0.0	28	18946.30	Body size effect: ≤ or >100 mm fork length
$p_{\le >\text{100mm+stream}}$	5329.99	47.21	0.0	32	18922.44	Body size effect (≤ or >100 mm) has constant stream effect
$p_{\le >\text{71 mm}}$	5333.61	50.84	0.0	28	18934.26	Body size effect: ≤ or > 71 mm fork length
$p_{\le >\text{71 mm +t}}$	5329.23	46.45	0.0	32	18921.68	Body size effect (≤ or > 71 mm) has constant time effect
$p_{\le >\text{71 mm *t}}$	5310.55	27.77	0.0	34	18898.90	Body size effect (≤ or > 71 mm) varies by time
$p_{\text{CONDUCTIVITY}}$	5338.36	55.59	0.0	27	18941.06	Stream conductivity

Appendix A. Concluded.

$p_{\mathrm{age+CONDUCTIVITY}}$	5337.10	54.32	0.0	30	18933.65	Stream conductivity has constant age effect
$p_{\mathrm{age*CONDUCTIVITY}}$	5333.96	51.18	0.0	32	18926.42	Stream conductivity effect varies by age
p_{WIDTH}	5329.26	46.48	0.0	27	18931.95	Stream width effect
$p_{\mathrm{age+WIDTH}}$	5324.85	42.07	0.0	30	18921.40	Stream width has constant age effect
$p_{\mathrm{age*WIDTH}}$	5327.70	44.92	0.0	32	18920.16	Stream width effect varies by age
$p_{\leq >100\mathrm{mm} + \mathrm{WIDTH}}$	5325.13	42.35	0.0	29	18923.73	Fish body size effect (≤ or >100 mm) has constant stream width effect
$p_{\leq \mathrm{or} >100\ \mathrm{mm} * \mathrm{WIDTH}}$	5328.82	46.04	0.0	31	18923.33	Stream width effect varies by fish body size (≤ or >100 mm)
$p_{\mathrm{t+age+WIDTH}}$	5309.99	27.21	0.0	30	18906.54	Additive (constant) effects of time, age, and width

Notes: Akaike's Information Criterion corrected for small sample sizes ($\mathrm{AIC_c}$) based on the log likelihood and number of parameters (K) was used to select models for inference. The difference in $\mathrm{AIC_c}$ between the highest-ranking and subsequent models ($\Delta\mathrm{AIC_c}$), and $\mathrm{AIC_c}$ weights (w_i) provide an index of relative support for each model. Deviance is defined as the difference in –2Log(Likelihood model|data) of the current model and –2Log(Likelihood model|data) of the saturated model. The saturated model is the model with the number of parameters equal to the sample size.

APPENDIX B: MODEL SELECTION RESULTS FOR SURVIVAL PROBABILITIES OF CUTTHROAT TROUT

Appendix B. Model selection for apparent survival ($\hat{\phi}$) of cutthroat trout in four streams under the robust design with Huggins' population estimator. Selection proceeded with capture probabilities ($\hat{p}^*$) held at full two-way effects (i.e., stream × age, age × time, stream × time), and movement parameters (γ' and γ'') and recapture parameter (c) were fixed to zero. To account for model uncertainty, model averaging was used to derive parameter estimates for inference.

Hypothesized model	AIC$_c$	ΔAIC$_c$	w_i	K	Deviance	Description of effects on apparent survival
$\phi_{\text{age*t*stream}}$	5282.78	0.00	0.478	55	18827.62	Full 3-way model: age effect depends on time and stream
$\phi_{\text{age*t, t*stream, age*stream}}$	5283.52	0.74	0.330	53	18832.52	All two-way interactions
$\phi_{\text{t*stream, age*stream}}$	5285.84	3.06	0.103	48	18845.27	Stream effect varies by time; stream effect varies by age
$\phi_{\text{JUVENILES:age*t*stream, ADULTS: stream}}$	5286.97	4.19	0.0599	44	18854.69	Juveniles (ages 0 and 1) vary by time and stream; adults (age-2+) vary by stream
Global model	5288.94	6.16	0.022	62	18819.11	Full 3-way model for ϕ and p
$\phi_{\text{age*t, t*stream}}$	5290.92	8.14	0.008	47	18852.42	Age effect varies by time; stream effect varies by time
$\phi_{\text{JUVENILES:age*t*stream, ADULTS: t}}$	5304.02	21.24	0.00001	43	18873.81	Juveniles vary by time and stream; adults vary by time

Appendix B. Continued.

$\phi_{\text{JUVENILES:age*t*stream, ADULTS: }\bullet}$	5305.89	23.11	0.0	41	18879.81	Juveniles vary by time and stream; adults constant
$\phi_{\text{age*t, age*stream}}$	5306.37	23.59	0.0	47	18867.87	Age effect varies by time; age effect varies by stream
$\phi_{\text{age*ANNDEG}}$	5308.13	25.35	0.0	35	18894.42	Age interacts with annual degree days
$\phi_{\text{ELEV* TRT, TRT *age}}$	5308.52	25.74	0.0	37	18890.69	Elevation effect interactions with treatment; treatment interacts with age
$\phi_{\text{age*SUMDEG}}$	5311.95	29.17	0.0	35	18898.24	Summer degree days varies by age
$\phi_{\text{t+age*stream}}$	5315.11	32.33	0.0	42	18886.98	Age effect varies by stream; constant time effect
$\phi_{\text{age*BKTDENS}}$	5316.61	33.83	0.0	35	18902.90	Brook trout density effect varies by age
$\phi_{\text{age+t*stream}}$	5321.51	38.73	0.0	43	18891.30	Stream effect varies by time; constant age effect
$\phi_{\text{age-0 TRT *t, age-1 TRT *t, age-2+}}$	5323.35	40.57	0.0	37	18905.53	Treatment effects for ages 0 and 1 vary by time; age-2+ constant
$\phi_{\text{age-0 TRT*t, age-1 TRT*T, age-2+ TRT+T}}$	5324.48	41.70	0.0	39	18902.53	Treatment effect for age-0 varies by time, treatment effect for age-1 has linear trend which differs by treatment group, age-2+ treatment effect varies has linear trend
$\phi_{\text{age*t+stream}}$	5324.67	41.89	0.0	41	18898.60	Age effect varies by time; constant stream effect

Appendix B. Continued.

$\phi_{\text{age+BKTDENS}}$	5326.11	43.33	0.0	33	18916.51	Constant age effect on brook trout density
$\phi_{\text{age-0 TRT*t, age-1 TRT*T, age-2+ TRT*T}}$	5326.72	43.94	0.0	39	18904.78	Treatment effect for age-0 varies by time, treatment effect for age-1 has linear trend which differs by treatment group, age-2+ treatment effect has linear trend differing by treatment group
$\phi_{\text{TRT*age}}$	5327.62	44.84	0.0	35	18913.91	Treatment effect varies by age
$\phi_{\text{age-0 TRT *t, age-1 TRT+t, age-2+}}$	5329.89	47.11	0.0	37	18912.07	Treatment effect for age-0 varies by time, treatment effect for age-1 constant (additive) over time, age-2+ constant
$\phi_{\text{age-0 TRT*t, age-1 TRT+T, age-2+}}$	5329.99	47.21	0.0	38	18910.10	Treatment effect for age-0 varies by time, treatment effect for age-1 has linear trend, age-2+ constant
$\phi_{\text{age-0 TRT*t, age-1 TRT *T, age-2+}}$	5331.42	48.64	0.0	39	18909.47	Treatment effect for age-0 varies by time, treatment effect for age-1 has linear trend which differs by treatment group, age-2+ constant
$\phi_{\text{age-0 TRT *T, age-1=age-2+}}$	5331.80	49.02	0.0	34	18920.14	Linear trend on treatment effect for age-0 varies by group
$\phi_{\text{age-0 TRT*t, age-1 TRT*T, age-2+ TRT+t}}$	5332.16	49.38	0.0	39	18910.21	Treatment effect for age-0 varies by time, treatment effect for age-1 has linear trend which differs by treatment group, age-2+ treatment effect constant over time

Appendix B. Continued.

$\phi_{\text{age-0 TRT +t, age-1=age-2+}}$	5332.26	49.48	0.0	34	18920.61	Additive (constant) time effect on age-0 treatment effect
$\phi_{\text{age-0 TRT, age-1=age-2+}}$	5333.94	51.16	0.0	32	18926.40	Treatment effect for age-0
$\phi_{\text{age-0 TRT *t, age-1, age-2+}}$	5334.34	51.68	0.0	37	18916.63	Treatment effect for age-0 varies by time; age-1 and age-2+ survival different and constant
$\phi_{\text{age-0 TRT+T, age-1=age-2+}}$	5335.58	52.80	0.0	33	18925.98	Treatment effect for age-0 has linear trend
$\phi_{\text{age-0 TRT *t, age-1=age-2+}}$	5335.72	53.05	0.0	36	18920.07	Treatment effect for age-0 varies by time
$\phi_{\text{age*JULTEMP}}$	5337.14	54.36	0.0	35	18923.44	July temperature effect varies by age
$\phi_{\text{age-0 TRT *t, age-1 TRT, age-2+}}$	5337.72	54.94	0.0	37	18919.90	Treatment effect for age-0 varies by time; constant treatment effect for age-1, age-2+ constant
$\phi_{\text{ELEV+t*age}}$	5339.22	56.44	0.0	39	18917.27	Age effect varies by time; constant elevation effect
$\phi_{\text{ELEV*age, t*age}}$	5340.97	58.19	0.0	41	18914.89	Elevation effect varies by time; age effect varies by time
$\phi_{\text{age*t}}$	5341.98	59.20	0.0	38	18922.09	Age effect varies by time
$\phi_{\text{age+ANNDEG}}$	5345.79	63.01	0.0	33	18936.19	Age effect additive on annual degree days
ϕ_{ANNDEG}	5350.05	67.27	0.0	31	18944.56	Annual degree days

Appendix B. Continued.

$\phi_{ELEV*TRT}$	5352.47	69.69	0.0	33	18942.88	Treatment effect varies by elevation
$\phi_{size+stream}$	5353.27	70.49	0.0	34	18941.62	Additive (constant) stream effect on size
$\phi_{size*t+stream}$	5353.35	70.57	0.0	38	18933.46	Size effect varies by time and has constant stream effect
$\phi_{size*stream}$	5354.73	71.95	0	35	18941.02	Size effect varies by stream
$\phi_{BKTDENS}$	5355.05	72.27	0.0	31	18949.56	Brook trout density
$\phi_{age+SUMDEG}$	5364.94	82.16	0.0	33	18955.35	Constant age effect on summer degree days
ϕ_{age+t}	5367.81	85.03	0.0	34	18956.16	Constant time effect on age
$\phi_{age\text{-}0\ TRT*t,\ age\text{-}1\ TRT*T,\ age\text{-}2\ TRT*t}$	5368.06	85.28	0.0	39	18946.12	Treatment effect for age-0 varies by time, treatment effect for age-1 has linear trend which differs by treatment group, age-2+ treatment effect varies by time
$\phi_{SUMMDEG}$	5369.17	86.39	0.0	31	18963.67	Summer degree days
$\phi_{ELEV+age}$	5372.18	89.40	0.0	33	18962.58	Constant age effect on elevation
$\phi_{a+JULTEMP}$	5374.26	91.48	0.0	33	18964.66	Constant age effect on mean July temperature
$\phi_{ELEV*age}$	5375.12	92.34	0.0	35	18961.40	Elevation effect varies by age

Appendix B. Continued.

$\phi_{\text{TRT*t}}$	5378.27	95.49	0.0	35	18964.57	Treatment effect varies by time
ϕ_{ELEV}	5379.60	96.82	0.0	31	18974.11	Elevation effect
$\phi_{\text{size+t}}$	5380.26	97.48	0.0	34	18970.66	Constant time effect on size
ϕ_{size}	5380.63	97.85	0.0	31	18975.14	Size effect
$\phi_{\text{ELEV+t}}$	5380.79	98.01	0.0	33	18971.19	Constant time effect on elevation
$\phi_{\text{size+T}}$	5381.44	98.66	0.0	32	18973.89	Linear trend on size
$\phi_{\bullet}$	5382.17	99.39	0.0	30	18978.72	Constant
ϕ_{JULTEMP}	5382.22	99.44	0.0	31	18976.72	Mean July water temperature by year and stream
$\phi_{\text{size*T}}$	5383.21	100.43	0.0	33	18973.61	Linear trend varies by size
$\phi_{\text{size*t}}$	5383.48	100.70	0.0	35	18969.77	Size effect varies by time
$\phi_{\text{ELEV*t}}$	5384.93	102.15	0.0	36	18969.17	Elevation effect varies by time
$\phi_{\text{TRT+age}}$	5389.58	106.80	0.0	33	18979.98	Additive (constant) age effect on treatment
ϕ_{age}	5392.64	109.86	0.0	32	18985.10	Age class effect
$\phi_{\text{age-0, age-1=age-2+}}$	5398.03	115.25	0.0	31	18992.53	Age-0 survival different than age-1 and age-2+

Appendix B. Concluded.

ϕ_{TRT}	5421.52	138.74	0.0	31	19016.03	Treatment effect
ϕ_{TRT+t}	5422.30	139.52	0.0	33	19012.71	Constant time effect on treatment

Notes: abbreviations for variables and covariates used in model structure for ϕ are: size – body size ≤ or > 71 mm fork length based on divisions between age classes across streams, T – linear trend in logit scale, TRT – treatment group (i.e., brook trout removal = treatment, no brook trout removal = control), ELEV – elevation block (2500 – 3000 m, > 3000 m), ADULTS – trout age 2 or older (i.e., age-2+), JUVENILE – trout age 0 or age 1, JULTEMP – mean July water temperature at end of year over which survival is estimated, ANNDEG – annual degree days over the interval where survival is estimated, SUMDEG – degree days during May through August at end of year over which survival is estimated, BKTDENS – brook trout (competitor) density of equivalent age or size class to cutthroat trout.

APPENDIX C: MODEL SELECTION RESULTS FOR CAPTURE PROBABILITIES OF BROOK TROUT IN CONTROL STREAMS

Appendix C. Model selection for capture probabilities ($\hat{p}^{*}$) of brook trout in control streams under the robust design with Huggins population estimator. Selection proceeded with apparent survival held constant ($\hat{\phi}_{\bullet}$), and movement parameters (γ' and γ'') and recapture parameter (c) were fixed to zero. The most-supported model structure for $\hat{p}^{*}$ (i.e., $p_{\text{age*t, age*stream, t*stream}}$) is over 20 times more likely than the next best model, and was subsequently used to model apparent survival.

Hypothesized model structure	AIC$_c$	ΔAIC$_c$	w_i	K	Deviance	Description of capture probabilities
$p_{\text{age*t, age*stream, t*stream}}$	12047.62	0.00	0.953	19	66340.18	Age effect varies by stream, time; time effect varies by stream (2-way model)
$p_{\text{age*t*stream}}$	12053.66	6.04	0.046	22	66340.18	Full 3-way model
$p_{\text{age*t, t*stream}}$	12062.27	14.65	0.00063	17	66358.85	Stream and age both vary by time
$p_{\text{age*t, age*stream}}$	12068.95	21.34	0.00002	15	66369.56	Age varies by both time and stream
$p_{\text{age*t}}$	12072.82	25.20	0.0	13	66377.44	Age effect varies by time
$p_{\text{age*t+stream}}$	12074.58	26.96	0.0	14	66377.19	Age effect varies by time, stream effect constant
$p_{\text{age+t}}$	12421.94	374.32	0.0	7	66738.60	Age effect has constant time effect
$p_{\text{age+t+str}}$	12423.73	376.11	0.0	8	66738.38	Stream, age, and time effects additive (constant)
$p_{\text{stream*t}}$	12460.14	412.53	0.0	9	66772.79	Stream effect varies by time

Appendix C. Concluded.

$p_{\text{stream+t}}$	12479.38	431.76	0.0	6	66798.05	Stream effect constant over time
p_{t}	12479.83	432.21	0.0	5	66800.50	Time effect
$p_{\text{stream*age}}$	12551.99	504.37	0.0	6	66870.65	Age effect varies by stream
$p_{\text{stream+age}}$	12553.37	505.75	0.0	5	66874.03	Age effect constant over stream
p_{age}	12555.06	507.44	0.0	4	66877.73	Age effect
$p_{\text{juv; high TRT} \neq \text{others}}$	12580.89	533.28	0.0	3	66905.57	Juveniles (ages 0 and 1) in high-elevation treatment ≠ others, all constant over time
$p_{\bullet}$	12581.17	533.55	0.0	2	66907.84	Constant
$p_{\text{juv; high TRT} \neq \text{others*t}}$	12581.22	533.60	0.0	6	66899.89	Juveniles (ages 0 and 1) in high-elevation treatment ≠ others, all others vary by time
p_{stream}	12582.66	535.04	0.0	3	66907.33	Stream effect
$p_{\text{juv; high TRT*; others} \bullet}$	12585.62	538.00	0.0	8	66900.27	Juveniles (ages 0 and 1) in high-elevation treatment vary by time, all other groups constant

APPENDIX D: MODEL SELECTION RESULTS FOR SURVIVAL PROBABILITIES OF BROOK TROUT IN CONTROL STREAMS

Appendix D. Model selection for apparent survival ($\hat{\phi}$) of brook trout in control streams under the robust design with Huggins' population estimator. Selection proceeded with capture probabilities ($\hat{p}^*$) held at full two-way effects (i.e., stream × age, age × time, stream × time), and movement parameters (γ' and γ'') and recapture parameter (c) were fixed to zero. The most-supported model (i.e., $\phi_{\text{age*stream, str*t, age*t}}$) was almost six times more likely than the second-best model, and was used to make inferences.

Hypothesized model structure	AIC_c	ΔAIC_c	w_i	K	Deviance	Model description
$\phi_{\text{age*stream, stream*t, age*t}}$	11747.44	0.00	0.819	32	66013.78	Full 2-way model
$\phi_{\text{age*stream, age*t}}$	11750.98	3.54	0.140	30	66021.35	Age effect varies by both stream and time
$\phi_{\text{age*stream*t}}$	11755.05	7.61	0.018	36	66013.30	Full 3-way model
$\phi_{\text{t*age+stream}}$	11755.62	8.18	0.014	28	66030.04	Age effect varies by time, constant (additive) stream effect
$\phi_{\text{age*stream*t}}$ $p_{\text{age*stream*t}}$	11757.50	10.06	0.0053	40	66007.65	Global model: 3-way model for both survival and capture
$\phi_{\text{t*stream, age*t}}$	11759.50	12.06	0.00197	30	66029.88	Time effect varies by both stream and age
$\phi_{\text{t+age*stream}}$	11761.35	13.91	0.00078	24	66043.84	Age effect varies by stream, constant time effect
$\phi_{\text{mid-elev: T+age, high-elev: age-2+T, juv*t}}$	11762.87	15.43	0.00037	23	66047.37	Mid-elevation stream (mid-elev): linear trend (T) on age, High-elevation (high-elev): linear trend for adults (age-2+) and juveniles vary by time

Appendix D. Continued.

$\phi_{\text{T+age*stream}}$	11763.05	15.61	0.00033	23	66047.56	Age effect varies by stream, linear trend
$\phi_{\text{mid elev: age+t, high elev: age*t}}$	11763.16	15.72	0.00032	24	66045.65	Mid-elev: constant age effect over time; High-elev: age effects vary by time
$\phi_{\text{t*stream, age*stream}}$	11765.37	17.92	0.0001	28	66039.78	Stream effect varies by both time and age
$\phi_{\text{T*age, T*stream, age*stream}}$	11765.62	18.17	0.00009	28	66040.03	Linear trends vary by both age and stream; age effect varies by stream
$\phi_{\text{T*age+stream}}$	11767.77	20.33	0.00003	25	66048.23	Linear trend varies by age, constant stream effect
$\phi_{\text{t+age+stream}}$	11769.81	22.36	0.00001	24	66052.29	Time, age, and stream effects constant (additive)
$\phi_{\text{T+age+stream}}$	11771.32	23.87	0.00001	23	66055.81	Trend, age, and stream effects constant
$\phi_{\text{T*age*stream}}$	11769.46	22.02	0.00001	30	66039.83	Linear trend varies by age and stream
$\phi_{\text{T*age, T*stream}}$	11769.60	22.16	0.00001	26	66048.05	Linear trends vary by both age and stream
$\phi_{\text{mid elev: t, high elev: age*t}}$	11779.20	31.76	0.0	25	66059.68	Mid-elev: time effect; High-elev: age effects vary by time
$\phi_{\text{mid elev :age-0+T \& age-1/age-2+T high elev: age-2}}$	11780.09	32.65	0.0	27	66056.52	Mid-elev: linear trend on age effect (age-0 or age-1/age-2+), High-elev: juveniles vary by time, adults constant
$\phi_{\text{mod elev: T, high elev: age-2+T}}$	11783.83	36.39	0.0	25	66064.30	Mid-elev: linear trend; High-elev: linear trend on adults; juveniles vary by time

Appendix D. Continued.

$\phi_{\text{ANNDEG*age}}$	11815.93	68.49	0.0	24	66098.41	Annual degree days effect varies by age
$\phi_{\text{ANNDEG+age}}$	11827.09	79.65	0.0	21	66115.62	Constant age effect on annual degree days
ϕ_{ANNDEG}	11847.22	99.78	0.0	20	66137.76	Annual degree days (October – September)
$\phi_{\text{JULTEMP*age}}$	11876.14	128.70	0.0	23	66160.64	July temperature varies by age
$\phi_{\text{SUMMDEG*age}}$	11962.41	214.97	0.0	23	66246.91	Summer degree days effect varies by age
$\phi_{\text{SUMMDEG+age}}$	12001.24	253.79	0.0	21	66289.77	Constant age effect on summer degree days
ϕ_{SUMMDEG}	12016.04	268.60	0.0	20	66306.59	Summer degree days (May – August) by year and stream
$\phi_{\text{JULTEMP+age}}$	12034.87	287.43	0.0	22	66321.38	Constant age effect on July temperature
ϕ_{JULTEMP}	12039.02	291.58	0.0	19	66331.58	Mean July water temperature by year and stream
$\phi_{\bullet}$	12047.62	3.18	0.0	19	66340.18	Constant
ϕ_{stream}	12039.12	291.68	0.0	20	66329.67	Stream effect
ϕ_{age}	12044.96	297.51	0.0	21	66333.49	Age effect
ϕ_t	11836.70	89.26	0.0	21	66125.24	Time effect
ϕ_T	11838.66	91.22	0.0	20	66129.21	Linear trend

Appendix D. Concluded.

$\phi_{t+\text{stream}}$	11783.90	36.46	0.0	22	66070.42	Stream effect constant over time
$\phi_{t*\text{stream}}$	11781.70	34.25	0.0	24	66064.18	Stream effect varies by time
$\phi_{T+\text{stream}}$	11786.17	38.73	0.0	21	66074.71	Stream effect has linear trend
$\phi_{T*\text{stream}}$	11786.73	39.29	0.0	22	66073.25	Linear trend varies by stream
$\phi_{t+\text{age}}$	11810.37	62.92	0.0	23	66094.86	Constant age effect over time
$\phi_{t*\text{age}}$	11796.13	48.69	0.0	27	66072.57	Age effect varies by time
$\phi_{T+\text{age}}$	11809.22	61.78	0.0	21	66097.75	Age effect has linear trend
$\phi_{T*\text{age}}$	11804.59	57.14	0.0	24	66087.07	Linear trend varies by age

Notes: abbreviations for model variables and covariates as are in Appendix B.

APPENDIX E: MODEL SELECTION RESULTS FOR CAPTURE PROBABILITIES OF BROOK TROUT IN TREATMENT STREAMS

Appendix E. Model selection for brook trout capture probabilities ($\hat{p}$) in treatment streams under a closed capture model. Hypothesized models include main factors of time (t), age class (age), and stream. Population estimates ($\hat{N}$) were structured to produce an estimate for each age class in each stream during each time.

Hypothesized model structure	AIC$_c$	ΔAIC$_c$	w_i	K	Deviance	Description of capture probabilities
p_{age}	-12765.38	0.00	0.453	26	98.13	Age effect
$p_{\text{stream+age}}$	-12764.46	0.92	0.286	27	97.01	Constant (additive) stream effect on age
$p_{\text{stream*age}}$	-12762.66	2.72	0.116	29	94.71	Age effect varies by stream
$p_{\text{t+age}}$	-12761.19	4.19	0.056	29	96.18	Constant time effect on age
$p_{\text{stream*age+t}}$	-12760.16	5.22	0.033	31	93.11	Age effect varies by stream; constant time effect
$p_{\text{stream+t+age}}$	-12760.00	5.39	0.031	30	95.32	Stream, time, and age effects all constant (additive)
$p_{\text{stream*t+age}}$	-12758.50	6.88	0.015	33	90.66	Stream effect varies by time, constant age effect
$p_{\text{t*age}}$	-12756.74	8.64	0.006	35	88.30	Age effect varies by time

Appendix E. Concluded.

$p_{stream*t,\ stream*age}$	-12756.08	9.30	0.004	35	88.96	Stream effect varies by both time and age
$p_{stream*t*age}$	-12749.00	16.39	0.0001	46	73.28	Full 3-way model
p_t	-12731.36	34.02	0.0	27	130.10	Time effect
p_{stream}	-12731.09	34.30	0.0	25	134.47	Stream effect
$p_{stream+t}$	-12730.81	34.57	0.0	28	128.61	Stream effect constant over time
$p_{stream*t}$	-12728.30	37.08	0.0	31	124.97	Stream effect varies by time

APPENDIX F: APPARENT SURVIVAL, ABUNDANCE, AND CAPTURE PROBABILITIES FOR BROOK TROUT AND CUTTHROAT TROUT

Appendix F. Parameter estimates for apparent survival ($\hat{\phi}$), population size ($\hat{N}$), and capture probabilities ($\hat{p}^*$) for trout in the four study streams during 1998 through 2001. Abbreviations are: mid = mid-elevation (2500 – 2700 m), high = high-elevation (3100 – 3200 m), CTL = control stream where trout populations are not manipulated, and TRT = treatment streams where brook trout are annually removed.

					Parameter estimates					
					Brook trout			Cutthroat trout		
Stream	Year	Segment length (m)	Survey dates	Age class	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)
Mid CTL	1998	700	9/24 – 9/27	0	0.483 (0.029)	362.2 (9.9)	0.709 (0.039)	0.0601 (0.0192)	199.2 (7.0)	0.710 (0.0539)
(E. Fk. Parachute Creek)	1999	700	9/3 – 9/9	0	0.163 (0.011)	1616.3 (42.1)	0.591 (0.025)	0.0126 (0.0117)	118.6 (6.4)	0.687 (0.0722)
	2000	800	9/27 – 9/30	0	0.059 (0.006)	1720.4 (24.4)	0.696 (0.018)	0.00136 (0.00239)	24.8 (1.2)	0.805 (0.0819)
	2001	800	9/25 – 9/28	0	–	390.9 (4.1)	0.849 (0.023)	–	52.2 (1.5)	0.842 (0.0640)

					Parameter estimates					
					Brook trout			Cutthroat trout		
Stream	Year	Segment length (m)	Survey dates	Age class	$\hat{\phi}$ (SE)	$\hat{N}$ (SE)	$\hat{p}^*$ (SE)	$\hat{\phi}$ (SE)	$\hat{N}$ (SE)	$\hat{p}^*$ (SE)
	1998	700	9/24 – 9/27	1	0.479 (0.026)	302 (7.5)	0.749 (0.038)	0.371 (0.0907)	37.4 (1.6)	0.792 (0.0798)
	1999	700	9/3 – 9/9	1	0.287 (0.025)	320.7 (8.9)	0.747 (0.031)	0.291 (0.0927)	30.6 (2.2)	0.763 (0.0852)
	2000	800	9/27 – 9/30	1	0.078 (0.018)	398.4 (16.2)	0.642 (0.037)	0.0198 (0.0281)	22.0 (2.5)	0.686 (0.135)
	2001	800	9/25 – 9/28	1	–	215.1 (4.8)	0.846 (0.031)	–	3.0 (0.13)	0.928 (0.0665)
	1998	700	9/24 – 9/27	2+	0.435 (0.0249)	527.3 (10.8)	0.732 (0.030)	0.622 (0.101)	41.2 (0.42)	0.936 (0.0316)
	1999	700	9/3 – 9/9	2+	0.307 (0.0229)	465.3 (12.9)	0.691 (0.028)	0.310 (0.0729)	54.6 (5.0)	0.635 (0.0842)

					Parameter estimates					
					Brook trout			Cutthroat trout		
Stream	Year	Segment length (m)	Survey dates	Age class	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)
	2000	800	9/27 – 9/30	2+	0.0564 (0.0146)	331.8 (8.9)	0.781 (0.031)	0.102 (0.0656)	34.7 (4.2)	0.647 (0.114)
	2001	800	9/25 – 9/28	2+	–	230.2 (6.8)	0.800 (0.038)	–	8.0 (0.13)	0.974 (0.0245)
High CTL (Indiana Cr.)	1998	950	8/20 – 8/23, 8/29	0	0.0 (0)	4.9 (1.7)	0.574 (0.265)	–	–	–
High CTL	1999	950	8/17 – 8/19	0	0.0 (0)	13.5 (9.2)	0.249 (0.212)	–	–	–
High CTL	2000	1082	8/14 – 8/18	0	0.0 (0)	5.9 (1.7)	0.444 (0.257)	–	–	–
High CTL	2001	1090	8/13 – 8/15	0	–	18.5 (3.7)	0.582 (0.217)	–	–	–

					Parameter estimates					
					Brook trout			Cutthroat trout		
Stream	Year	Segment length (m)	Survey dates	Age class	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^{*}$ (*SE*)	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^{*}$ (*SE*)
High CTL	1998	950	8/20 – 8/23, 8/29	1	–	–	–	0.290 (0.131)	28.4 (14.3)	0.252 (0.155)
High CTL	1999	950	8/17 – 8/19	1	0.850 (0.294)†	3‡	0 (0.0018)†	0.448 (0.135)	27.5 (4.8)	0.521 (0.172)
High CTL	2000	1082	8/14 – 8/18	1	0.869 (0.274)†	5‡	0 (0.0016)†	0.698 (0.346)	2.5 (1.0)	0.427 (0.216)
High CTL	2001	1090	8/13 – 8/15	1	–	1‡	0 (0.0036)†	–	33.3 (8.1)	0.494 (0.169)
High CTL	1998	950	8/20 – 8/23, 8/29	2+	0.875 (0.109)	51.2 (3.2)	0.733 (0.098)	0.574 (0.0660)	97.1 (4.9)	0.716 (0.0739)
High CTL	1999	950	8/17 – 8/19	2+	0.441 (0.0859)	49.1 (8.2)	0.484 (0.103)	0.551 (0.0596)	131.0 (11.8)	0.527 (0.0661)

					Parameter estimates					
					Brook trout			Cutthroat trout		
Stream	Year	Segment length (m)	Survey dates	Age class	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)
High CTL	2000	1082	8/14 – 8/18	2+	0.374 (0.0985)	40.7 (3.4)	0.695 (0.099)	0.450 (0.0484)	149.2 (12.6)	0.532 (0.0629)
High CTL	2001	1090	8/13 – 8/15	2+	–	36.7 (5.8)	0.644 (0.146)	–	129.1 (2.2)	0.844 (0.0397)
Mid TRT (Little Muddy Cr.)	1998	877	9/10 – 9/13	0	–	269.1 (10.2)	0.632 (0.0341)	–	180.7 (49.8)	0.309 (0.114)
Mid TRT	1999	877	9/10 – 9/13	0	–	215.0 (8.5)	0.637 (0.0350)	0.282 (0.0723)	71.3 (7.0)	0.581 (0.1012)
Mid TRT	2000	877	9/21 – 9/24	0	–	30.5 (2.4)	0.639 (0.0390)	0.355 (0.0477)	272.8 (15.4)	0.604 (0.0596)
Mid TRT	2001	877	9/18 – 9/21	0	–	73.8 (4.28)	0.629 (0.0367)	–	283.8 (124.6)	0.250 (0.136)

					Parameter estimates					
					Brook trout			Cutthroat trout		
Stream	Year	Segment length (m)	Survey dates	Age class	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)
Mid TRT	1998	877	9/10 – 9/13	1	–	179.5 (5.2)	0.732 (0.0347)	0.274 (0.0495)	182.7 (18.2)	0.512 (0.0881)
Mid TRT	1999	877	9/10 – 9/13	1	–	112.4 (3.7)	0.736 (0.0348)	0.517 (0.0590)	163.6 (4.8)	0.759 (0.0483)
Mid TRT	2000	877	9/21 – 9/24	1	–	41.4 (2.0)	0.737 (0.0365)	0.471 (0.0711)	66.5 (9.1)	0.536 (0.1037)
Mid TRT	2001	877	9/18 – 9/21	1	–	27.5 (1.6)	0.729 (0.0380)	–	269.7 (22.9)	0.541 (0.0663)
Mid TRT	1998	877	9/10 – 9/13	2+	–	90.8 (1.7)	0.840 (0.0259)	0.359 (0.0465)	167.5 (3.85)	0.791 (0.0435)
Mid TRT	1999	877	9/10 – 9/13	2+	–	41.5 (1.1)	0.843 (0.0263)	0.356 (0.0484	159.45 (10.0)	0.618 (0.0572)

					Parameter estimates					
					Brook trout			Cutthroat trout		
Stream	Year	Segment length (m)	Survey dates	Age class	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)
Mid TRT	2000	877	9/21 – 9/24	2+	–	55.9 (1.3)	0.844 (0.0271)	0.386 (0.0448)	167.55 (14.8)	0.483 (0.0535)
Mid TRT	2001	877	9/18 – 9/21	2+	–	59.0 (1.4)	0.839 (0.0266)	–	117.2 (3.1)	0.767 (0.0549)
High TRT (Willow Cr.)	1998	950	9/17 – 9/20	0	–	106.6 (6.1)	0.613 (0.0427)	–	–	–
High TRT	1999	1002	8/10 – 8/13	0	–	29.8 (2.6)	0.622 (0.0438)	–	–	–
High TRT	2000	1200	8/8 – 8/11	0	–	–	–	–	–	–
High TRT	2001	1200	8/7 – 8/10	0	–	174.7 (8.8)	0.614 (0.0420)	–	–	–

Stream	Year	Segment length (m)	Survey dates	Age class	Parameter estimates					
					Brook trout			Cutthroat trout		
					$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)
High TRT	1998	950	9/17 – 9/20	1	–	13.5 (1.2)	0.725 (0.0486)	–	–	–
High TRT	1999	1002	8/10 – 8/13	1	–	23.2 (1.5)	0.732 (0.0480)	–	–	–
High TRT	2000	1200	8/8 – 8/11	1	–	38.3 (2.1)	0.732 (0.0485)	–	–	–
High TRT	2001	1200	8/7 – 8/10	1	–	13.5 (1.2)	0.725 (0.0489)	–	–	–
High TRT	1998	950	9/17 – 9/20	2+	–	240.3 (3.5)	0.821 (0.0219)	0.5678 (0.0888)	40.0 (0.17)	0.973 (0.0274)
High TRT	1999	1002	8/10 – 8/13	2+	–	92.3 (1.9)	0.827 (0.0222)	0.674 (0.1002)	28.8 (4.3)	0.534 (0.1042)

					Parameter estimates					
					Brook trout			Cutthroat trout		
Stream	Year	Segment length (m)	Survey dates	Age class	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)	$\hat{\phi}$ (*SE*)	$\hat{N}$ (*SE*)	$\hat{p}^*$ (*SE*)
High TRT	2000	1200	8/8 – 8/11	2+	–	107.7 (2.0)	0.827 (0.0225)	0.466 (0.1008)	27.0 (1.4)	0.800 (0.0895)
High TRT	2001	1200	8/7 – 8/10	2+	–	117.2 (2.2)	0.822 (0.0224)	–	21.2 (0.81)	0.889 (0.08332)

Notes: apparent survival estimates are for the annual interval beginning in the year indicated (i.e., $\hat{\phi}_{1998}$ is for 1998-1999 interval). A dash (–) indicates no estimate was possible or no trout were captured.

† Estimates are poor because few fish of this age class were captured.

‡ Values are total numbers captured because too few fish were captured to calculate an estimate.

APPENDIX G: AGE CLASS DESIGNATION CRITERIA FOR BROOK TROUT AND CUTTHROAT TROUT

Appendix G. Age-class designation for brook trout and cutthroat trout captured during two-pass depletion electrofishing in four streams in Colorado during 1998 to 2001. Divisions were based on separations of modal peaks in length-frequency histograms and confirmed with age-length relationships estimated from otoliths. Abbreviations are: mid = mid-elevation (2500 – 2700 m), high = high-elevation (3100 – 3200 m), CTL = control stream where trout populations are not manipulated, TRT = treatment streams where brook trout are annually removed, and '–' indicates that no trout of that age were captured.

			Sizes (fork length in mm) used to divide trout age classes					
			Brook trout age class			Cutthroat trout age class		
Stream	Year	Survey date	0	1	2+	0	1	2+
Mid CTL	1998	24 Sept – 27 Sept	< 110	> 110	> 160	< 100	> 100	> 145
(East Fork Parachute Cr.)	1999	3 Sept – 6 Sept	< 110	> 110	> 157.5	< 80	> 80	> 140
	2000	27 Sept – 30 Sept	≤ 105	> 105	> 147.5	< 90	> 90	> 130
	2001	25 Sept – 28 Sept	< 105	> 105	> 150	< 90	> 90	> 135
Mid TRT	1998	10 Sept – 13 Sept	< 85	> 85	> 140	< 55	> 55	> 92.5
(Little Muddy Cr.)	1999	10 Sept – 13 Sept	< 85	> 85	> 135.5	< 55	> 55	> 92.5

Appendix G. Concluded.

	2000	21 Sept – 24 Sept	< 90	> 90	> 135.5	≤ 62.5	> 62.5	> 87.5
	2001	18 Sept – 21 Sept	< 90	> 90	> 135	≤ 60.5	> 60.5	> 97.5
High CTL	1998	20 Aug – 23 Aug, 29 Aug	< 65	–	> 185	–	< 65	> 65
(Indiana Cr.)	1999	17 Aug – 19 Aug	< 65	> 65	> 85	–	< 65	> 65
	2000	14 Aug – 18 Aug	< 65	> 65	> 110	–	< 65	> 65
	2001	13 Aug – 15 Aug	< 65	> 65	> 100	–	< 80	> 80
High TRT	1998	17 Sept – 20 Sept	< 65	> 65	> 100	–	–	≥ 95
(Willow Cr.)	1999	10 Aug – 13 Aug	< 45	> 45	> 90	–	–	≥ 95
	2000	8 Aug – 11 Aug	–	> 65	> 95	–	–	≥ 95
	2001	7 Aug – 10 Aug	< 60	> 60	> 105	–	–	≥ 95